SPECIES INTERACTIONS DURING SUCCESSION IN ROCKPOOLS: ROLE OF HERBIVORES AND PHYSICAL FACTORS

by

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ABSTRACT

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Species Interactions During Succession In Rockpools:
Role Of Herbivores And Physical Factors

Positive interactions are increasingly recognised to be important as community structure processes. Bertness and Callaway's model predicts positive interactions to be important under high consumer pressure or high environmental stress. Associational defences between organisms, when palatable algae take advantage of living with less palatable ones, will be the dominant structuring forces under high consumer pressure and low physical stress. Habitat ameliorations become more important under harsh physical conditions and low consumer pressure. This model was tested at Wembury Bay, Devon, Southwest England, using rockpools and emergent rock habitats distributed over the vertical height of the shore to generate gradients of environmental stress.

Relationships between rockpool physico-chemical parameters and assemblage composition were investigated across the shore. Highest rockpool communities on the shore experienced the harshest environmental stress. Consumer pressure measured in rockpools was twice that recorded on emergent rock owing to high tide limpet movements from the surroundings into the pool rather than herbivore densities. Over these gradients, experimental plots were maintained at natural and reduced grazer density to control consumer pressure. Species interactions during succession were examined. Experimental plots distributed at three shore heights (high, mid, low) were scraped in both habitats to initiate succession and were then sampled regularly over a 2 year period. Species susceptibility to grazing drove different trajectories of succession under high and low consumer pressure suggesting that palatability influences species interactions. Physical stress affected species recruitment and development of the successional sequence in both habitats and over the intertidal gradient. Selective removal of early ephemeral and later perennial colonising algal species provided some evidence of positive interactions under both elevated levels of physical stress and high consumer pressure. These results are discussed in the context of the Bertness and Callaway model with which they are consistent and other models of succession.

RESUMÉ

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Interactions Entre Espèces Durant La Succession Des Cuvettes Rocheuses:
Le Rôle Des Herbivores Et Des Facteurs Physiques

L'importance des interactions positives, en tant que processus structurant les communautés, est de plus en plus reconnue. Le modèle de Bertness et Callaway prédit une dominance des interactions positives dans les milieux soumis à un fort stress environnemental ou de la part des consommateurs. Lorsque des algues sensibles aux herbivores se dévelopent parmi des algues moins comestibles, elles beneficient d'une protection définie comme défense associative. Ces associations structurent majoritairement les milieux soumis à de fortes pressions herbivores et à un faible stress physique. Des améliorations de l'habitat par certaines espèces sont communes aux milieux présentant des conditions physiques extrêmes et une faible pression herbivore. Ce modèle a été testé à Wembury Bay, Devon, au sud-ouest de l'Angleterre, en utilisant comme habitat les cuvettes rocheuses et le rocher émergent repartis le long de l'estran afin d'obtenir un gradient de stress environnemental.

Les relations entre les paramètres physico-chimiques et la composition des assemblages des cuvettes ont été étudiées sur la hauteur de l'estran. Les communautés des cuvettes situées en haut de l'estran sont soumises à un plus fort stress environnemental. La pression herbivore mesurée dans les cuvettes est deux fois plus importante que sur le rocher émergent. Ce résultat s'explique, à marée haute, par une intrusion dans les cuvettes des patelles avoisinantes et non par une abondance plus élevée d'herbivores. Afin d'examiner les interactions entre espèces lors de la succession en fonction d'un gradient de stress herbivore, les sites expérimentaux ont été maintenus à une densité naturelle et réduite de brouteurs. Dans les deux habitats (cuvettes et émergent), des cadrats expérimentaux distribués à trois hauteur sur l'estran (haut, milieu, bas) ont été nettoyés pour initier la succession et ont été échantillonés régulièrement durant une période de deux ans. La sensibilité des espèces au broutage a généré différentes trajectoires de succession en fonction de la pression herbivore (forte ou faible) suggérant une influence de la comestibilité des espèces sur la nature de leurs interactions. Le stress physique a affecté le recrutement des espèces ainsi que le déroulement de la succession dans les deux habitats et le long du gradient intertidal. La suppression sélective des algues colonisatrices, soit des espèces éphémères précoces, soit des espèces pérennes tardives, a montré l'exsistence d'interactions positives liées à un fort stress physique ou à une pression herbivore élevée. Ces résultats sont discutés par rapport au modèle de Bertness et Callaway et aux autres modèles de succession.

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AUTHOR'S DECLARATION

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award without prior agreement of the Graduate Committee.

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A programme of advanced study was undertaken, which included:

- Multivariate statistical PRIMER course in November 2003 conducted by Dr. K.R. Clarke.
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Relevant scientific seminars and conferences were regularly attended at which work was often presented.

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- Posters presented each year since April 2002 at the council meetings of the Marine Biological Association of the UK.
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- Graduate Research Forum (GRF), February 2003, Plymouth, UK. Oral presentation.
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Contents

Chapter 1

General introduction

1.1 Background

Rocky shores have been the subject of numerous ecological studies during the last 50 years (see Lewis, 1964; Hawkins and Jones, 1992; Little and Kitching, 1996; Raffaelli and Hawkins, 1996; Underwood, 2000; Bertness *et al.*, 2001, for reviews). Rocky shore habitats are amenable to study as they are easily accessible and are two-dimensional at low tide. Many of the species present are sessile or slow moving allowing easy identification, rapid quantification and manageable experimental manipulations, such as species transplantation, exclusion or removal. Moreover, the rocky shore environment is regulated by the tidal cycle and receives input from the seawater during regular submergence as well as by wave splash. This pattern of emersion and immersion generates a very strong vertical gradient of stress in a relatively small limited spatial extent. Accordingly, the organisms living on rocky shores have to cope with environmental stresses such as desiccation, thermal stress, wave exposure, oxygen availability, and nutrient variation. Finally, biological interactions including grazing, competition, and predation play a major role in influencing the distribution of species. Thus, rocky shores are tractable model systems for experimental ecology.

Patterns of distribution of organisms living in the intertidal have been studied throughout the world and general features of zonation along the vertical gradient have been described (Stephenson and Stephenson, 1949; Lewis, 1964; Raffaelli and Hawkins, 1996, for reviews). Patterns of vertical distribution vary from place to place depending on the wave exposure and the geographical location of the shore. The potential causes of these patterns of zonation have been the subject of numerous studies, which have shown that high shore species are able to survive for long periods of emersion and their upper vertical limits of distribution are largely set by physical factors (e.g. desiccation) (e.g. Baker, 1909; Gowanloch and Hayes, 1926; Biebl, 1952; Dayton, 1975; Schonbeck and Norton, 1978; Hawkins and Hartnoll, 1985), (see Newell, 1979; Norton, 1985, for reviews). However, observations made by Southward and Southward (1978) after the Torrey Canyon oil spill and removal experiments have shown that upper limits of seaweeds can also be set by biological interactions such as competition for space (e.g. Hawkins and Hartnoll, 1985) or grazing (Underwood, 1979, 1980; Underwood and Jernakoff, 1981; Boaventura *et al.*, 2002) (see Raffaelli and Hawkins, 1996, for review). In the same way, transplantation and removal experiments showed that lower limits of species distribution are generally set by biological factors: competition for primary space and food (Connell, 1961a,b; Hawkins, 1983; Schonbeck and Norton, 1980; Lubchenco, 1980; Chapman, 1990a), grazing (Lodge, 1948; Burrows *et al.*, 1954) (see Hawkins and Hartnoll, 1983b; Boaventura *et al.*, 2002, for reviews) and predation (Connell, 1961b; Paine, 1971, 1974).

During the last 40 years, the increasing use of experimental manipulation has allowed the testing of hypotheses about ecological patterns and processes (Underwood, 2000), and has enriched our knowledge of community dynamics and informed our understanding of ecology as a whole. The activity of grazers has been shown to limit the distribution and abundance of algae (see Hawkins and Hartnoll, 1983b; Lubchenco and Gaines, 1981, for reviews). Competition for space and food has been found to be an important factor influencing community structure (Lubchenco and Gaines, 1981; Connell, 1983; Connell and Sousa, 1983; Hawkins and Hartnoll, 1983b; Dayton, 1984; Sousa, 1984b; Underwood and Denley, 1984; Vadas, 1985; Menge and Farrell, 1989). Predation, for example by starfish and whelks, has been shown to limit the abundance of barnacles and mussels and influence the diversity of intertidal assemblages (Paine, 1969; Connell, 1970). Moreover, these biological interactions can have an indirect negative or positive effect on other species (Menge, 1995; Underwood, 2000, for review). For instance, if a predator consumes a superior competitor, it can cause large changes in the diversity and abundance of species in an assemblage. However, this keystone predation, reviewed by Underwood (2000), does not occur on every rocky shore. These biological and physical factors vary along vertical and horizontal gradients (see Raffaelli and Hawkins, 1996). Furthermore, community structure and dynamics are also be affected by other less predictable processes such as variation in arrival of propagules, larval and juvenile supply (Levin and Paine, 1974; Roughgarden *et al.*, 1988; Underwood, 2000; Jenkins and Hawkins, 2003), which will influence species abundance and the outcome of biological interactions (see Underwood, 2000, for review). In addition, physical disturbances such as wave action (Dethier, 1984), bashing by logs or scouring (Clement, 1916; Dayton, 1971; Lubchenco, 1983; Dethier, 1984; Benedetti-Cecchi and Cinelli, 1996) have a major effect, leading to high species diversity by providing new bare substrate for sessile organisms to colonise (Dayton, 1971; Sousa, 1979b,a, 1980; Farrell, 1989; McGuinness, 1987a,b) with highest diversity often at intermediate levels of disturbance (Lubchenco, 1978; Connell, 1978).

Most of the work described so far has been conducted on open freely draining rock and rockpools have been much less extensively studied. Underwood (1981) even considered rockpools as not being part of intertidal habitat because they are immersed during low tide. Rockpools and emergent rock are both regulated by the tidal cycle and receive a similar influence from the seawater. In addition, the variation in physical factors associated with tidal height is similar for both habitats even if fluctuations are less important in rockpools than on open rock. However, rockpools differ because of their extra dimension: the water column. Biological interactions can be more intense in pools because they generally have greater diversity than the adjacent areas of open rock. Some taxa are more abundant in pools (e.g. algae, gastropods) while others are absent or fewer (e.g. fucoids, barnacles) than on adjacent open rocks (Metaxas and Scheibling, 1993).

The overall aim of this thesis is to advance our understanding of rockpool community dynamics and the role of pools within rocky shore ecosystems. This thesis will focus on succession and modification of biological interactions that are caused by the physical environment. This introduction will first summarise the environment of rockpools; second, it will review studies made on rockpool communities; third, it will review work on the interactions between species and ecosystem functioning. Finally, I will summarise the Bertness and Callaway (1994) model, which provided a framework for much of the experimental work in this thesis and that I tested in the model system of intertidal rocky shore using rockpools and emergent rock.

1.2 Environment of rockpools

Rockpools can be considered as isolated habitat patches with well-defined boundaries (Chapman, 1990b; Metaxas and Scheibling, 1993). Each pool differs in its shape, size, volume, surface area, depth, height on the shore, exposure to wave and splash, degree of shading and drainage and therefore individual pools are rarely comparable (Astles, 1993; Metaxas and Scheibling, 1993). However, using experimental pools of a series of standard diameters, Underwood and Skilleter (1996) showed that pool diameter had little influence on the assemblage of organisms. The influence of tidal height on patterns of occupancy has been investigated in several studies (e.g. Dethier, 1982; Wolfe and Harlin, 1988a,b; Kooistra *et al.*, 1989). However, a lack of replicate pools at each heights in some of the experiments may have influenced results, given that variations found could be due to physical differences (e.g. due to time exposure), which were apparent between pools (Astles, 1993). Accordingly, Astles (1993) chose not to consider height in her study. Nevertheless, physical factors vary with tidal height such that lower pools experience less variable conditions than higher pools (Metaxas and Scheibling, 1993). Moreover, the ecology of rockpools will be affected by weather conditions (wind velocity and direction, precipitation) and input of nutrients and organism immigrating from the open sea (Ganning, 1971).

The physical environment of rockpools does not fluctuate as much as that of emergent freely draining rocky shores - except for the very high shore pools - but fluctuations are larger than those of the open sea. The greatest diurnal variation is in oxygen saturation with higher values during the day due to photosynthetic activity in pools and lower values at night when respiration dominates biological processes (Morris and Taylor, 1983). A vertical stratification of oxygen has been observed during the day but not at night (Daniel and Boyden, 1975). In the same way, total carbon dioxide varies daily but inversely to oxygen concentrations (Morris and Taylor, 1983). Temperature was found to vary daily up to 10°C during daytime at spring tide and decreasing at night (Morris and Taylor, 1983; Huggett and Griffiths, 1986) and thermal stratification within pools has also been reported (McGregor, 1965; Morris and Taylor, 1983). Salinity may increase up to 5 units during the emerged period (Lami, 1931; Pyefinch, 1943; Green, 1971; Morris and Taylor, 1983). Alkalinity is relatively stable and varies less than 0.2 meq.l^{-1} (Morris and Taylor, 1983). These daily variations of oxygen, pH, and alkalinity are predominantly caused by biological processes (Pyefinch, 1943; McGregor, 1965; Ganning, 1971; Green, 1971; Daniel and Boyden, 1975; Morris and Taylor, 1983). Fluctuations in temperature, salinity, oxygen and total carbon dioxide concentration also depend on the height of the pool on the shore (Pyefinch, 1943; Metaxas and Scheibling, 1993). With the incoming tide, changes in the physico-chemical factors occur rapidly (a few minutes) and their direction and magnitude will depend on the time of the day. For instance, for a daylight immersion, oxygen saturation will decrease and total carbon dioxide will increase but with a slightly smaller range. On the contrary, a night-time immersion will induce opposite changes: oxygen saturation will increase and total carbon dioxide will decrease (Morris and Taylor, 1983). The magnitude of diurnal variation also depends on the height of the pool; if the pool is covered only during spring tides then extreme change will occur whereas for a pool with long periods of immersion fluctuations will be much smaller (Morris and Taylor, 1983).

Salinity, temperature and pH show seasonal variations in the magnitude of their daily fluctuation (Ganning, 1971; Morris and Taylor, 1983). Salinity stratification can vary due to evaporation in the summer, rainfall and freezing in the winter (Naylor and Slinn, 1958; Ganning, 1971; Morris and Taylor, 1983). Within rockpools, gradients and discontinuity can appear in oxygen saturation and temperature with warmer temperatures and higher oxygen values at the bottom of the pool (Morris and Taylor, 1983). The influence of the wind will play a major role in breaking down stratification but this will vary between pools due to differences in shape, depth, and shore height. Therefore, individual tidepools can be unique in their physical regime (Metaxas and Scheibling, 1993). These factors will influence assemblages and the distribution of invertebrates and algae.

1.3 Biology of rockpools

1.3.1 Distribution patterns in rockpools

Shore height distribution The first attempts to classify rockpools were based on the position of pools in relation to the height of the shore, salinity, vegetation and the permanence of the water (Forsman, 1951; Droop, 1953; Gustavsson, 1972). A number of studies have shown variation in the abundance of species along the tidal gradient. Phytoplankton communities in pools were examinated by Droop (1953) and Metaxas and Lewis (1992) who found variation in microalgal abundance with tidal height. Variation in the abundance of macroalgae with tidal height has also been reported. Commonly, green algae such as *Ulva* spp., *Cladophora* spp. and *Chaetomorpha* spp. have been found in high shore rockpools while *Spongomorpha* spp., corallines *Lithothamnion* spp. and *Corallina* spp. and the brown algae *Fucus* spp., *Laminaria* spp. and *Scytosiphon* spp.

were found in lower pools (see Metaxas and Scheibling, 1993, for review). Many other species from meiofauna (flatworms, rotifers, oligochaetes, cladocerans, copepods, ostracods, barnacles, amphipods, isopods) to fishes show vertical pattern of distribution in relation to tidal height (Fraser, 1936; Ganning, 1971; Goss-Custard *et al.*, 1979; Femino and Mathieson, 1980; Sze, 1982; Huggett and Griffiths, 1986; Dethier, 1980; Bennett and Griffiths, 1984). These patterns of vertical distribution are most probably a direct result of variation in physical conditions along this gradient.

Within rockpool distribution Vertical zonation of macroalgae within rockpools has also been described by Kooistra *et al.* (1989) and van Tamelen (1996). Kooistra *et al.* (1989) used multivariate analyses to examine pools on exposed shores in Brittany (France). For high littoral rockpools, they observed monospecific strands (e.g. *Chaetomorpha aerea*, *Hildenbrandia rubra*) that probably resulted from high physical stress (high temperatures, high salinity fluctuation and evaporation). In mid tidal pools, four zones were determined from top to bottom: first, a zone of *Pseudolithophyllum orbiculatum* possibly maintained by the grazing of limpets which prevented the establishment of annual algae; a second zone of *Corallina elongata* most likely protecting green algae from grazing; a third zone of *Bifurcaria bifurcata* which sets its lower limit probably by self shading and finally a deeper one with shade tolerant species *Corallina elongata* and *Phymatolithon polymorphum* that seemed protected from grazing by *Corallina* spp. In lower rockpools, these zones "spill over" the pool edges to the surrounding substrate. Rockpools of the Oregon coast were studied by van Tamelen (1996) who found three zones from the shallower to the deepest parts: a foliose algal zone at the pool rim, a crustose coralline algal zone at the pools sides and at the pool bottoms a bare zone. By manipulating physical disturbance (cobbles) and biotic interactions (limpets, coralline algae), he showed that distribution was largely determined by a strong vertical gradient of scouring and by coralline algae pre-empting space from fleshy crustose algae.

1.3.2 Rockpool assemblage composition: differences from open rock

Several studies have described the assemblages found in rockpools (e.g. Fraser, 1936; Ganning, 1971; Goss-Custard *et al.*, 1979; Femino and Mathieson, 1980). Commonly, the species are similar to those of rocky shores but with differing relative abundance, distribution and diversity due to differences in the physical environment (Metaxas and Scheibling, 1993). Rockpool communities include phytoplankton, zooplankton and fish - due to the extra dimensional water column - in addition to algae and benthic invertebrates (Ganning, 1971; Green, 1971; Metaxas and Scheibling, 1993). Rockpools are immersed during low tide, therefore, organisms are protected from desiccation inducing an uplift of species limits. Species are found higher on the shore in pools than on adjacent areas of open rock. For instance, *Ulva intestinalis* has been found 1.80 m higher than on the emerged substrate in Maine (USA) while *Chondrus crispus*, *Hildenbrandia rubra*, *Pseudendoclonium submarinum* and *Ralfsia verrucosa* extended 2.44 m higher (Femino and Mathieson, 1980). Similar patterns were observed for invertebrates including *Gibbula cineraria*, *Actinia equina*, *Patella ulyssiponensis* and *Littorina saxatilis*, which also extended higher up the shore in pools (Lewis, 1964). Conversely, some species are intolerant of pool conditions and are found in lower densities. For example, barnacles are frequently absent in pools as found by Singletary and Shadlou (1983) in New England (USA), by Goss-Custard *et al.* (1979) in Ireland and by Lewis (1964) in England. Other animals are only rarely found submerged such as *Osilinus* spp., *Nucella lapillus*, *Gibbula umbilicalis*, *Littorina obtusata* and *Melaraphe neritoides* (Lewis, 1964). Some algae are also rare in pools: fucoids such as *Fucus vesiculosus* (Goss-Custard *et al.*, 1979; Lubchenco, 1982) and *Ascophyllum nodosum* and the red alga *Porphyra umbilicalis* (Femino and Mathieson, 1980; Lubchenco, 1982). In contrary, some species (e.g. *Corallina officinalis* and *Chladophora sericea*) are found on emergent rock in lower proportions than in rockpools (see Femino and Mathieson, 1980, for review). Overall, rockpools tend to have much more diverse assemblages than adjacent areas of open rock.

1.4 Processes and dynamics regulating assemblage structure

The structure and dynamics of rockpool communities are influenced by several factors. Biological interactions are more intense in rockpools than on open rock and induce differences between these habitats (Metaxas and Scheibling, 1993). Physical disturbance plays a major role in structuring the biological assemblages that inhabit rockpools. In addition, fluctuations in physical conditions may lead to seasonal and spatial variations in community organisation.

1.4.1 Biological interactions

Assemblage composition is strongly influenced by biological factors including competition, herbivory and predation, often driven by recruitment dynamics. Each is considered in turn.

1.4.1.1 Competition

Studies have demonstrated that competition, mainly for space, has a major role in regulating rockpool community assemblages. Dethier (1984) observed that at similar tidal heights, Washington State rockpools (USA) were dominated by one species (either the surfgrass *Phyllospadix scouleri*, articulated coralline algae, the mussel *Mytilus californianus*, the anemone *Anthopleura elegantissima*, the red algae *Rhodomela larix*, the green algae *Cladophora* spp.) which monopolizes space and prevents potential competitors from settling and surviving. In Nova Scotia, Chapman (1990b) reported that ephemeral algae induced a decrease in *Fucus* canopy cover. By experimentally removing the canopy of *Cystoseira* spp. in the Mediterranean, Benedetti-Cecchi and Cinelli (1992a) showed a strong negative interaction between *Cystoseira* spp. and *Corallina elongata*, *Padina pavonica* and *Rytiphloea tinctoria*. After removing *Cystoseira* spp., they recorded an increase in the abundance of articulated corallines, corticated branched, thick bladed and branched algae. van Tamelen (1996) removed corallines from rockpools on the Oregon coast and observed an increase in the abundance of fleshy crustose algae. He deduced that corallines pre-empt space from fleshy crustose algae. At the bottom of deep rockpools in Brittany, Kooistra *et al.* (1989) suggested that *Halichondria panicea* and thick coralline crustose algae were superior competitors for space by overgrowing other species. Arrontes and Underwood (1991) found that the limpets *Cellana tramoserica* had a negative effect on the growth and abundance of the starfish *Patiriella exiga* in rockpools of New South Wales.

1.4.1.2 Herbivory

The influence of grazers on intertidal assemblages has been studied in numerous experimental manipulations. Herbivores have been shown to restrict the distribution and abundance of algae in rockpools. In experimental rockpools, Underwood and Jernakoff (1984) recorded greater percentage of cover and biomass of algae in pools from which herbivores had been excluded compared to control pools. In shallow intertidal pools on the Washington coast, Paine and

Vadas (1969) found that sea urchin grazing had a major impact on algal abundance and diversity. Benedetti-Cecchi and Cinelli (1995) showed that filamentous algae and *Cystoseira* spp. were reduced by sea urchins grazing in rockpools in the western Mediterranean. In addition, Wolfe and Harlin (1988a,b) reported that pools with the highest density of *Littorina littorea* had the smallest algal diversity. In contrast, work on the Oregon coasts showed that herbivores have no effect on algal distribution in rockpools but influence abundance of fleshy algae at different levels of wave exposures (van Tamelen, 1996). For instance, at exposed sites, herbivorous snails were scarce and fleshy algae were more abundant than at sheltered sites where herbivorous snails were much more abundant leading to an assemblage dominated by grazer resistant *Corallina* spp. and more bare space.

Herbivores reduce algal recruitment by consuming newly settled algae (Lubchenco, 1982). Grazers, especially limpets, can reduce the abundance of *Cystoseira* spp. embryos and juveniles (Benedetti-Cecchi and Cinelli, 1992b). Chapman (1990b) found that grazers have a strong negative effect on the density of *Fucus distichus* juveniles, which are more affected than adults, whereas herbivores have an enhancing effect on ephemeral algae. In Washington tidepools, Dethier (1982, 1984) suggested that herbivores could play a key role in algal seasonality patterns and in exclusion of certain intertidal algae. She showed that *Littorina* spp. have a negative effect on the abundance of green algae *Collinsiella* spp., the red algae *Rhodomela* spp. and on diatoms. Moreover, grazing seems more intense in rockpools than on adjacent rock, possibly because of the lack of desiccation allowing limpets to forage constantly (Dethier, 1982); thus such herbivores can remove most of the germlings. Herbivores (*Littorina littorea*, *Littorina obtusata* and *Acmaea testudinalis*) together with algal competition excluded fucoids in mid-littoral protected tidepools of New England (Lubchenco, 1982). Some algae can also resist grazing by being unpalatable or by reproducing and growing during seasonal reduction of grazer abundance and then attaining a size refuge (Dethier, 1982).

1.4.1.3 Predation

Few studies have been made on predation and its role in regulating the abundance and diversity of species in rockpools. However, Paine (1966, 1971) showed that predation can maintain high species diversity in Washington state. In *Ulva* spp. dominated rockpools of New England, Lubchenco (1978) suggested that many green crabs *Carcinus maenas* occur probably due to protection from gulls by the canopy. She showed that *Carcinus* prey upon small *Littorina littorea* inducing a low periwinkle density, which protects *Ulva* spp. from grazing. She also showed that algal diversity was higher at intermediate levels of predation which acted as a biological disturbance. In the same way, Coull and Wells (1983) highlighted that substrate complexity is an important factor in reducing predation. They studied predation by fish upon meiofauna in rockpools of New Zealand and showed that the complex structure of *Corallina officinalis* was used as a refuge from the predatory blenny *Helcogramma medium*. In Washington, Dethier (1980) had shown that the copepod *Tigriopus californicus* found refuge in high shore tidepools because predation pressure was much less than in low shore pools. Fairweather (1987) observed that addition of whelks to tide pools of New South Wales had a negative effect on limpet abundance.

1.4.1.4 Recruitment

Recruitment variability has been shown to be a very important factor influencing the abundance of organisms in shallow water habitats (e.g. Connell, 1985; Gaines and Roughgarden, 1985; Roughgarden *et al.*, 1988; Menge, 1991), however few studies have been made on the influence of recruitment in rockpools. The availability of algal spores and invertebrate larvae may vary seasonally in density and according to patterns of reproduction influencing species structure (Paine and Vadas, 1969; Dethier, 1984). For instance, Benedetti-Cecchi and Cinelli (1996) and Benedetti-Cecchi (2000b) suggested that there was non-hierarchical competition between *Cystoseira* spp. and algal turf, the outcome depending upon the reproduction period of each species. In addition, herbivores can remove settling organisms and affect species distribution by reducing or preventing recruitment (see 1.4.1.2 Herbivory).

1.4.2 Disturbance

In addition to deterministic and biological processes such as stress related to tidal height and pool size, wave exposure, herbivory, predation and competition, stochastic events such as physical disturbance are important structuring factors producing complex mosaics of species assemblage in rockpools (Dethier, 1984). According to Dethier (1984), disturbing agents include waves, excessive heat, wave-driven logs or rocks, unusual influxes of predators or herbivores. She studied disturbance among six monopolizing dominant species in Washington State rockpools, observing that severe disturbance occurred in high shore pools during summer due to heat stress and in low pools in winter, principally due to wave action. Moreover, depending on the vagaries of planktonic recruitment, up to three years could be required for recovery following a large disturbance (Dethier, 1984). She concluded that concomitance of high disturbance frequencies and slow recovery did not allow the same population structure in pools of the same tidal level. van Tamelen (1996) studied the effect of scouring by cobbles and noticed that the abundance of organisms was reduced and/or limited to the top part of the pools on the Oregon coasts. On the west coast of Italy, Benedetti-Cecchi and Cinelli (1996) observed patterns of disturbance and recovery in rockpools with a mosaic assemblages of canopy forming species, turf-forming and encrusting algae patches. By monitoring provision of open space, they found that an interaction between the size of a clearance and the timing of its initiation affected patterns of algal colonization. In the Northern Baltic Sea rockpools, the disturbance from ferry washes increased *Ulva intestinalis* cover (Ostman and Ronnberg, 1991). Physical disturbance can also affect fish populations in pools. Richkus (1978) studied movement of the woolly sculpin *Clinocottus analis* between pools of southern California and recorded that by moving large stones, storms affected fish abundance. In the Northern Gulf of California, winter-kill due to low temperatures was recorded to limit diversity by eliminating tropical species (Thomson and Lehner, 1976).

1.4.3 Variations in rockpool assemblages

Interaction between biological and physical factors generates patterns in species distributions, assemblages composition and structure but these pattern are frequently obscured by spatial and temporal variability in rockpool communities.

1.4.3.1 Spatial variations

As for assemblages on open rock, species composition in rockpools varies predictably from the low to the high intertidal zone due to differences in tolerance to the physical stress gradient (Dethier, 1984). However, the distribution of organisms related to their intertidal height is less clear (Metaxas and Scheibling, 1993). Several studies have recorded differences in species assemblages among pools at similar heights (Pyefinch, 1943; Femino and Mathieson, 1980; Sze, 1980; Dethier, 1982; Wolfe and Harlin, 1988a,b; Arrontes and Underwood, 1991). Sze (1980) suggested that these differences were related to the degree of wave exposure with high wave action moderating competitive interactions and grazing effects. Variation among pools at a given tidal height cannot be ascribed to differences in environmental factors alone but to differences in species rates of recovery (see 1.4.2 Disturbance) from disturbance (Dethier, 1984). In Nova Scotia, horizontal spatial variability in percentage cover of macroalgae due to differential recruitment of opportunistic forms and/or to differences in physical characteristics of the pools was observed (Metaxas *et al.*, 1994; Metaxas and Scheibling, 1994). They also reported significant variation in the abundance of benthic species among pools at the same tidal height with greatest variability among high shore pools. Astles (1993) studied the abundance and distribution of algae and animals in rockpools near Sydney, Australia at different spatial scales. At large spatial scales, she detected no significant differences for most species abundance between sites but at smaller spatial scales, she found very large fluctuation in abundances between pools. She suggested that disturbance was not the major structuring process, but that it may affect pools differentially because of the diverse composition of assemblages and differences in pool shape. The history of pools may have a more significant role in influencing assemblage composition (Astles, 1993) by the variation in time of creation of free space, recruitment regime (Sutherland, 1974, 1981) or by the competitive outcome (Kay and Keough, 1981; Keough, 1984). Therefore, assemblage composition might be set by complex interactions between extrinsic and intrinsic factors.

1.4.3.2 Temporal variations

Assemblages in rockpools can show considerable temporal variation with season. Femino and Mathieson (1980) observed a maximum number of taxa in late spring owing to a large number of annuals and a minimum taxa number in winter in rockpools of Maine, USA. They recorded a greater biomass in summer with few red algae and large kelps normally restricted by warm temperature. They suggested that ecological factors determine seasonal growth and abundance of tidepool algae. Dethier (1982) found seasonal patterns were evident in rockpools in Washington State with peaks for *Collisiella tuberculata* and diatoms in winter, *Rhodomela larix* in winter in high shore pools and in summer in low shore pools, and finally *Prionitis* spp. and articulated corallines in spring and summer. She attributed these variations to wave drag in winter, increase in temperature and light intensity in summer and seasonal fluctuation in herbivore abundances. Seasonal changes in macroalgal cover in Rhode Island pools were associated with changes in water temperature, light intensity and day length (Wolfe and Harlin, 1988a,b). It was assumed that seasonal changes in grazing activity contribute to seasonality in macroalgae (Lubchenco and Cubit, 1980; Underwood, 1981; Dethier, 1982). In the Northern Gulf of California, Thomson and Lehner (1976) reported seasonal variation in fish communities physically controlled by variation in sea temperature. However, Astles (1993) found no significant seasonal differences in abundance for most species at large spatial scales when comparing rockpools in Australia. She assumed that no disturbance or perturbation had affected the pools, or, that when subject to disturbance, species were not affected or recovered quickly enough between each sampling.

1.5 Succession

Succession can be defined as a change in species over time on substrata created by a disturbance (Walker and Moral, 2003). It was first studied in terrestrial ecosystem by Clement (1916, 1928) who considered succession as linear and ending up reaching a climax. A more modern view is that succession is not so predictable with varying trajectories set by disturbances occurring along the species replacement sequence (Walker and Moral, 2003). A disturbance can be defined as an event affecting community structure, its impact depend on its frequency through time, its magnitude and size creating a mosaic of patches (Sousa, 1979a; Farrell, 1989). Temporal fluctuation, intensity and spatial extent of the disturbance can dictate the successional sequence in regards with the reproduction, recruitment and dispersal of the colonists (Bertocci *et al.*, 2005). Studying succession in terrestrial ecosystem often necessitate weeks (for grass growth) to centuries (trees) whereas in marine ecosystem algal replacement occurs within months which represent an obvious advantage. In marine ecosystem, the first definitions of species interactions during succession, namely facilitation, tolerance and inhibition, were inferred by Connell and Slatyer (1977)(see chapter 4 for definitions). They focused on the overall effect of early colonist on later ones in terms of positive, negative or neutral interactions (Connell *et al.*, 1987). Connell and Slayter models have little predictive power (Benedetti-Cecchi, 2000a) and perhaps can be best considered as a classification of modes of succession. Several authors have also emphasised that in any successional sequence different processes can act at different times or several process can occur together (Hawkins, 1981; Farrell, 1991). Plant-animal interactions have been integrated to the three Connell and Slayter successsional modes by Farrell (1991) who predicted the influence of grazing on the successional rates. Recently, Benedetti-Cecchi (2000a) provided a qualitative key to predict successional trajectories with regard to the life history traits (i.e. recruitment, size), the space utilisation (i.e. sparse or monopolisation) and the susceptibility to consumer of pioneer and later colonists. He also emphasised that precaution was needed when applying it to marine habitat as more investigations were necessary on the relation between species life history and their performance.

1.6 Thesis rationale, objectives and structure

Interactions between species, together with extrinsic events, play a major role in structuring intertidal communities. In addition, the physical environment greatly influences the outcome of species interactions (Bertness and Callaway, 1994). Therefore, these parameters need to be studied holistically. Disturbance is also an important factor in structuring intertidal assemblages. A recovery period with a succession through species replacements usually follows disturbance events. This thesis will examine interactions between macroalgae, herbivores, and the influence of environmental stress on those interactions during succession.

Several authors have developed models to describe successional events based on species interactions (e.g. Connell and Slatyer, 1977; Farrell, 1991; Benedetti-Cecchi, 2000a). This thesis focuses mainly on the model proposed by Bertness and Callaway (1994). They predicted that positive direct interactions are common under harsh physical conditions and high consumer pressure (fig. 1.1) in both climax communities and during succession. In benign environments and at low consumer pressure, they assumed that competitive interactions are the dominant structuring forces. Moreover, under high physical stress, they demonstrated that positive interactions are characterized by habitat ameliorations by the primary space-holders. They concluded that under high grazing pressure, associational defences - when unpalatable algae protect against grazing palatable ones that have recruit among them - occur among potential competitors. This conceptual model originated from observations made on salt marsh where the lower part experience anoxic soil condition, the intermediate marsh have high soil salinities because of its position at the limit of the tidal flush and the high marsh being less stressful as influenced by terrestrial run-off (Bertness and Leonard, 1997). Several positive interactions during secondary succession and among adults have been documented such as aeration of the anoxic soil by lower salt marsh plants (e.g. Bertness, 1991b; Hacker and Bertness, 1995) and reduction of soil salinity by shading from early colonists in intermediate marsh (Bertness, 1991a; Bertness and Shumway, 1993) (but see Bertness and Leonard, 1997, for review). Some evidences of neighbor habitat ameliorations from other intertidal system such as rocky shores have also been shown between barnacles (Bertness, 1989) and mussels (Bertness and Grosholz, 1985). Bertness and Callaway (1994) emphasised on the fact that positive interactions should be predictable under stressful environments (either mediated by harsh physical condition or high consumer pressure) and must be included in community paradigms. Since their paper, although, habitat ameliorations have been well documented in marine habitats (see Bruno and Bertness, 2001, for review) little attention have been given to the role of associational defences (Stachowicz, 2001) and their model have never been tested as a whole on an ecosystem.

According to those models, prediction of a sequence of colonization will depend on the model of succession involved, the successional status of the species most affected by grazers, the intensity of consumption by herbivores, the understanding of the life history of the species (reproduction, recruitment, dispersal), the time of disturbance occurrence, and the size patch affected (Sousa, 1984a; Farrell, 1991; Benedetti-Cecchi, 2000a,b). Therefore, succession can be driven by constant patterns, which lead to canalized succession and by less predictable and more variable patterns, which lead to contingent succession (Berlow, 1997).

Studies of species interactions during succession on open rock in the intertidal generally support Farrell's predictions (1991) with resulting negative interactions between colonists (see Sousa and Connell, 1992, for review). However, very few studies have been made on succession in rockpool habitats (e.g. Benedetti-Cecchi and Cinelli, 1996; Benedetti-Cecchi, 2000b). Given the environmental differences between these habitats - emergent rock experiencing more desiccation and heat stress than rockpools - rockpool and emergent communities provide a contrasting set of conditions within a small scale in which to test Bertness and Callaway's model. The main objectives are: (1) to investigate species interactions during the first stages of succession in rockpools and to compare them to those of the emergent substrate; (2) to examine the influence of consumer pressure on these interactions and on the succession trajectory. The general hypothesis

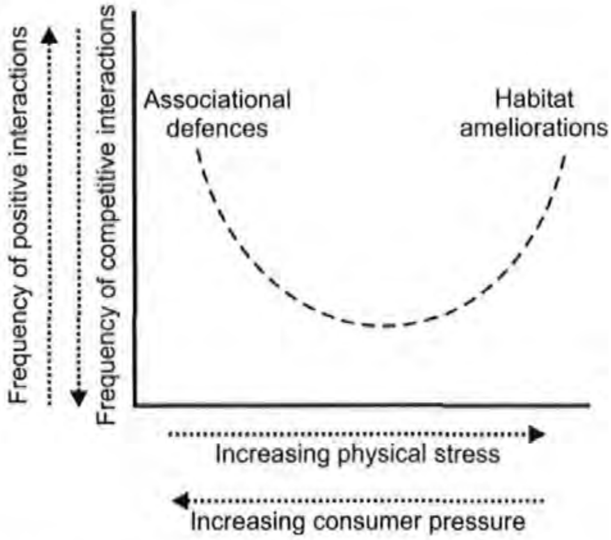

Figure 1.1: Bertness and Callaway conceptual model (1994) on direct positive interactions predicted to be common under harsh physical conditions and high consumer pressure.

is that among positive interactions, associational defences (e.g. palatable algae growing within *Corallina* spp. which protected them against grazing) will occur more often in rockpools where consumer pressure is speculated to be high (Dethier, 1982; Lubchenco, 1982; Chapman, 1990b) and physical stress low, and that habitat ameliorations will be found on the emergent substrate where consumer pressure is hypothesized to be low and physical stress high.

From the different conceptual model of succession (Connell and Slatyer, 1977; Farrell, 1991; Bertness and Callaway, 1994; Benedetti-Cecchi, 2000a), predictions can be done: (1) As the physical stress increase with the shore elevation, the rate of positive interactions will increase from the low to the high shore level in both rockpools and emergent rock. (2) In low physical stress environment and at high consumer pressure (i.e. in rockpools), facilitation from early colonists for later ones is expected as associational defences. This involves a recruitment of unpalatable species in the first instance to enhance the establishment of more palatable later colonist. Manipulation removal of early colonist should reduce the abundances of the later species. (3) At high physical stress and low consumer pressure (i.e. emergent rock where herbivores were removed), habitat amelioration from early colonist are expected to be necessary for the later one to establish. Therefore, early green ephemerals or barnacles will facilitate Fucus development. On the contrary, a decrease in Fucus abundance is expected when green ephemerals or barnacles are experimentally removed. (4) Negative interaction such as competition can be predicted in benign environment at medium consumer pressure (i.e. rockpools at reduced grazer density and emergent rock with natural herbivores abundances). There will be an inhibition from the early colonists which could even stop the succession. Its relaxation by removal of the early species will enhance the recruitment of later colonists. Those predictions were tested in turn in the different chapters of this thesis.

Chapter 2 describes the physico-chemical environment of rockpools and patterns of algal communities at the study site, their relationship and the influence of herbivores on both abiotic and biotic parameters in order to establish the influence of the physical stress gradient among shore levels on species distribution in rockpools and the relative role of algal assemblages on the physico-chemical environment.

Chapter 3 quantifies consumer pressure by measuring grazing intensity in rockpools and on adjacent emergent rock and investigates the possible causes of the greater grazing pressure that was observed in rockpools (e.g. higher herbivore density, grazer movements) in order to define a grazing gradient between rockpools and emergent rock and to relate it to the Bertness and Callaway model (1994).

In chapter 4, the influence of grazing pressure and physical stress, on algal species interactions during succession is studied in rockpools and on emergent rock. In addition, initiation time of succession and effect of early and later colonisers on each other is assessed in order to increase our understanding of species interactions and examine these relations to various successional models.

In chapter 5, the results of my work will be integrated to test the Bertness and Callaway model and the hypotheses that (1) associational defences will only occur in benign environments under high grazing pressure (i.e. in rockpools at natural herbivore density); (2) habitat ameliorations will only occur in harsh physical conditions and low grazing pressure (i.e. on emergent rock where herbivores are removed) and (3) at low levels of physical stress and consumer pressure, competition will be the main interaction between algal species.

Chapter 2

Relationships between physico-chemical factors and grazing in regulating community composition in rockpools

2.1 Introduction

Compared to the emergent intertidal substrata, few attempts have been made to disentangle the factors regulating community composition in rockpools and relate these to physico-chemical variables (but see Huggett and Griffiths, 1986; Metaxas *et al.*, 1994). Unlike organisms that are exposed to the air during low tide, organisms living in rockpools are protected from desiccation (Newell, 1979). They do, however, still experience considerable variation in the physical environment (salinity, temperature, oxygen, carbon dioxide levels and pH) over the tidal cycle (Huggett and Griffiths, 1986). The rockpool environment can be quite erratic and changes can be sudden when the tide returns to connect a pool to the sea once again (Johnson and Skutch, 1928; Naylor and Slinn, 1958; Morris and Taylor, 1983; Huggett and Griffiths, 1986).

Major environmental gradients such as elevation (Morris and Taylor, 1983; Johnson and Skutch, 1928; Pyefinch, 1943; Wolfe and Harlin, 1988b) and wave action, together with topographical factors, such as the slope of the surrounding rock and the pool walls (Johnson and Skutch, 1928; Astles, 1993), shade (Pyefinch, 1943), and pool dimensions, all influence physical conditions in rockpools (Pyefinch, 1943; Ambler and Chapman, 1950; Goss-Custard *et al.*, 1979;

Sze, 1980; Therriault and Kolasa, 1999). Physico-chemical conditions also vary over the emersed period, with tidal, spring-neap and seasonal cycles (Pyefinch, 1943; Ambler and Chapman, 1950; Morris and Taylor, 1983; Metaxas and Scheibling, 1996; Huggett and Griffiths, 1986). For example, timing of low water can have a major influence, with greater physico-chemical variations experienced when low water occurs in the middle of the day (Huggett and Griffiths, 1986). In addition, a longer period of tidal isolation of rockpools during spring tides generates greater variation in physico-chemical factors, leading to extreme conditions in high shore pools (Pyefinch, 1943; Ambler and Chapman, 1950; Morris and Taylor, 1983). The duration and the frequency of the period of emergence directly influence the amount of solar irradiance received by rockpools and therefore their water temperature (Johnson and Skutch, 1928; Morris and Taylor, 1983; Metaxas and Scheibling, 1996), which in turn influences evaporation. Greater insolation stress in summer generally leads to more extreme conditions in particular in temperature and salinity. Temperature will also vary with pool size and depth (Ambler and Chapman, 1950), according to heat radiation from the surrounding rock (Johnson and Skutch, 1928; Ganning, 1971), the ratio of daylight to night time (Johnson and Skutch, 1928; Ambler and Chapman, 1950; Gustavsson, 1972; Morris and Taylor, 1983), and the air temperature (Ambler and Chapman, 1950; Femino and Mathieson, 1980). Rockpool salinity depends on evaporation and freshwater inputs, such as rainwater, and the interaction of these factors with the size and depth of the pool. For example, Goss-Custard *et al.* (1979) found that salinity was greater in shallow pools than in deeper pools in Ireland owing to evaporation. The greatest variations in salinity have been recorded on hot or rainy days (Gustavsson, 1972; Femino and Mathieson, 1980) with extreme changes in very high shore pools that were rarely connected with the sea (Naylor and Slinn, 1958). Vertical stratification of temperature and salinity has also been observed in rockpools (Ambler and Chapman, 1950; Morris and Taylor, 1983; Kooistra *et al.*, 1989).

The chemical composition of pools, particularly hydrogen ion (pH) and oxygen concentrations, are closely related to biological factors, in particular with the density rather than the composition of the biota (Klugh, 1924; Johnson and Skutch, 1928; Stephenson *et al.*, 1934; Pyefinch, 1943). The pH provides an index of the ratio of oxygen to carbon dioxide (Ambler and Chapman, 1950) and is related to the balance of photosynthetic and respiratory activity. It has been used as an index of photosynthesis (Moore *et al.*, 1923; Morris and Taylor, 1983), and to estimate the relative proportions of plants and animals (Ambler and Chapman, 1950). Oxygen can become supersaturated in rockpools (Ambler and Chapman, 1950). Temperature and oxygen concentrations vary in relation to the height of the pool on the shore and show the greatest variation with higher values during daytime at high shore (Morris and Taylor, 1983), and may therefore play an important role in influencing the community in pools via stress. Temperature variation increases progressively with vertical height on the shore (Stephenson *et al.*, 1934; Pyefinch, 1943; Ambler and Chapman, 1950; Naylor and Slinn, 1958; Daniel and Boyden, 1975). Oxygen, temperature, pH and salinity have all been well studied, but little is known about the importance of nutrient levels in pools on the community (Metaxas *et al.*, 1994).

In parallel with physico-chemical parameters, the biota of rockpools has been described, but work has mainly focused on mid to high shore pools (Naylor and Slinn, 1958; Gustavsson, 1972; Sze, 1980; Metaxas *et al.*, 1994; Bjork *et al.*, 2004) and early studies were poorly replicated with very few pools (e.g. Klugh, 1924; Ambler and Chapman, 1950; Naylor and Slinn, 1958). Community composition has been shown to change along the vertical gradient of the shore (Klugh, 1924; Huggett and Griffiths, 1986; Kooistra *et al.*, 1989) with high shore pools being dominated by green algae (Gustavsson, 1972; Sze, 1980; Wolfe and Harlin, 1988b; Bjork *et al.*, 2004) and low shore pools having greater algal biomass (Femino and Mathieson, 1980) and faunal species richness (Therriault and Kolasa, 1999). Johnson and Skutch (1928) classified rockpools in relation to their species vertical distribution and occurrence, either restricted to pools, found both in pools and on emergent rock at similar shore height or when species reached their upper limit in pools. Rockpool communities are also subject to seasonal variations (Femino and Mathieson, 1980; Sze, 1982; Dethier, 1982; Wolfe and Harlin, 1988a,b), for example, with an increase in annual species during the spring (Femino and Mathieson, 1980). Some studies have used a functional group approach to describe patterns of spatial distribution and seasonality in algal communities with, for example, thick leathery and crustose macroalgal forms in higher abundances in low shore pools (Steneck and Dethier, 1994; Metaxas *et al.*, 1994) (but see Padilla and Allen, 2000, for discussion of limitations). Relationships between the abiotic environment and biotic parameters have also been investigated (Huggett and Griffiths, 1986; Wolfe and Harlin, 1988b; Metaxas *et al.*, 1994; Therriault and Kolasa, 1999). For example, Huggett and Griffiths (1986) showed that the density and relative proportions of the fauna and flora can drastically influence oxygen concentration in pools. However, the indirect effect of grazers on physico-chemical factors, such as oxygen, temperature, salinity, has not been examined, although it is recognized that herbivores play a major role in structuring the algal community of rockpools (Paine and Vadas, 1969; Lubchenco, 1978; Dethier, 1982; Lubchenco, 1982; Sze, 1982; Steneck and Dethier, 1994).

The overall aim of this chapter was to describe changes in macroalgal community composition over the vertical tidal gradient and examine the extent to which distribution patterns are either driven by, or in turn drive, physico-chemical factors. In addition, the effect of herbivory and seasonality on macroalgal abundance, and the indirect influence of these algae on the physico-chemical environment, was also investigated. In order to examine the effect of grazing on algal recruitment and development, grazers were removed at different times of the year. After a preliminary survey, a grazer removal experiment was carried out in rockpools during summer and winter in order to establish: (1) how the algal community changed over the emersion gradient under a varying consumer pressure; (2) how the rockpool physico-chemical factors pH, temperature, salinity and dissolved oxygen changed over the tidal gradient under differing consumer pressure; (3) the relationship between assemblage composition and physico-chemical rockpool parameters.

2.2 Material and methods

Experiments were conducted at Wembury Bay (50° 18' N, 4° 5' W) Southwest England, a moderately exposed to sheltered shore with flat and smooth sloping bedrock, interrupted by small sandy beaches. Rockpools are common over the whole vertical extent of the shore. The mid tide level (MTL) was dominated by barnacles, with patches of *Fucus serratus* and *Ascophyllum nodosum* lower on the shore. At the upper limit of the barnacle zone, patches of *Fucus spiralis*, *Lichina pygmaea*, *Pelvetia canaliculata* and the lichen *Verrucaria maura* covered the rock surface. Common herbivores included the limpets *Patella vulgata*, *P. depressa*, *P. ulyssiponensis* (the latter mostly found in pools), the periwinkle *Littorina littorea* and the trochids *Gibbula umbilicalis* and *Osilinus lineatus*. Predators such as the dogwhelk *Nucella lapillus* and the shore crab *Carcinus maenas* were also present.

2.2.1 Preliminary broadscale survey

A preliminary descriptive survey was made in order to describe the general community composition of rockpools in relation to shore height and pool size. A total of 96 rockpools were selected at each of two shore levels: high level pools between 3 and 4m above lowest astronomical tides (MTL-MHWN), and low level pools between 0.5 and 1m above lowest astronomical tides (MLWS-MLWN). The selected tidal heights excluded very high shore rockpools above MHWN, which were dominated by *Ulva* spp. Two pool sizes were considered: small (0.25-0.75 m^2 in surface area) and large (1.2-1.6 m^2). In March and April 2002, the percentage cover of macroalgae forming primary and secondary layers was quantified using a method developed by Viejo (1997). Primary cover was assessed by moving aside the canopy species forming the secondary cover. A string with 10 knots was randomly placed ten times in each large pool and five times in each small pool (Viejo, 1997). At the intersection of each knot with the substratum, macroalgal cover was estimated. Seaweed floating at the pool surface in contact with a knot was considered as 1% of secondary cover which was then pushed aside in order to identify the seaweed covering the bedrock under the knot as 1% of primary cover. In addition, any macrofauna encountered were also recorded as number of individual.

Organisms (seaweeds and animals) present in the pools, but not recorded by this method, were also assessed by a broadscale survey of the pool and a value of 1% abundance was allocated to them. Seaweeds were identified in the field to species when possible, but when there was any doubt samples were collected for further identification in the laboratory using identification keys (Hiscock, 1979; Irvine, 1983; Hiscock, 1986; Irvine and Chamberlain, 1991; Burrows, 1991; Dixon and Irvine, 1977; Fletcher, 1987; Maggs and Hommersand, 1993). In addition, any macrofauna encountered were also recorded.

Shannon Diversity index (H') (Pielou, 1969) was calculated for the preliminary survey of species recorded at high and low levels in March-April 2002 as:

$$H' = -\sum_{i=1}^{n} P_i \ln P_i \tag{2.1}$$

where P_i is the proportion of ith species in each pool (n=24). Analysis of variance (ANOVA) was used to determine the effect of two fixed and orthogonal factors: tidal height (High or Low) and pool size (Large or Small) on the diversity of organisms in rockpools. Cochran's test was used to test for the assumption of homogeneity of variances (Winer, 1971). When required, *Post-hoc* multiple comparisons of the means were effectuated using Student-Newman-Keuls tests (SNK) (Underwood, 1997). These analyses were carried out using WinGmav5 (Underwood and Chapman 1997).

Multivariate analyses were conducted in order to compare community composition. These were performed on the fourth-root transformed data to reduce the influence of the most abundant species on overall assemblage structure (Clarke and Warwick, 2001). Assemblages were analysed using a Bray-Curtis matrix of similarity (Bray and Curtis, 1957; Clarke and Warwick, 2001). From this an ordination of each sample was carried out using non-metric multidimensional scaling (nMDS). An analysis of similarity (ANOSIM) was used in order to test for differences between tidal height and pool size for the preliminary survey. Analyses were performed using PRIMER-E v6.1.5 (Clarke and Warwick, 2001) (for nMDS, ANOSIM).

2.2.2 Effects of emersion gradient, season and grazing regime on algal community composition and physico-chemical parameters

2.2.2.1 Experimental design and implementation

An experimental manipulation was carried out in order to examine the relationship between physico-chemical parameters, algal functional groups and herbivores over the vertical intertidal gradient. A total of 18 medium sized rockpools (depth 8-15 cm, area 0.35-1 m^2), were selected at Wembury point with 6 pools at each of three shore levels (high level pools between 3-4m above lowest astronomical tides (MTL-MHWN); mid level between 1-3m above lowest astronomical tides (MLWS-MTL) and low level pools between 0.5-1m above lowest astronomical tides (MLWS-MLWN)). After selection, the absolute height of each pool above LAT was determined by recording the time of emersion on several occasions and referring to a tide level prediction program (Poltips3, Proudman Oceanographic Laboratory, NERC, Liverpool, UK). High shore rockpools dominated by *Ulva* spp. were not used. In order to investigate the effect of herbivores on the algal community and on the physico-chemical environment of the pools, grazers were removed from two rockpools at each shore level in summer 2002 (reduced grazer density: -G) and these pools were compared to two others left at a natural grazer density (controls: +G). An additional grazer removal was initiated six months after the beginning of the experiment, in two other pools at each shore level in winter 2003 (-G6), in order to assess changes due to seasonal algal recruitment. These treatments were randomly allocated to selected pools and grazers were removed every month from August 2002 to February 2005 (-G6 removal started in February 2003). All detectable by eye molluscan herbivores (e.g. *Patella vulgata*, *P. depressa*, *P. ulyssiponensis*, *Littorina littorea*, *Gibbula umbilicalis*, *Osilinus lineatus* but also Chitons and *Aplysia* spp.) were removed by hand from inside the rockpool and from a one metre area around each pool to minimise grazer recolonization from the surrounding area.

2.2.2.2 Biotic sampling: algal functional groups

The macroalgal community of those rockpools was described according to functional group composition as outlined by Littler (1980), Littler and Littler (1980) and Steneck and Dethier (1994). After identification at the species level whenever possible, macroalgae were grouped in six functional groups: crustose algae, articulated calcareous, filamentous, foliose algae, coarsely branched macroalgae and leathery macrophytes (See appendix A.1 for species breakdown). An additional group representing the macrofauna encountered during sampling was also considered. In each rockpool, two random quadrats of 10x10cm subdivided into 16 sections were sampled in August 2004 and February 2005. For each section, individual algae received a score from 0 to 4: 0 (species absent), 1 (species cover 1/4 of the section), 2 (species cover 50% of the section), 3 (species cover 3/4 of the section), 4 (100% cover) (see Dethier *et al.*, 1993, for details). Species present in each section, but with a score lower than 1, were recorded as 1% cover. Species percentage cover was then estimated and used to asses the proportion of each functional group. Macroalgal cover forming primary and secondary layers was assessed in all pools. Primary cover was assessed by moving aside the canopy species forming the secondary cover. Any macrofauna, other than manipulated herbivores, encountered using this method were also recorded as number of individual.

A permutational multivariate analysis of variance (PERMANOVA, PERMANOVA program (Anderson, 2001; McArdle and Anderson, 2001)) was performed on a Bray-Curtis matrix of similarity in order to compare the percentage of algal cover between summer and winter, between shore heights (High, Mid, Low) and between grazer treatments (+G, -G, -G6) and also to test for any interactions among these factors. When statistical differences were found, pairwise comparisons were used to investigate the data further. Finally, to interpret the pattern of individual species or functional group abundance, a SIMPER (PRIMER-E v6.1.5.) procedure was then applied to the data.

2.2.2.3 Abiotic sampling: physico-chemical parameters

Physico-chemical parameters were measured in the 18 rockpools in order to investigate any relationships between the distribution of functional groups, the vertical intertidal gradient and the influence of grazer density (+G, -G, -G6). The surface area of the pools was measured from digital pictures using the Image J software (Abramoff and Magelhaes, 2004). The mean maximum depth (hereafter referred to as depth) was assessed from 3 measurement points, from the bottom of the pool to its surface, with a ruler. The volume of each pool was estimated, based on the assumption that the shape of the rockpools was between a cylinder and a cone (Volume = (1/2) x surface x height). Measurements of changes in physico-chemical parameters (temperature, dissolved oxygen concentration, pH and salinity) over the daytime low water period were taken in each pool in summer (August 2004) and winter (February 2005). Equipment used for the measurements were an Orion model 1230 pH/mV/ORP/Conductivity/Dissolved Oxygen/Salinity/Temperature Meter (QCL laboratories Ltd, England) in August 2004, and a portable pH/DO meter (HQ20 Hatch portable LDO^{TM}, Loveland USA) in February 2005. Before each measurement, the water of the pool was mixed by stirring it in order to avoid any stratification effect. Measurements were taken hourly between the emersion of each pool and subsequent immersion on three consecutive days. For all measurements, the period of emersion was on average five hours for the high shore pools and three hours for the low shore pools, with low tide corresponding to the middle of the day. Weather conditions on the three replicate days within each season were similar in terms of solar irradiance, air temperature and wind speed and there was no rainfall (data on these conditions were based on the records of the Plymouth Marine Laboratory weather station, PML, Plymouth, U.K.).

Physico-chemical parameters were compared among treatments using analysis of variance (ANOVA), with two fixed and orthogonal factors: tidal heights (High, Mid, Low) and treatments (+G, -G, -G6). Analyses were done for time 0, when the pool was just disconnected from the sea and just before the pool was reconnected with the sea (after 3 hours in Winter 2005 and 4 hours in Summer 2004). Measurements were recorded over a longer time in the summer owing to a longer low tide period than in winter. Dissolved oxygen was expressed as mg of oxygen produced per dm^2 of pool bottom surface area, assuming that the surface at the top of the rockpool was equivalent to the bottom. Cochran's test was used to test for the assumption of homogeneity of variances. When this assumption was not verified, data were logarithmicaly transformed to achieve homogeneity of variance. When required, *Post-hoc* multiple comparisons of the means were made using Student-Newman-Keuls test (SNK).

In order to examine any relationships between physico-chemical variables and functional groups, Pearson's correlation coefficient was calculated between each variable. In addition, draftman plots (pairwise scatter plots between all variables, PRIMER-E v6.1.5) were plotted and were presented in appendix B. Abiotic data used were the average of the maximum value measured at the end of the low tide of the 3 days measurements for each of the two replicate pools and were compared with the mean abundances of the functional groups recorded in those replicate pools in summer 2004 and winter 2005 (n=18).

In addition, in order to relate physico-chemical variables to the biotic assemblage, a BIOENV procedure was carried out on the data from the 18 rockpools. The maximum value at hte end of the low tide of the physico-chemical parameters over a four-hour period was related to functional group cover in a BIOENV procedure. Spearman's rank correlation of the two triangular matrices: (1) a Bray-Curtis matrix of similarity of the functional groups with a fourth-root transformation and (2) the normalised Euclidian distance matrix of the physico-chemical factors were calculated for summer 2004 and winter 2005 in order to find the subset of abiotic variables which match the best the biotic assemblage. BIOENV was performed using PRIMER-E v6.1.5.

2.3 Results

2.3.1 Preliminary broadscale survey

A list of the species encountered in high and low level pools is presented in table 2.1. The composition of the algal species in rockpools differed between high and low shore levels. Distinct clusters for high and low level rockpools were apparent on the multidimensional scaling ordination map (see fig. 2.1) and differences were confirmed by the ANOSIM (R=0.534, p<0.01). Simper analysis showed that *Phymatolithon lenormandii* characterised most of the high level pools with 22% contribution to the similarity within this group. *Mesophyllum lichenoides* was the third most important species characterising the low level group with 11% contribution to the similarity after *Lithophyllum incrustans* (SIMPER, 18%) and *Corallina elongata* (SIMPER, 18%). Among the species contributing the most to the dissimilarity between the high and the low level, *Mesophyllum lichenoides* and *Phymatolithon lenormandii* were the most important, contributing 7% and 6% respectively (SIMPER). Species diversity characterized by the Shannon diversity index H' was

Table 2.1: Macroalgal species abundance in rockpools at high and low shore levels for the preliminary survey (March-April 2002). Data are mean percentage cover ±SE (n=48). Species <0.5% are represented by (+), numbers are % cover, species not found are represented by (-). Primary and secondary algal cover was sampled and represented after species name by (1c) and (2c) respectively. Algae are ordered by division (Rhodophyta, Chlorophyta, Phaeophyceae).

Species	High level	Low level	Species	High level	Low level
Rhodothamniella floridula	-	2.2±0.1	*Halopteris scoparia*	+	0.5±0.1
Corallina officinalis	+	-	*Halopteris filicina*	-	-
Corallina elongata	21.5±0.1	19.6±1.3	*Colpomenia peregrina*	+	0.4±0.1
Jania rubens	+	-	*Scytosiphon lomentaria* (1c)	+	+
Osmundea spp.	0.9±0.3	+	*Scytosiphon lomentaria* (2c)	+	-
Osmundea spp. (2c)	+	-	*Himanthalia elongata*(1c)	-	1.9±0.6
Lithophyllum incrustans	10.9±1.5	19.5±1.3	*Himanthalia elongata* (2c)	-	5.8±1.7
Phymatolithon lenormandii	27.9±2.2	10.8±1.2	*Fucus vesiculosus* (1c)	+	-
Phymatolithon purpureum	-	6.2±0.9	*Fucus vesiculosus* (2c)	0.7±0.3	-
Mesophyllum lichenoides	+	11.3±1.3	*Fucus serratus* (1c)	+	+
Mastocarpus stellatus	1.2±0.5	+	*Fucus serratus* (2c)	0.8±0.4	0.7±0.3
Chondrus crispus (1c)	+	+	*Halidrys siliquosa* (1c)	+	-
Chondrus crispus (2c)	-	+	*Halidrys siliquosa* (2c)	+	-
Calliblepharis jubata (1c)	-	0.7±0.2	*Cystoseira baccata* (1c)	-	+
Calliblepharis jubata (2c)	-	+	*Cystoseira baccata* (2c)	-	+
Gigartina acicularis	-	+	*Cystoseira tamariscifolia* (1c)	+	0.9±0.2
Gigartina pistillata	+	+	*Cystoseira tamariscifolia* (2c)	+	1.0±0.3
Gelidium spp.	2.7±0.5	0.6±1.4	*Bifurcaria bifurcata* (1c)	1.2±0.4	-
Osmundea pinnatifida	0.6±0.1	+	*Bifurcaria bifurcata* (2c)	2.3±0.9	-
Gastroclonium ovatum	+	1.1±0.3	*Laminaria saccharina* (1c)	-	+
Plocamium cartilagineum	-	+	*Laminaria saccharina* (2c)	-	+
Champia parvula	-	+	*Laminaria ochroleuca* (1c)	-	-
Chylocladia verticilata	-	+	*Laminaria ochroleuca* (2c)	-	-
Ceramium spp.	0.5±0.2	1.7±0.3	*Laminaria digitata* (1c)	-	+
H. hypoglossoides	-	+	*Laminaria digitata* (2c)	-	1.0±0.3
Polysiphonia spp.	+	1.0±0.3	*Saccorhiza polyschides* (1c)	-	+
Dumontia contorta	+	+	*Saccorhiza polyschides* (2c)	+	0.5±0.2
Palmaria palmata (1c)	+	+	*Ascophyllum nodosum* (2c)	+	-
Palmaria palmata (2c)	-	+	*Ralfsia verrucosa*	+	1.0±0.1
Petrocelis	0.9±0.2	1.2±0.3	*Sargassum muticum* (1c)	4.4±0.5	3.0±0.4
Hildenbrandia rubra	+	+	*Sargassum muticum* (2c)	13.2±2.0	5.2±1.0
Ulva intestinalis (1c)	1.2±0.3	-	*Patella* spp.	1.0±0.2	0.8±0.3
Ulva intestinalis (2c)	0.5±0.4	-	*Gibbula* spp.	+	+
Ulva spp. (1c)	3.4±0.7	1.0±0.4	*Osilinus lineatus*	+	-
Ulva spp. (2c)	+	+	*Anemonia* spp.	+	+
Cladophora spp.	0.6±0.2	2.3±0.1	*Actinia* spp.	+	-
Bryopsis plumosa	-	+	Sponge	-	0.3±0.1
Codium spp. (1c)	-	+	Rock	14.2±2.0	7.9±0.7
			Sand	3±0.1	0.4±0.2

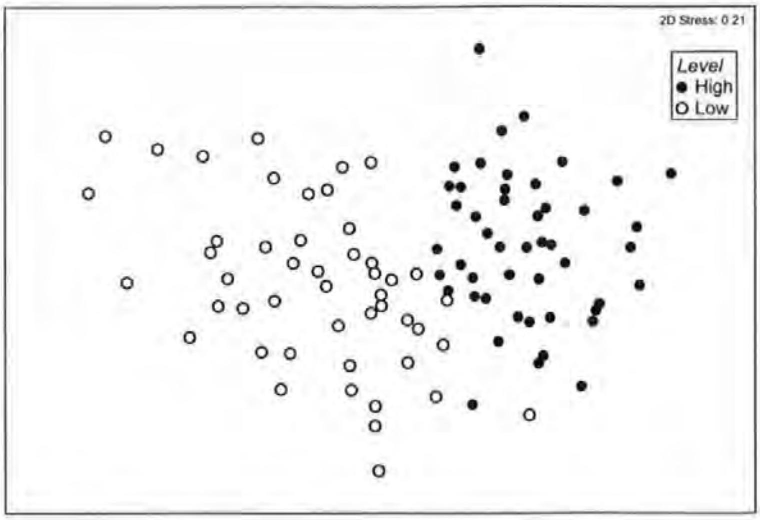

Figure 2.1: nMDS ordination of the algal percentage cover in rockpools on the upper shore (High, n=48) and on the lower shore (Low, n=48) at Wembury during the preliminary survey (March-April 2002 based on a fourth root transformed Bray-Curtis similarity (stress 0.21).

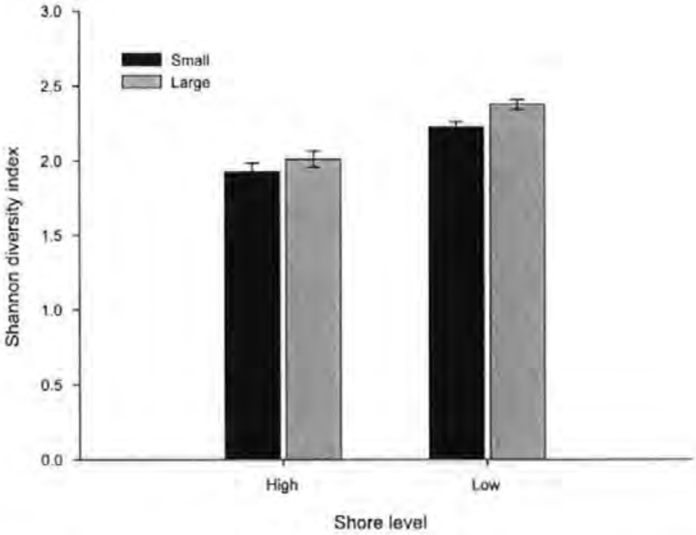

Figure 2.2: Shannon diversity index representation for the species present in rockpools on the upper and lower shore in relation to pool size. Data are mean Shannon diversity index (±SE) of the preliminary survey (March-April 2002). (n=24). There were significant differences between High and Low shore levels (ANOVA, $p<0.01$) and between pool size (ANOVA, $p<0.05$).

significantly higher in low shore rockpools than in the high level ones (fig. 2.2) (Cochran's test, $C=0.39$, $p>0.05$; 2-way ANOVA, $F=54.88$, $p<0.01$). No differences in species composition were detected between large and small pools (ANOSIM, $p>0.05$). No interaction was found for species diversity between shore level and pool size (2-way ANOVA, $F=0.53$, $p>0.05$). However, species diversity was higher in larger rockpools than in small ones (2-way ANOVA, $F=6.66$, $p<0.05$) (fig. 2.2).

2.3.2 Effects of emersion gradient, season and grazing regime on algal community composition and physico-chemical parameters

2.3.2.1 Rockpool volumes

Although careful selection of rockpools was undertaken in order to use similar sizes, the low shore level pools had significantly larger volumes (70L ±7 SE) than in the mid (40L ±6 SE) and high shore level (34L ±2 SE) (table 2.2). However, no significant differences in volume were detected between experimental treatments and for the depths or the surface areas of the pools (ANOVA, table 2.2).

Table 2.2: 2-way ANOVA comparing volumes of rockpools selected to study biotic and abiotic parameters at three shore levels (Le: High, Mid, Low) with three treatments allocated (Tr: grazer removal (-G), grazer removal initiated 6 months later (-G6), natural grazer density (+G)). (n=2). (Cochran's test non significant). ns: non significant; $***$: $P<0.001$; $**$: $P<0.01$; $*$: $P<0.05$. SNK: factor levels of the same group are represented with: =, factor levels with significant differences are represented with < or > according to their rank order.

Source	SS	DF	MS	*F*	*P*
Level (Le)	4447.09	2	2223.55	9.98	**
Treatment (Tr)	202.01	2	101.01	0.45	ns
Le×Tr	836.72	4	209.18	0.94	ns
Residual	2005.41	9	222.82		
SNK of Levels: High=Mid<Low					

2.3.2.2 Algal Functional groups

The algal community varied according to seasons, shore height and grazer treatments (fig. 2.3). These effects were also highlighted by the PERMANOVA (table 2.3). Changes in algal abundance occurred from one season to the other. In winter most algae died back (fig. 2.3), causing a reduction in cover of most of the erect fleshy functional groups. A greater abundance of crustose and articulated calcareous algae was recorded in the winter (mainly *Corallina* spp.). However, this most probably resulted from an underestimation in summer as they were partially covered by other algae. A higher but more variable proportion of corticated and leathery macrophyte, filamentous and foliose algae in rockpools during the summer showed that summer samples were more variable than winter ones, which was confirmed by their average similarities (SIMPER, summer: 47%, winter: 66%, see Appendix, B.1, for details). Table B.1 lists the functional groups and the species that contributed the most to the dissimilarity between summer and winter seasons.

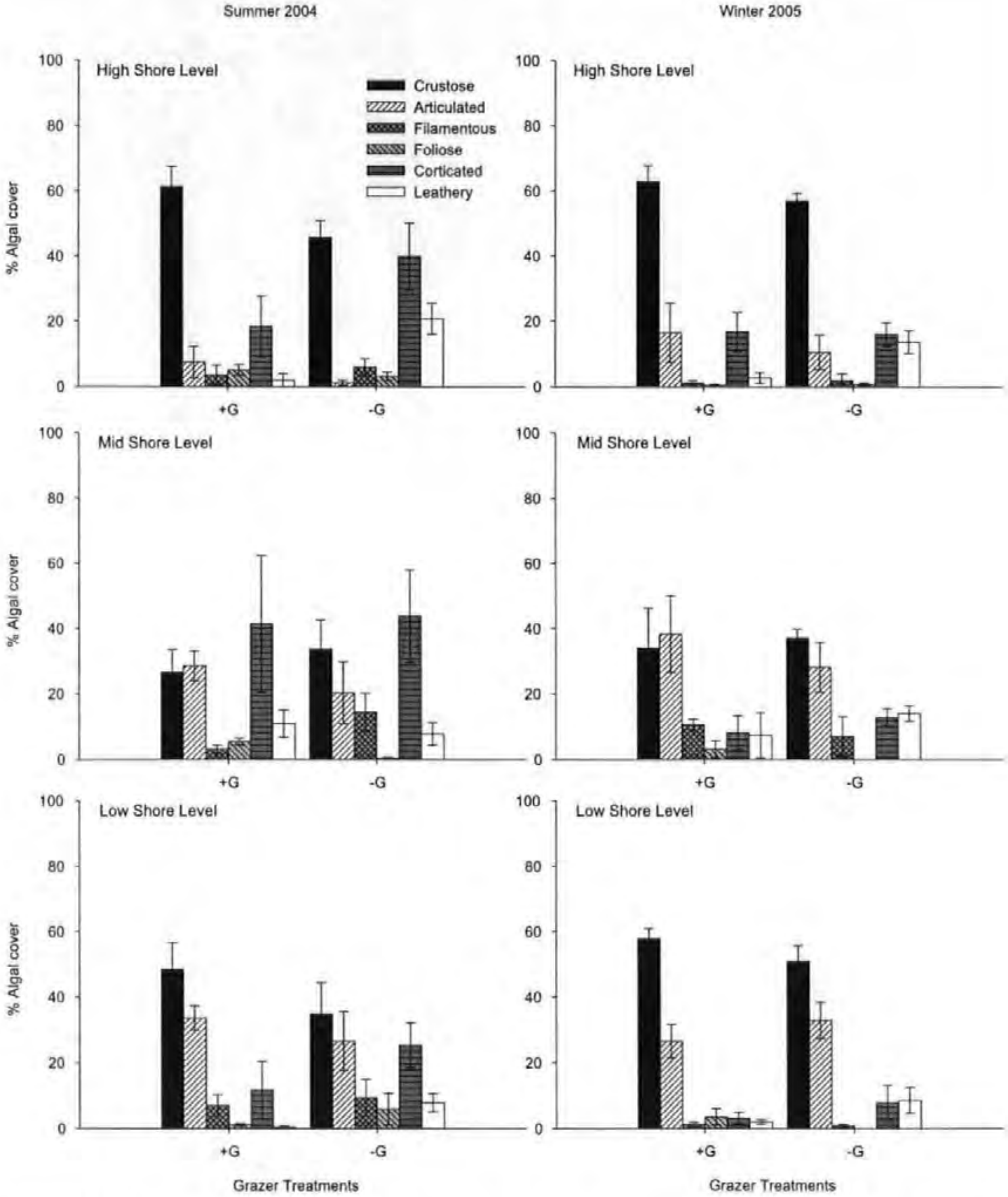

Figure 2.3: Total functional group algal cover (mean ±SE; n = 4 quadrats) in different grazer treatments: Natural grazer density (+G), reduced grazer density (-G) with removal started in summer 2002 at the 3 shore levels (High, Mid, Low) for the summer 2004 and winter 2005.

Table 2.3: PERMANOVA and Pair-wise *a posteriori* comparisons based on Bray-Curtis dissimilarity comparing percentage algal cover in rockpools sampled at two different seasons (Se: Summer, Winter), at three shore levels (Le: High, Mid, Low) for the three treatments (Tr): Natural grazer density (+G), reduced grazer density (-G) with removal started in summer 2002, reduction of grazer induced 6 months after in winter 2003 (-G6). ns: non significant; * * *: $P<0.001$; **: $P<0.01$; *: $P<0.05$.

Source	df	SS	MS	F	P(perm)	P(MC)
Season (Se)	1	2014.22	2014.22	6.25	* * *	* * *
Level (Le)	2	2339.37	1169.67	3.63	* * *	* * *
Treatment (Tr)	2	1787.10	893.54	2.77	**	**
Se × Le	2	333.09	166.54	0.52	ns	ns
Se×Tr	2	373.79	186.89	0.58	ns	ns
Le×Tr	4	1892.86	473.22	1.47	ns	ns
se×Le×Tr	4	805.62	201.41	0.63	ns	ns
Residual	18	5797.22	322.07			
Total	35	15343.26				

Pair-wise *a posteriori* comparisons

Level			Treatment		
Groups	*t*	*P*	Groups	*t*	*P*
(High,Mid)	1.68	*	(+G, -G)	1.78	**
(High,Low)	1.90	**	(+G,-G6)	1.22	ns
(Mid,Low)	1.55	**	(-G,-G6)	1.42	ns

Crustose and articulated calcareous algae, corticated and leathery macrophytes were identified as good discriminators between seasons. In summer, the cover of crustose and articulated calcareous algae was less abundant than in winter, as corticated macrophytes such as *Ceramium* spp. and leathery macrophytes such as *Sargassum muticum* partially covered them, leading to an underestimation of their cover.

A gradient in algal community composition was evident in rockpools between the shore heights (*a posteriori* pair-wise test, table 2.3). Three trends were apparent for functional groups and species abundances: some were decreasing, others were increasing down the shore and finally some had their highest or lowest proportion at the mid shore. Cover of leathery macrophytes, mostly *Sargassum muticum* and *Fucus* spp., declined with shore height and this functional group was generally a good discriminator for the high shore level (SIMPER, appendix B.2). In contrast, articulated calcareous algae *Corallina* spp. and corticated macrophytes increased down the shore and SIMPER analysis showed they contributed largely toward discriminating the low shore level (table B.2). Within the crustose functional group, opposite species trends were observed over the shore levels. The abundance of *Phymatolithon* spp. decreased from the high to the low shore whilst *Lithophyllum incrustans* increased (fig. 2.4). Consequently, the mid shore level had the lowest proportion of crustose cover. Furthermore, the filamentous functional group, particularly

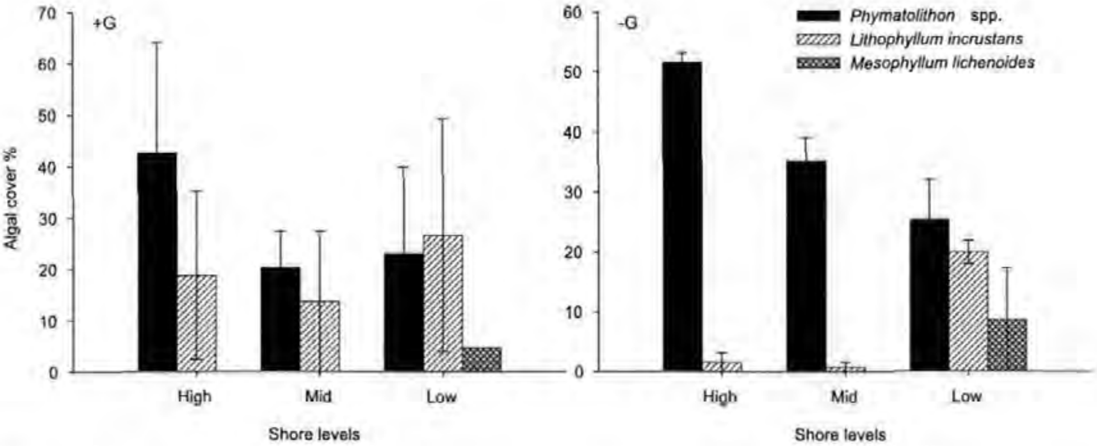

Figure 2.4: Percentage cover of calcareous encrusting algal species in winter 2005 (±SE; n=4) in different grazer treatments: Natural grazer density (+G), reduced grazer density (-G) with removal started in summer 2002 at the three shore levels: High, Mid, Low.

Cladophora spp., and *Sphacelaria* spp. showed the highest percentage cover in rockpools of the mid shore (table B.2).

Effects of grazer abundance were also apparent. Algal community composition showed significant differences between controls (+G) and the grazer exclusion (-G) treatments (*a posteriori* pair-wise test, table 2.3). Algal assemblages in rockpools where grazers were removed 6 months after (-G6) were more variable than in rockpools at natural grazer density (+G), and rockpools at reduced grazer density (-G) (table 2.4). The total cover of encrusting and articulated calcareous algae was generally greater in controls than in reduced grazer density rockpools (fig. 2.3 and fig. 2.4), showing a clear discrimination (table B.3). In contrast, corticated and leathery macrophytes, such as *Ceramium* spp., *Gelidium* spp. and *Sargassum muticum* respectively, were more abundant in pools at reduced grazer density (-G) (fig. 2.3). Filamentous algae such as *Cladophora* spp. followed the same trend (fig. 2.3, table B.3).

Table 2.4: Average similarity percentage (in bold) between rockpools for each treatment: grazer removal (-G), grazer removal 6 month later (-G6), natural grazer density (+G) and dissimilarity between the three shores levels given by SIMPER

Treatments	+G	-G	-G6
+G	**61.99**		
-G	39.96	**63.03**	
-G6	42.92	42.82	**54.25**

2.3.2.3 Physico-chemical parameters

Owing to the difficulty of reaching all pools immediately after emersion, values at the first sampling point differed among treatments and shore levels for some parameters (table 2.5, 2.7). However, differences were small compared to those observed between treatments at the end of the low water period. Each season was analysed separately. Dissolved oxygen measurements were not made in summer 2004 due to equipment failure.

In summer 2004, for all three grazer treatments, at all three shore levels, the mean pH of pools increased over the low water period, showing the pools became more alkaline. Mean pH immediately after emersion was 8.55 ±0.02 SE, which increased to a value of 9.31 ±0.03 SE averaged over all treatments. The change in pH over the low water period was generally not linear,

Table 2.5: Summer 2004. 2-way Anova for effects of grazer manipulation and shore height on a) pH, b) temperature, c) salinity mean values for the rockpools sampled at 3 shore levels (Le: High, Mid, Low) for the 3 treatments (Tr: reduced grazer density stated in summer 2002: -G, reduced grazer density started 6 months later in winter 2003: -G6, natural grazer density: +G) at time 0 and at time 4 hours at the end of the low tide on 3 consecutive days (n=3). (Cochran's test non significant). ns: non significant; * * *: $P<0.001$; **: $P<0.01$; *: $P<0.05$. SNK: factor levels of the same group are represented with: =, factor levels with significant differences are represented with < or > according to their rank order.

		Time 0			Time 4		
a) pH	DF	MS	*F*	*P*	MS	*F*	*P*
Levels (Le)	2	0.05	5.95	*	0.02	3.82	*
Treatment (Tr)	2	0.03	3.54	*	0.12	18.57	* * *
Le×Tr	4	0.03	3.94	*	0.1	15.69	* * *
Residual	18	0.01			0.01		
SNK (Le×Tr)							
Time 0:	Tr(Le)	High: +G<-G6 and -G<-G6					
Time 4:	Tr(Le)	High: -G<+G<-G6 Mid: -G<+G=-G6 Low: +G<-G			Le(Tr)	-G: High=Mid<Low -G6: Mid>Low +G: High=Mid=Low	

		Time 0			Time 4		
b) Temperature	DF	MS	*F*	*P*	MS	*F*	*P*
Levels (Le)	2	0.30	0.59	ns	3.17	2.80	ns
Treatment (Tr)	2	0.16	0.30	ns	5.17	4.56	*
Le×Tr	4	0.15	0.29	ns	0.4	0.36	ns
Residual	18	0.52			1.13		
SNK (Tr)					Time 4: -G<+G=-G6		

		Time 0			Time 4		
c) Salinity	DF	MS	*F*	*P*	MS	*F*	*P*
Levels (Le)	2	0.15	0.62	ns	0.14	0.21	ns
Treatment (Tr)	2	0.03	0.13	ns	0.75	1.10	ns
Le×Tr	4	0.08	0.33	ns	0.67	1.01	ns
Residual	9	0.24			0.69		

but slightly asymptotic with a decline in the rate of change with time (fig. 2.5). There was a lower increase of pH in the pools at reduced grazer density (-G) on the high and mid shore (fig. 2.5) indicated by the SNK test for samples at the end of the low water period (table 2.5). The pools where grazers were removed in winter 2003 (-G6), 6 months after the start of the experiment, and the pools at natural grazer density showed no significant differences. No pH gradient was observed over the shore heights but maximum pH was recorded in the lower pools at reduced grazer density (-G), and in mid shore rockpools at natural grazer density (+G) (table 2.5, SNK and table 2.6). In addition, pH was negatively correlated with depth and a strong positive correlation was recorded with temperature and salinity (table 2.8).

Temperature also increased asymptotically during emersion for all the treatments and at all the shore levels. Mean temperature was 16.1°C ±0.1 SE after pools became separated from the sea and was 20.7°C ±0.2 SE at the end of the low tide period, averaged over all the treatments (fig. 2.5). At the end of the low water period, the temperature for rockpools at reduced grazer density (-G) was lower than in pools at natural grazer density (+G) (SNK, table 2.5). Pools where grazers were removed 6 months after the start of the experiment (-G6) were no different from the controls (SNK, table 2.5). No gradient in temperature was observed over the shore heights (table 2.5). However, an opposite trend between grazer treatments appeared with highest mean temperatures in mid and low shore rockpools where herbivores were removed (-G) and highest mean temperatures in mid and high shore rockpools at natural grazer density (+G) (table 2.6). In addition, temperature was negatively correlated with pool depth (table 2.8).

Salinity followed the same trend as temperature with a linear increase over the emersion time from 34.9 ±0.1 SE to 37.5 ±0.3 SE ppt, averaged for all treatments (fig. 2.6). Although, no significant differences were observed owing to high levels of variability (table 2.5), shore heights and grazer treatments influenced salinity. The increase in salinity over the emersion period was

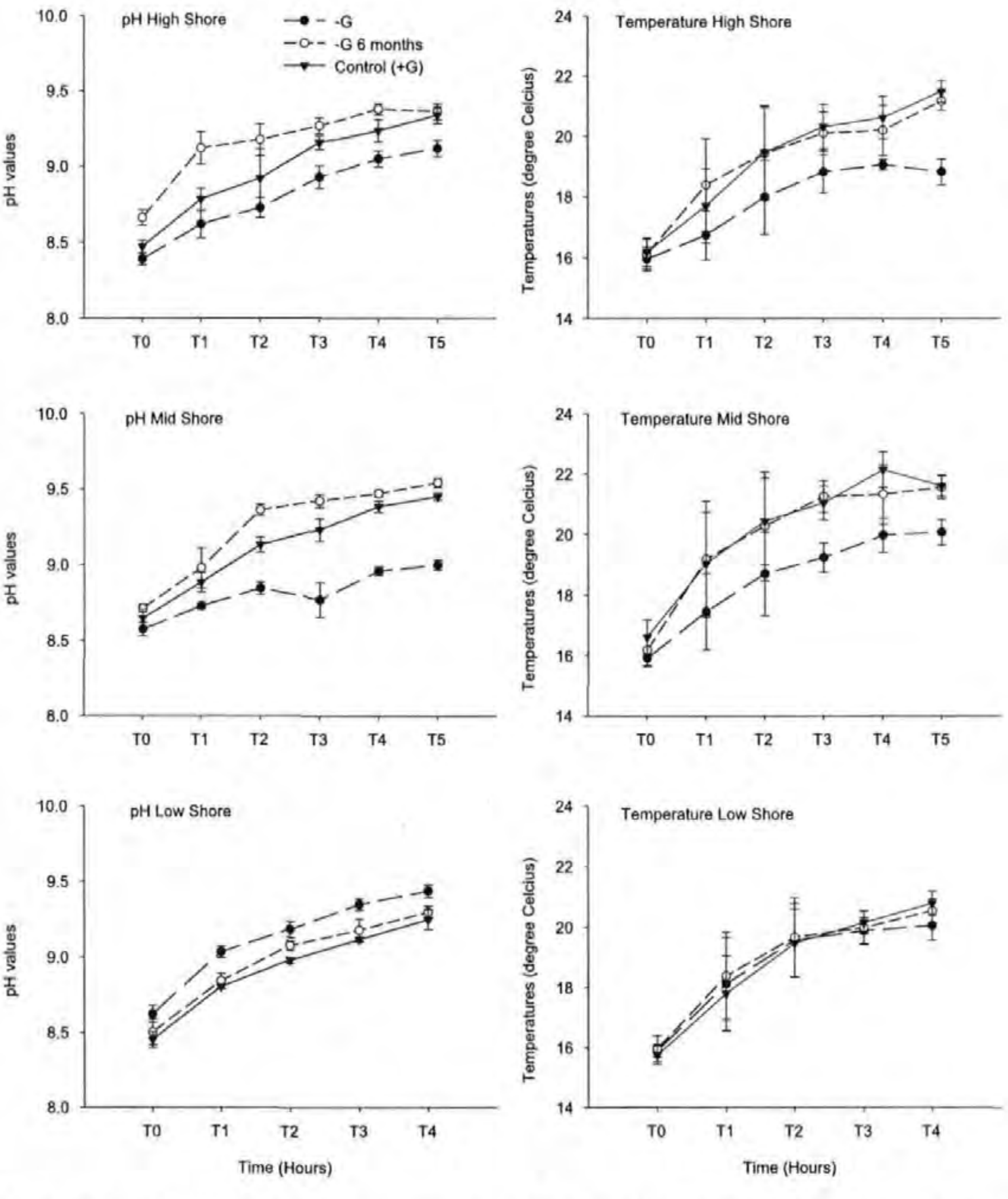

Figure 2.5: SUMMER 2004. pH and temperature mean value (±SE) measured every hour in rockpools of 3 replicate sampling days over an emersion period in August 2004 at the 3 shore levels (High, Mid, Low) for the 3 treatments (reduced grazer density stated in summer 2002: -G, reduced grazer density started 6 months later in winter 2003: -G 6 months, natural grazer density: +G). Seawater pH was 8.64 ±SE 0.11 and temperature was 17 degree Celsius ±0.8 SE.

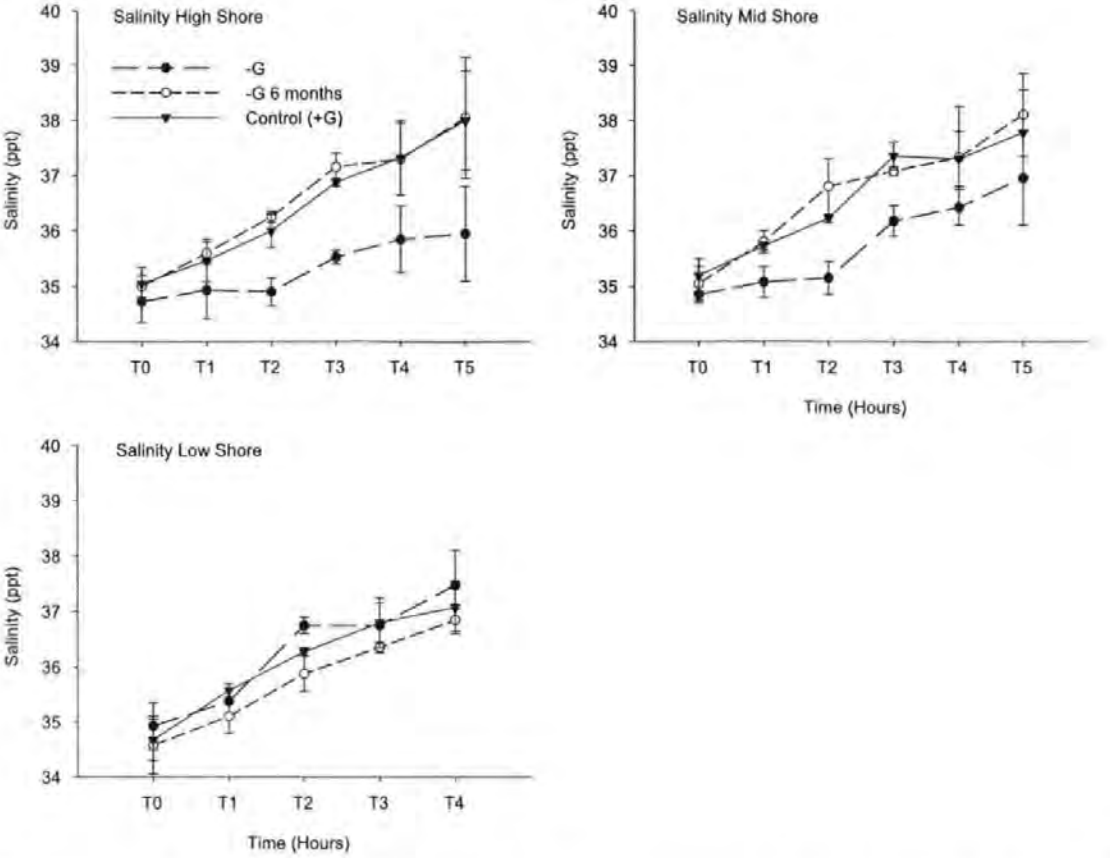

Figure 2.6: SUMMER 2004. Salinity mean value (±SE) measured every hour in rockpools of 3 replicate sampling days over an emersion period in August 2004 at the 3 shore levels (High, Mid, Low) for the 3 treatments (reduced grazer density stated in summer 2002: -G, reduced grazer density started 6 months later in winter 2003: -G 6 months, natural grazer density: +G). Seawater salinity was 35.4 ppt ±0.3 SE

Table 2.6: Summer 2004. Average abiotic values (±SE) of pH, temperature (Degree Celsius) and salinity (ppt) for each shore level (Low, Mid, High) at natural (+G) and reduced grazer density (-G) measured at the end of the low tide period (after 4-5 hours of disconnection from the sea). (n=2). In bold: extreme values.

	pH			Temperature		
Grazer	High	Mid	Low	High	Mid	Low
-G	9.12±0.05	9.0±0.03	**9.44**±0.04	18.81±0.42	**20.07**±0.42	**20.05**±0.48
+G	9.34±0.06	9.45±0.02	9.25±0.06	**21.48**±0.35	**21.60**±0.35	20.78±0.40

	Salinity		
Grazer	High	Mid	Low
-G	35.95±0.85	36.95±0.85	**37.48**±0.63
+G	**38.00**±0.90	37.78±0.76	37.08±0.48

lower in pools at reduced grazer density (-G) at high and mid shore levels than in the two other treatments (+G and -G6). Measurements made at the end of the emersion period showed opposite gradients in salinity mean values as shore height increased according to grazer treatments: a decrease in pools at reduced grazer density (-G) and an increase in pools at natural herbivores density (+G) (table 2.6). Salinity was positively correlated with temperature and surface area but negatively with depth (table 2.8).

In the winter, fewer differences between treatments were observed (table 2.7). All parameters had a linear increase during the low water period (fig. 2.7 and fig.2.8), except for dissolved oxygen (fig. 2.9). Changes in pH values over the low water period were similar to those in summer with a general increase from an average of 8.3 ±0.05 SE to 9.21 ±0.04 SE (fig. 2.7). At the mid shore level, lower pH values were recorded in pools at reduced grazer density (-G) at the end of the

Table 2.7: Winter 2005. 2-way Anova for effects of grazer manipulation and shore height on a) pH, b) temperature, c) salinity mean values for the rockpools sampled at 3 shore levels (Le: High, Mid, Low) for the 3 treatments (Tr: reduced grazer density stated in summer 2002 (-G), reduced grazer density started 6 months later in winter 2003 (-G6), natural grazer density (+G) at time 0 and at time 3 hours at the end of the low tide on 3 consecutive days (n=3).(Cochran's test non significant). ns: non significant; $* * *$: $P<0.001$; $**$: $P<0.01$; $*$: $P<0.05$. SNK: factor levels of the same group are represented with: =, factor levels with significant differences are represented with < or > according to their rank order.

		Time 0			Time 3		
a) pH	DF	MS	*F*	*P*	MS	*F*	*P*
Levels (Le)	2	0.06	0.74	ns	0.19	17.26	* * *
Treatment (Tr)	2	0.01	0.12	ns	0	0.36	ns
Le×Tr	4	0.01	0.12	ns	0.04	4.38	*
Residual	9	0.08			0.01		
SNK (Le×Tr) Time 3:	Tr(Le)		High: -G=-G6<+G Mid: -G<+G Low: -G=-G6=+G		Le(Tr)	-G: High<Low -G6: High=Mid=Low +G: High<Mid>Low	

		Time 0			Time 3		
b) Temperature	DF	MS	*F*	*P*	MS	*F*	*P*
Levels (Le)	2	4.92	25.03	* * *	2.5	4.75	*
Treatment (Tr)	2	0.17	0.87	ns	1.65	3.14	ns
Le×Tr	4	0.2	1	ns	0.32	0.61	ns
Residual	18	0.2			0.53		
SNK (Le)		Time 0: High=Mid<Low			Time 3: High<Mid=Low		

		Time 0			Time 3		
c) Salinity	DF	MS	*F*	*P*	MS	*F*	*P*
Levels (Le)	2	0.04	1.03	ns	0.07	0.43	ns
Treatment (Tr)	2	0	0.02	ns	0.04	0.24	ns
Le×Tr	4	0	0.04	ns	0.07	0.41	ns
Residual	18	0.04			0.17		

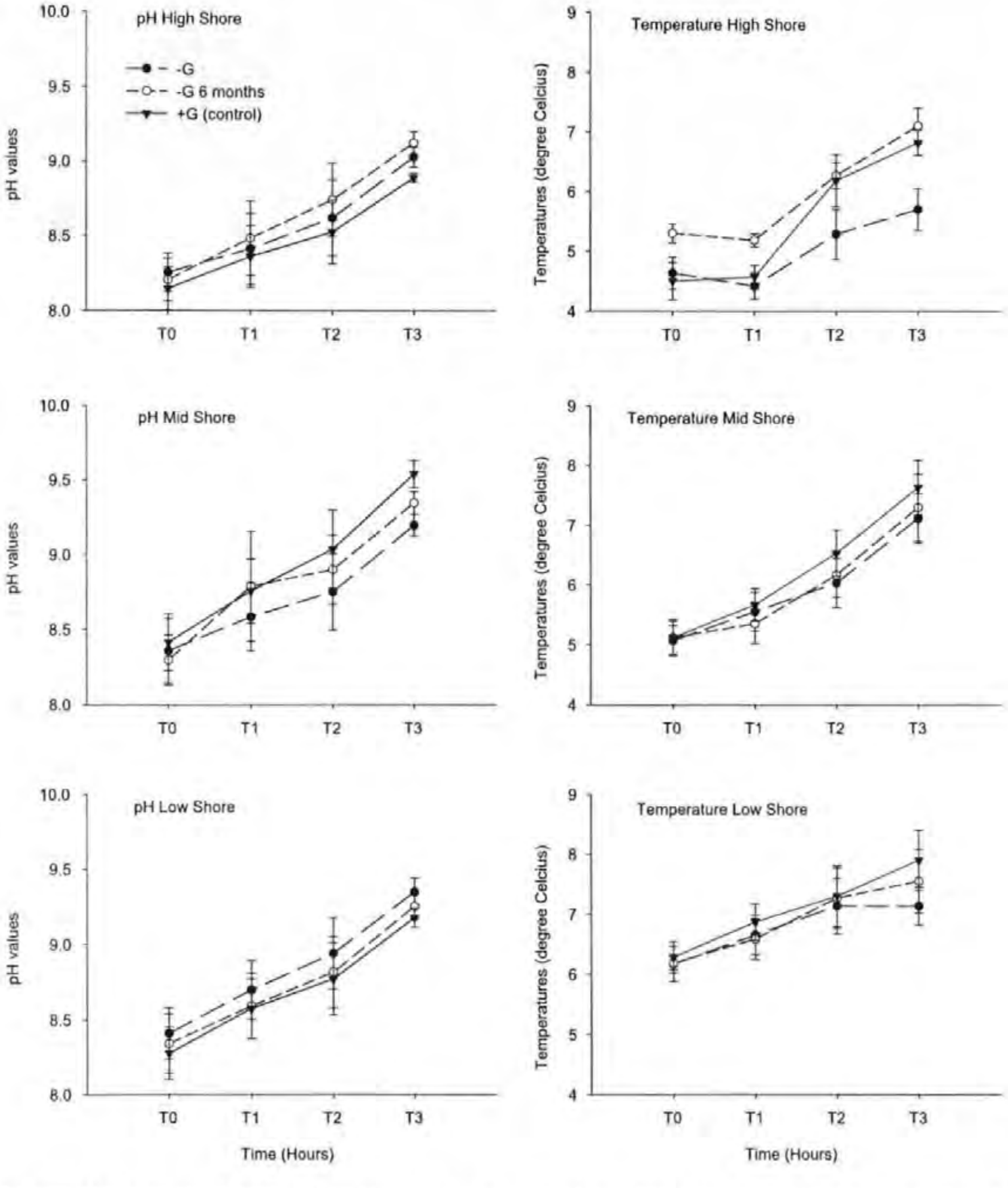

Figure 2.7: WINTER 2005. pH and temperature mean value (±SE) measured every hour in rockpools of 3 replicate sampling days over an emersion period in February 2005 at the 3 shore levels (High, Mid, Low) for the 3 treatments (reduced grazer density stated in summer 2002: -G, reduced grazer density started 6 months later in winter 2003: -G 6 months, natural grazer density: +G). Seawater pH was 8.30 ±SE 0.15 and temperature was 7.3 degree Celsius ±0.3 SE.

emerged period than in the two other treatments (+G and -G6). This was highlighted by the significant interaction of shore levels × treatments and the SNK test (table 2.7). No other treatments appeared to have significant differences (table 2.7). As in summer, no gradient over the shore height of pH was observed (table 2.7, SNK), but the highest pH values were recorded in low shore pools at reduced grazer density (-G) and in mid shore pools left at natural grazer density (+G) (table 2.9). In addition, a positive correlation was detected between pH and dissolved oxygen (table 2.8).

Temperature variations in winter were much lower than in summer and only increased from a mean across all treatments of 5.4°C ±0.1 SE to 7.1°C ±0.2 SE over the low tide period. During the three days of measurements, air temperature at the beginning of the low tide was extremely cold (around 3°C at 9:30 am) and was lower than the sea temperature (6.6°C ±0.3 SE) causing an initial decrease in pool water temperatures in contact with the cold air in the morning, that then increased as the air temperature increased later in the day. Just after rockpool emersion, mean temperatures (averaged across grazer treatments) decreased below sea temperature down to a mean of 4.8°C ±0.1 SE in high shore pools and 5.1°C ±0.1 SE in mid shore pools (fig. 2.7) and were significantly lower than in low shore pools with 6.2°C ±0.1 SE (table 2.7, time 0). At the end of the low water period, high shore rockpool temperatures were higher than in the mid and low shore pools (table 2.7, time 3). A significant gradient of temperature was observed (table 2.7, SNK) with lower temperatures in high shore rockpools for all grazer treatments (table 2.9). In addition, a positive correlation of temperature with the surface area of the rockpools was found (table 2.8).

There was a general small, but constant increase in salinity across grazer treatments and shore levels (much lower that observed in the summer) over the low tide period, from a mean of 34.60 ppt ±0.03 SE to 35.08 ppt ±0.07 SE (fig. 2.8). Experimental removal of grazer and tidal elevation had no effect on changes in salinity during emersion (table 2.7). No gradient of salinity was found over the shore heights (table 2.7, table 2.9). However, a negative correlation was found between salinity and depth of the pools (table 2.8).

In winter, the production of dissolved oxygen per unit area of substratum showed an asymptotic increase from 13.47 mg/l ±0.26 SE to 18.44 mg/l ±0.35 SE during the low water period (fig. 2.9) with an interaction between shore levels and treatments (table 2.10). Owing to

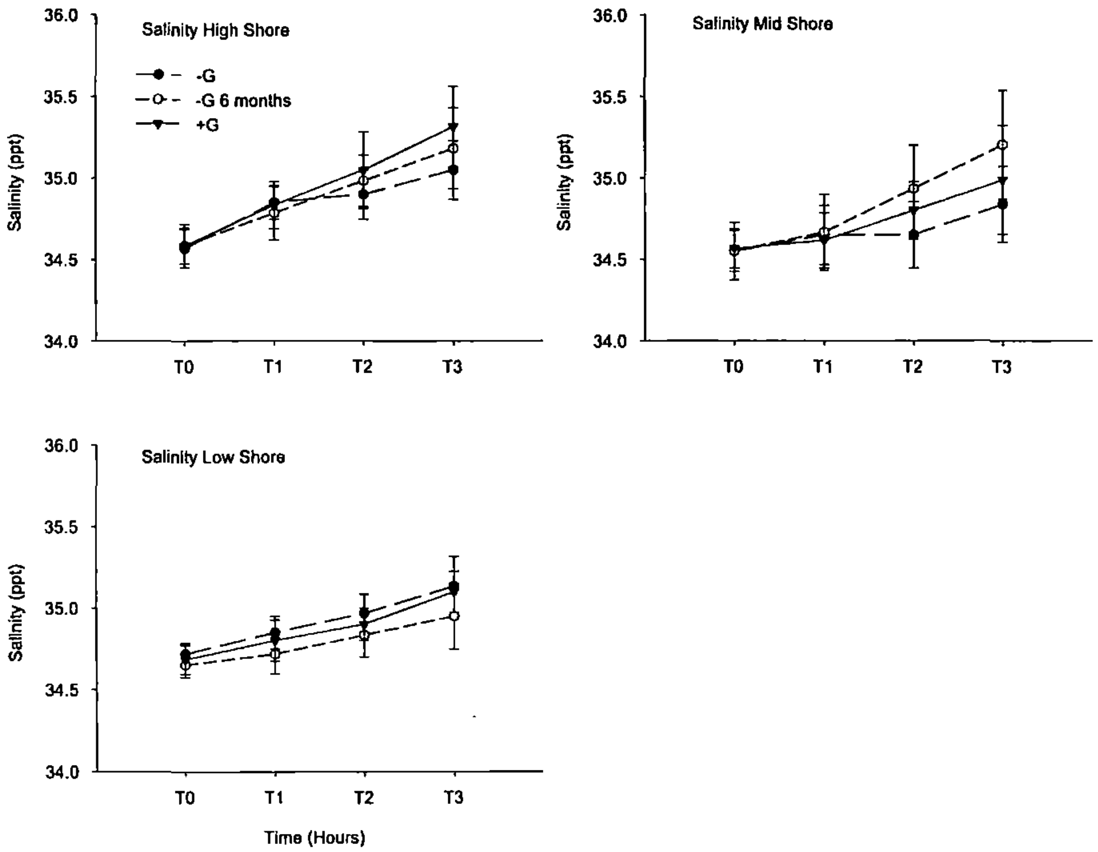

Figure 2.8: WINTER 2005. Salinity mean value (±SE) measured every hour in rockpools of 3 replicate sampling days over an emersion period in February 2005 at the 3 shore levels (High, Mid, Low) for the 3 treatments (reduced grazer density stated in summer 2002: -G, reduced grazer density started 6 months later in winter 2003: -G 6 months, natural grazer density: +G). Seawater salinity was 34.65 ppt ±0.06 SE

Table 2.8: Pearson correlation coefficient for abiotic factors (Surface area (Surface), maximum depth (Depth), pH, Temperature (Temp), Salinity and disolved oxygen (DO)) in Summer 2004 and Winter 2005. In bold: significant correlation coefficient (t-test, p<0.1), (n=18). Corresponding Draftman plots are presented in the appendix B.

	Summer 2004				Winter 2005				
	Surface	Depth	pH	Temp	Surface	Depth	pH	Temp	Salinity
Depth	-0.09				-0.09				
pH	0.28	**-0.45**			0.26	-0.08			
Temp	0.16	**-0.45**	**0.62**		**0.43**	-0.06	0.54		
Salinity	**0.47**	**-0.40**	**0.82**	**0.63**	0.18	**-0.60**	0.05	0.13	
DO					-0.14	**0.47**	**0.43**	0.09	**-0.48**

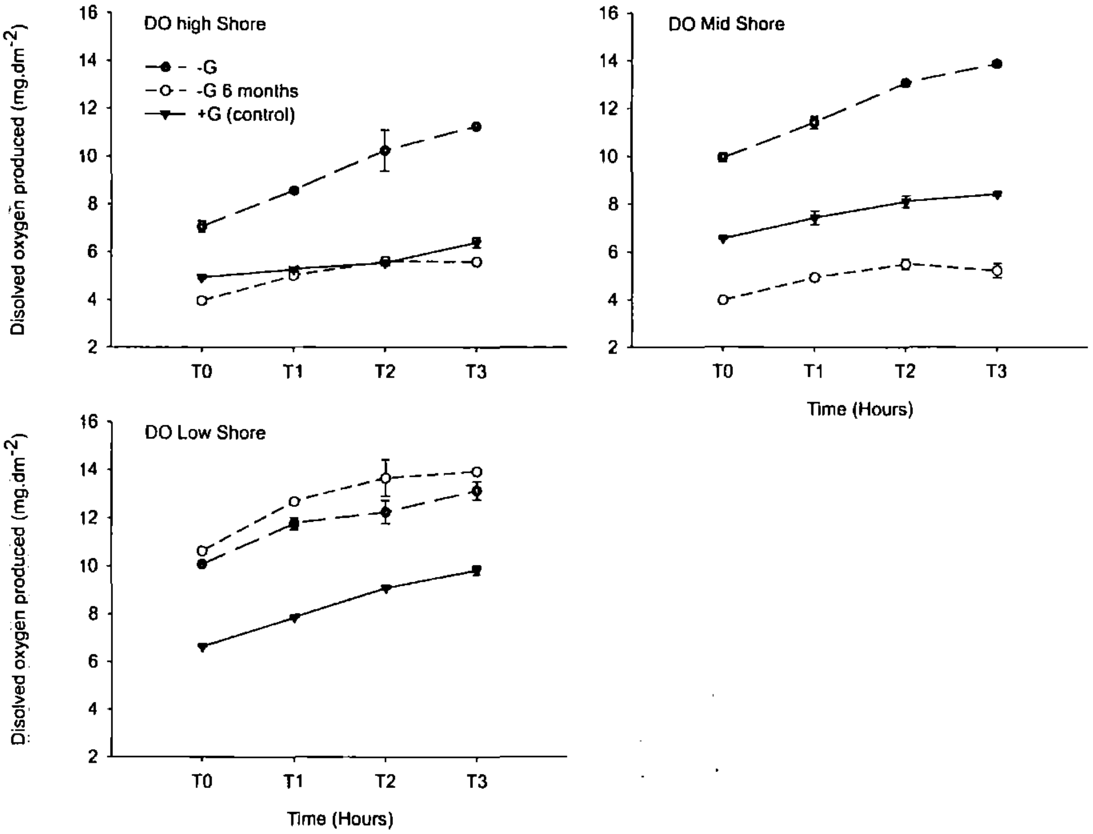

Figure 2.9: WINTER 2005. Production of dissolved oxygen (DO) per surface area. Mean value (±SE) measured every hour in rockpools of 3 replicate sampling days over an emersion period in February 2005 at the 3 shore levels (High, Mid, Low) for the 3 treatments (reduced grazer density stated in summer 2002: -G, reduced grazer density started 6 months later in winter 2003: -G6, natural grazer density: +G). Seawater dissolved oxygen was 12.18 mg.l^{-1} ±0.32 SE.

the difficulty of reaching all pools immediately after emersion, differences between measurements at the beginning of the low tide were recorded (see time 0 in fig. 2.9 and in table 2.10). At all shore levels, oxygen production at the end of the low water period was greater in pools where grazer density was reduced compared to pools at natural grazer density (fig. 2.9, table 2.10). The oxygen values in pools where grazers were removed 6 months after the start of the experiment (-G6) varied among shore levels. There was a general pattern of greater production on the low shore, which declined with shore height. However, the precise ranking of shore levels varied among treatments. A gradient in oxygen production was observed in pools at natural grazer density (+G) which decreased with shore height (table 2.9 and table 2.10, SNK). In addition, dissolved oxygen was positively correlated with pool depth and pH and negatively correlated with salinity (table 2.8).

Table 2.9: Winter 2005. Average abiotic values (±SE) of pH, temperature (Degree Celsius), salinity (ppt) and dissolved oxygen (DO) for each shore level (Low, Mid, High) at natural (+G) and reduced grazer density (-G) measured at the end of the low tide period (after 4-5 hours of disconnection from the sea). (n=2). In bold: extreme values.

Grazer	pH			Temperature		
	High	Mid	Low	High	Mid	Low
-G	9.03±0.07	9.20±0.07	**9.35±0.09**	**5.70±0.35**	7.12±0.41	7.13±0.32
+G	8.89±0.03	**9.54±0.09**	9.18±0.07	**6.82±0.21**	7.63±0.45	7.90±0.50
Grazer	**Salinity**			**DO**		
	High	Mid	Low	High	Mid	Low
-G	35.05±0.18	34.86±0.23	35.13±0.18	20.00±0.00	20.00±0.18	19.38±0.63
+G	35.31±0.25	35.00±0.33	35.10±0.13	**14.63±0.52**	19.83±0.16	19.63±0.38

Table 2.10: Winter 2005. 2-way Anova for effects of grazer manipulation and shore heights on dissolved oxygen (DO) mean values for the rockpools sampled at 3 shore levels (Le: High, Mid, Low) for the 3 treatments (Tr: reduced grazer density stated in summer 2002 (-G), reduced grazer density started 6 months later in winter 2003 (-G6), natural grazer density (+G) at time 0 and at time 3 hours at the end of the low tide on 3 consecutive days (n=3).(Cochran's test non significant). ns: non significant; * * *: $P<0.001$; **: $P<0.01$; *: $P<0.05$. SNK: factor levels of the same group are represented with: =, factor levels with significant differences are represented with < or > according to their rank order.

DO	DF	Time 0			Time 3		
		MS	*F*	*P*	MS	*F*	*P*
Levels (Le)	2	32.83	711.21	***	48.61	1266.89	***
Treatment (Tr)	2	25.42	550.73	***	61.36	1599.10	***
Le×Tr	4	11.48	248.49	***	19.21	500.49	***
Residual	18	0.05			0.04		
SNK (Le×Tr)		Time 0				Time 3	
	Le(Tr)	-G: High<Mid=Low -G6: High=Mid<Low +G: High<Mid=Low			Le(Tr)	-G: High<Mid>Low -G6: High>Mid<Low +G: High<Mid<Low	
	Tr(Le)	High: -G6<+G<-G Mid: -G6<+G<-G Low: +G<-G<-G6			Tr(Le)	High: -G6<+G<-G Mid: -G6<+G<-G Low: +G<-G<-G6	

2.3.2.4 Relating functional groups and physico-chemical variables

The BIOENV procedure showed weak correlations between the physico-chemical variables, such as depth, pH and temperature measured in summer 2004 and pH, temperature and dissolved oxygen measured in winter 2005, to explain the functional group assemblages (table 2.11).

However, Pearson coefficients confirmed that these physico-chemical variables were correlated with some of the functional groups. The correlations were not Bonferroni corrected for multiple tests, since the aim was to explore possible associations. Caution was therefore to be taken in interpreting these results. In summer 2004, foliose algae, leathery macrophytes and animal functional groups were negatively correlated with depth and the corticated macrophytes positively

Table 2.11: BIOENV analysis between abiotic factors (Surface area, maximum depth (Depth), pH, Temperature, Salinity and dissolved oxygen (DO)) and functional group assemblages (Crustose, Articulated calcareous, Filamentous, Foliose, Corticated macrophytes, Leathery macrophytes, Bare rock, Animals) in rockpools in Summer 2004 and Winter 2005. Only the 3 best correlations between biotic assemblages and the best combination of physico-chemical variables are presented (n=18).

Summer 2004		Winter 2005	
Correlation	Variables	Correlation	Variables
0.19	Depth	0.24	pH, Temperature
0.19	Depth, pH	0.23	pH, Temperature, DO
0.18	Depth, Temperature	0.22	pH

correlated with depth (table 2.12). A strong positive correlation was found between the foliose group and pH and the articulated calcareous algae with temperature (table 2.12). In addition, foliose algae were found to correlate positively with salinity and the corticated macrophytes negatively with salinity (table 2.12). In winter 2005, the animals were also strongly negatively correlated with depth (table 2.12), pH was negatively correlated with the crustose algae, positively correlated with the filamentous algae and, in contrast to summer, positively correlated with foliose algae (table 2.12). Temperature was, as in summer, correlated positively with the articulated calcareous algae and, in addition with foliose algae (table 2.12). Temperature was negatively correlated with leathery macrophytes (table 2.12). Salinity was positively correlated with the presence of animals in the pools (table 2.12). Finally, animals were negatively correlated with dissolved oxygen (table 2.12).

Table 2.12: Pearson correlation coefficient for abiotic factors (Surface area (Surf.), maximum depth (Depth), pH, Temperature (Temp), Salinity (Sal.) and dissolved oxygen (DO)) and algal functional group cover (Crustose, Articulated calcareous (Articulated), Filamentous, Foliose, Corticated macrophytes (Corticated), Leathery macrophytes (Leathery), Bare rock, Animals) in Summer 2004 and Winter 2005. In bold: significant correlation coefficient (t-test, p<0.1), (n=18). Corresponding Draftman plots are presented in the appendix B.

	Summer 2004					Winter 2005					
	Surf.	Depth	pH	Temp	Sal.	Surf.	Depth	pH	Temp	Sal.	DO.
Crustose	-0.01	-0.03	-0.16	-0.20	0.05	0.22	-0.12	**-0.51**	-0.35	0.13	-0.36
Articulated	0.12	0.10	0.36	**0.43**	0.30	0.09	0.16	0.40	**0.42**	-0.06	0.24
Filamantous	0.12	0.33	-0.03	-0.09	-0.08	-0.29	-0.02	**0.45**	0.31	-0.14	0.34
Foliose	0.10	**-0.51**	**0.63**	0.36	**0.45**	0.27	0.09	**0.44**	**0.41**	0.10	0.08
Corticated	-0.13	**0.62**	-0.40	-0.18	**-0.42**	-0.40	0.31	-0.15	-0.22	-0.20	-0.05
Leathery	-0.03	**-0.44**	-0.05	-0.20	-0.16	-0.25	-0.29	0.01	**-0.46**	-0.03	0.09
Bare rock	0.11	-0.29	-0.17	-0.22	0.11	-0.05	-0.30	-0.32	-0.32	0.40	-0.04
Animals	0.01	**-0.60**	0.29	0.24	0.12	0.18	**-0.63**	0.07	0.10	**0.45**	**-0.54**

2.4 Discussion

In rockpools of Wembury, the results showed the influence of shore elevation and herbivores on macroalgal assemblages and also on physico-chemical parameters. Some reciprocal relationships between physico-chemical parameters and the macroalgal community were also apparent. Thus, emphasing the fact that biotic and biotic parameters are interrelated and need to be studied holistically. In recent years, ecologists have tended to overlook the important role that the physical environment can play and therefore not consider its influence on the outcomes of species interactions (Bertness and Callaway, 1994). Some previous work has pointed out the relationship between macroalgal distribution and diversity, intertidal height and physico-chemical factors (e.g. Huggett and Griffiths, 1986; Metaxas *et al.*, 1994), but there is still limited understanding in this area. Huggett and Griffiths (1986) related biotic and abiotic parameters, but did not test these associations with formal statistics. Metaxas *et al.* (1994) did not look at chemical factors such as pH, dissolved oxygen and salinity, but only at nutrients and rockpool physical features such as surface, depth and volume.

Although low level rockpools had significantly greater volumes than mid and high shore ones, the results of this study were still valid with respect to oxygen observations, as these were corrected for volume. However, the differences observed between shore levels, particularly the physico-chemical factors, have to be considered with care. A potentially confounding effect in studies of rockpool community structure is that of pool size (Martins *et al.*, 2007). Whilst efforts were made to select rockpools of the same size, geomorphological processes seemed to have shaped larger pools on the low shore: stronger wave action has been reported at low tide levels on some shores by other studies (Dethier, 1984; Underwood and Jernakoff, 1984).

Changes in macroalgae and abiotic patterns were observed in rockpools over the intertidal gradient, as documented in previous studies (Femino and Mathieson, 1980; Huggett and Griffiths, 1986; Wolfe and Harlin, 1988b; Kooistra *et al.*, 1989). The preliminary survey showed that rockpools across shore heights were characterized by different community assemblages. Seaweed populations in high shore level pools were composed mostly of the encrusting alga, *Phymatolithon lenormandii*, whereas the low intertidal pools were occupied by other encrusting algae, *Lithophyllum incrustans* and *Mesophyllum lichenoides* and the turf species, *Corallina elongata*. Indeed, *Phymatolithon lenormandii* can be found from the eulittoral to the sublittoral zone but generally occurs above *Lithophyllum incrustans*. *Mesophyllum lichenoides* and *Corallina elongata* are also known to be infralittoral species (Cabioc'h et al 1992). Likewise, the distinct vertical distribution of functional groups in rockpools was also apparent. The proportion of leathery macrophytes decreased in pools down the shore, whereas articulated calcareous algae and corticated macrophytes increased. Filamentous algae and crustose algae were most abundant at mid shore level. In contrast, Metaxas *et al.* (1994) found a decrease in leathery macrophytes and crustose algae with increasing intertidal height in rockpools in Nova Scotia, but their study was based from the mid shore upwards. The lower pools of Metaxas *et al.* (1994) probably correspond to high-mid shore pools in the present study. On the shore at Wembury, crustose and articulated calcareous algae followed the model of Steneck and Dethier (1994), with increasing productivity potential at lower shore levels since in the present study crustose algae were replaced by larger canopy forming species. My work showed the crustose functional group was composed of different species with opposite distributions: *Phymatolithon lenormandii* characterized the higher pools whereas *Lithophyllum incrustans* the lower ones. This pattern would have gone unnoticed if community assemblage at only the functional group level had been looked at, reinforcing the concerns of Padilla and Allen (2000). The mid level is clearly a transitional zone where species characteristic of the high shore level are partially replaced by lower shore species. Species diversity also increased with decreasing shore height associated with a reduction in environmental stress (see also Femino and Mathieson, 1980; Huggett and Griffiths, 1986; Wolfe and Harlin, 1988b; Kooistra *et al.*, 1989). According to Metaxas *et al.* (1994), less macroalgal species would survive in high shore rockpools due to the harsh environment. Higher species diversity has also been observed in large sized pools compared to the small ones; this pattern was ascribed to differences in recruitment, or physical stress and disturbance that are influencing the pools, depending on their depth and shape (Astles, 1993).

Herbivores played a major role in structuring the algal community, having a significant effect on algal abundance over the intertidal gradient as well as inducing an indirect effect on physico-chemical factors. In the pools with normal grazer density, the crustose and articulated calcareous algae were more abundant than in the pools with reduced grazer density. The abundance of corticated and leathery macrophytes and filamentous algae increased as a consequence of grazer removal. Indeed, they were the groups that were most affected by grazing. Filamentous algae (i.e.

Cladophora spp.) and most corticated macrophytes, such as *Ceramium* spp., are palatable species (Dethier, 1982; Padilla, 1984) and leathery macrophytes are slow growing species with small juveniles suceptible to herbivory (Benedetti-Cecchi and Cinelli, 1992b). Similar observations were made by Steneck and Dethier (1994), with a change in dominant functional groups with grazer removal. In Washington State, rockpools with crustose algae, low algal biomass and low diversity became dominated by macrophytes with an increase in biomass and species diversity. They showed that grazer removal in low level pools led to increasing abundance of leathery macrophytes, as previously highlighted by Paine and Vadas (1969), and in mid level pools, an increase in foliose and corticated macrophytes.

The present study showed that herbivores had an indirect effect on the physico-chemical environment in pools by changing the macroalgal assemblage. There was a progressive increase in oxygen levels in all the pools during low tide. However its effect was higher in pools with reduced grazer density than in rockpools at normal grazer density. This can be explained by both the increase in algal abundance, and therefore an increase in photosynthetic activity, as well as the reduction in the proportion of animals, which reduced the respiratory consumption of oxygen. The presence of animals was also negatively correlated with the level of dissolved oxygen. In addition, higher dissolved oxygen was recorded at Wembury in mid level pools with reduced grazer density, that also had the greatest abundance of highly productive filamentous algae. Production of dissolved oxygen decreased with algal abundance and diversity as the shore height increased in control pools, as shown by Huggett and Griffiths (1986) in South Africa. The asymptotic increase of oxygen showed a reduction of the photosynthetic activity at the end of the emerged period, also recorded by Morris and Taylor (1983) and Griffin (pers. com.); this could be due to limiting factors such as a decrease in light intensity at the end of the day.

The relationship between biotic and abiotic factors was also illustrated by related seasonal changes. The percentage of leathery macrophytes, such as *Sargassum muticum*, corticated macrophytes, such as *Ceramium* spp., and filamentous and foliose algae all decreased in winter leaving crustose and articulated calcareous algae dominating rockpools. Reduction in algal abundance can be explained by a decrease in water temperature and in incident light (Wolfe and Harlin, 1988a; Dethier, 1982; Sze, 1982), but counteracted by a reduction in grazing activity (Dethier, 1982). In the present study, low winter temperatures had a negative effect on the canopy-forming leathery macrophyte abundances which obscured the primary algal layer, such as articulated calcareous algae, under estimated during summer sampling. This was confirmed by an indirect positive effect of winter temperatures on articulated calcareous species. In addition to low winter temperatures, storm loss could also accentuate the reduction of canopy cover. Lower consumer pressure (littorinids) in winter was reported as a major factor in structuring the algal community, with an increase in *Ulva* spp. (Dethier, 1982; Wolfe and Harlin, 1988b). However, this pattern was not confirmed at Wembury as no increase of palatable species or photosynthetic activity was recorded in winter either in pools at natural or reduced grazer density. In summer, the results of the present investigation showed that rockpool depth influenced assemblages structure, as shown in recent work (Martins *et al.*, 2007), with a negative effect on foliose algae, leathery macrophyte and animal abundances, but little temperature effect on the biota was recorded .

Differences in the increase of pH, temperature and salinity, over the low water period, were also recorded in the present study between summer and winter and grazer treatments. An alkaline pH reflected high rates of photosynthesis which slowed down in summer at the end of the day, limited by a reduction in solar irradiance. Higher pH was expected in pools at reduced grazer density, induced by greater algal biomass photosynthesis and corresponding to the higher oxygen production observed in these pools. The range of pH was lower in reduced grazer pools at high shore in both summer and winter. This correspond with what was found in previous studies (Morris and Taylor, 1983; Huggett and Griffiths, 1986). In the present investigation, temperature was affected by environmental and biotic factors. Air temperature and light intensity influenced rockpool temperatures in relation to pool depth and surface area in contact with the air, as shown in previous studies (Ambler and Chapman, 1950; Femino and Mathieson, 1980; Martins *et al.*, 2007), with major increases in temperature in summer and reductions to below sea water temperature in winter, due to colder air temperatures. In addition, greater algal biomass in pools at reduced herbivore density caused a lower increase in temperature, as suggested by Ambler and Chapman (1950) who found that canopy cover reduced the light irradiance and water mixing. Although, the increase in salinity over the low water period did not differ significantly between treatments, a lower range appeared in pools with reduced consumer pressure, and particularly in winter. Greater algal biomass, in particular canopy species, and cooler air temperatures in winter reduced the increase in rockpool temperatures, therefore reducing the evaporation rate. Salinity was also affected by the depth and surface area of the pools. There were no seasonal effects of grazer removal induced 6 months after the start of the experiment on algal recruitment, in contrast to Benedetti-Cecchi (2000b) who found differences in algal colonisation.

No abiotic gradients over the shore heights were found. However, the most extreme temperature values were recorded in the highest rockpools, with temperatures higher than seawater in summer and lower in winter, as found by Fernandez (1999). In winter, a pH gradient was only found in rockpools with reduced grazer densities with the lowest levels in high shore pools.

In summary, this study highlighted a reciprocal relationship between biotic and abiotic parameters and an indirect effect of herbivores and seasonality on the physico-chemical rockpool environment. Physical environmental parameters were found to affect physico-chemical rockpool processes, with air temperature, surface area and depth affecting pool temperature and therefore salinity value. Physico-chemical factors influenced biological processes, with low temperature or depth negatively affecting algal assemblage abundances, and light intensity affecting photosynthesis, and therefore oxygen production. In addition, higher algal cover, induced by the removal of herbivores, affected the rockpool physico-chemical parameters such as increasing oxygen production, or buffering temperature increase and therefore salinity. Finally, the highest rockpool communities on the shore experienced the most extreme physico-chemical values and therefore the harshest environmental and physiological stress.

Chapter 3

Grazing intensity and foraging behaviour of gastropods in and around rockpools

3.1 Introduction

Herbivores have an important role in structuring the macroalgal community of rocky shores (Lubchenco and Menge, 1978; Lubchenco and Gaines, 1981; Hawkins, 1981; Hawkins and Hartnoll, 1983b; Underwood and Jernakoff, 1984; Sousa, 1985; Farrell, 1991; Sousa and Connell, 1992; Benedetti-Cecchi, 2000a). The most common herbivores on the North-east Atlantic rocky shores are the limpets *Patella vulgata*, *Patella ulyssiponensis* and *Patella depressa*, the trochids *Gibbula umbilicalis*, *Osilinus lineatus* and the littorinids *Littorina littorea*, *Littorina obtusata* and *Littorina saxatilis* (Lewis, 1964; Hawkins and Hartnoll, 1983b). Their feeding pattern, behaviour and the consequences of such behaviour for community structure have been the subject of numerous studies (see Hawkins and Hartnoll, 1983b; Norton *et al.*, 1990, for reviews). The predominant influence of patellid limpets in structuring the rocky shore community in North West Europe has been widely demonstrated (Jones, 1948; Southward, 1964; Hawkins, 1981; Hawkins *et al.*, 1992; Jenkins *et al.*, 2005; Coleman *et al.*, 2006; Hawkins and Hartnoll, 1983b, for reviews). By scraping microbiofilm from the rock surface using strong radula strokes that often penetrate the substrate, limpets ingest diatoms, filamentous algae, cyanobacteria, macroalgal germlings and even macroalgae and barnacle shell (Underwood, 1979; Hawkins and Hartnoll, 1983b; Hawkins *et al.*, 1989a; Hill and Hawkins, 1991). With continuous radula movements (Santini and Chelazzi, 1996), limpets are completing a loop centered on a home scar. This loop is composed of overlapping outward and homeward journeys with a maximum foraging phase in the middle of the loop (Hartnoll and Wright, 1977; Little *et al.*, 1988; Cook *et al.*, 1969; Williams and Morritt, 1991; Santina *et al.*, 1995; Chelazzi *et al.*, 1994). The timing of foraging in relation to tidal and dial cycles varies among localities (see Branch, 1981; Hawkins and Hartnoll, 1983b; Little, 1989; Santina *et al.*, 1995; Chelazzi *et al.*, 1994; Santini and Chelazzi, 1996, for reviews). Evidence suggests foraging is timed in order to limit the risk of mortality owing to predation (starfish, crabs, birds) (Little *et al.*, 1990; Ewans and Williams, 1991; Coleman *et al.*, 1999), wave action, physiological stress such as heat and desiccation, and competition for home scars (Hartnoll and Wright, 1977; Branch, 1981; Little, 1989; Ewans and Williams, 1991; Hawkins and Hartnoll, 1982; Williams *et al.*, 1999).

The majority of studies on limpet activity have been on emergent rock and the rockpool environment has been relatively overlooked. The grazing intensity and movement of herbivores in rockpools and in relation to the emergent rock have received little attention. Dethier (1982), Lubchenco (1982) and Chapman (1990b) speculated that grazing pressure was higher in rockpools than on emergent rock due to the ability of grazers to forage constantly in pools (Dethier, 1982; Lubchenco, 1982) and/or a higher observed herbivore density (Lubchenco, 1982). Investigations of limpet distribution on rocky shores in Ireland and Scotland confirmed that adult *Patella ulyssiponensis* were confined to rockpools or damp areas (Davies, 1969; Delany *et al.*, 1998). In addition, *Patella ulyssiponensis* was also found predominantly in pools colonized by *Lithothamnion* spp. (Lewis, 1964; Fretter and Graham, 1976). Delany *et al.* (1998) also suggested that adult *Patella vulgata* migrated out of the tidepools after a nursery period, even though they could tolerate rockpool conditions.

Herbivores usually graze when immersed (Underwood, 1979; Hawkins and Hartnoll, 1983b) and therefore estimation of grazing intensity can be difficult. Various methods have been used to assess feeding behaviour: estimates of grazer density, direct observation, photography, telemetry, use of microphones and quantification of grazing marks on wax discs (see Hartnoll, 1986; Chelazzi *et al.*, 1994; Thompson *et al.*, 1997, for reviews). One of the most common methods is a direct estimate of grazer density which may not reflect actual grazing intensity. For example, Forrest *et al.* (2001) found a correlation between the density and grazing intensity for the limpet *Cellana tramoserica* but not for the neritid *Nerita atramentosa.* Local estimates of grazer density do not take into account the behaviour of herbivores that may feed far from their low tide location (Leving and Garrity, 1983; Hutchinson and Williams, 2003; Chelazzi *et al.*, 1983, for review). Another method of assessing grazing intensity relies on quantifying the radula scrapes left in the structure of wax discs placed into the substratum (Thompson *et al.*, 1997; Forrest *et al.*, 2001). Assessing grazing intensity with wax discs is an efficient and inexpensive method, which has been used successfully to demonstrate spatial and temporal patterns in the grazing activity of patellid limpets (Thompson *et al.*, 1997; Forrest *et al.*, 2001; Hutchinson and Williams, 2003). It is based on the assumption that when grazers move they are foraging (Vadas, 1985; Branch, 1971) and that encounters between grazers and the wax discs do not affect their behaviour (Thompson *et al.*, 1997; Jenkins and Hartnoll, 2001).

The overall aim of this study was to develop an understanding of the grazing intensity in the rockpool habitat and to establish a comparison with the emergent rock largely using the indirect wax disc method of Thompson *et al.* (1997) and some direct observations. The specific objectives were: (1) to test if grazing intensity was greater in rockpools than on emergent rock, and if it was related to herbivore density. If it was not related to grazer abundance, as suggested by preliminary observations, the aim was to investigate the possible causes of a greater consumer pressure in rockpools by: (2) establishing if specific differences in grazing intensity existed between *Patella ulyssiponensis*, which was constantly immersed in rockpools, and *Patella vulgata* which was commonly found on emergent rock; (3) establishing whether herbivore movements occurred from emergent rock into rockpools and quantify them; (4) if some movements were recorded, to test if limpets fed preferentially in rockpools rather than on emergent rock.

3.2 Material and methods

Most of the field experiments were conducted at Wembury Bay (Southwest England). The shore at Wembury is moderately exposed with flat and smooth sloping bedrock, interrupted with small sandy beaches. A further grazing behaviour experiment was set up at Downderry (N50:21:44 W4:22:00) and Wembury in order to study spatial variation in grazing. The shore at Downderry is situated 32 km west of Wembury with similar bedrock but with slightly greater exposure to wave action. The most common herbivore species encountered on these shores were the limpets *Patella vulgata*, *Patella ulyssiponensis* (previously *P. aspera*) and *Patella depressa*, the trochids *Gibbula umbilicalis* and *Osilinus lineatus*, and the littorinids *Littorina littorea* and *Littorina saxatilis*.

3.2.1 Grazing patterns in rockpools and on emergent rock

In order to establish whether there were differences in grazing intensity between pools and emergent substrata, and if grazing intensity was related to herbivore density, six rockpools and six emergent rock plots of similar size and community composition were randomly selected at each of three shore levels: high (3-4m above LAT), mid (1-3m above LAT) and low (0.5-1m above LAT). An array of nine wax discs in an area of 40×40cm were deployed on open rock, avoiding areas of erect algae, in each pool and on each emergent rock plots possessing similar barnacle cover. Wax discs were deployed for a period of 15 days every three months from May 2002 to March 2003 (see Thompson *et al.*, 1997; Forrest *et al.*, 2001, for method). At the time of each deployment, grazer density was counted in three replicate 20×20cm quadrats in each pool and on each emergent rock plot. Following deployment, all discs were returned to the laboratory and examined under a dissecting microscope. The percentage area scraped by radulae was estimated with the help of a circular acetate grid with twenty-five evenly spaced holes. All radula marks encountered under these 25 holes were recorded and percentage cover of grazing marks estimated. To allow easier distinction of the marks, a fine layer of printer toner powder was applied to the discs with a paint brush.

Grazing effort per experimental unit was estimated by calculating the mean percentage cover of grazing marks on wax discs deployed over the area studied (rockpools and emergent rock). Analysis of variance (ANOVA) (Underwood, 1997) was used to determine differences among experimental treatments. Grazing intensity and herbivore density were compared using a two-way ANOVA with two fixed and orthogonal factors: habitat (rockpool and emergent rock) and shore level (High, Mid and Low shore). In addition, Pearson's correlation coefficient was calculated to test if there was a relationship between grazer density and grazing intensity when looking at the overall grazing pressure in rockpools and emergent rock. Cochran's test was used prior to ANOVA to check the homosedastity of data and if necessary data were transformed (Winer, 1971). When required, *a post-hoc* multiple comparisons of the means were undertaken using Student-Newman-Keuls's test (SNK) (Underwood, 1997). These analyses were carried out using WinGmav5 (Underwood and Chapman 1997).

3.2.2 Causes of greater grazing intensity in rockpools

3.2.2.1 Influence of species specific environment on grazing intensity

To determine if greater grazing intensity in rockpools could be accounted for solely by greater grazing intensity of those grazers naturally found in rockpools (*Patella ulyssiponensis*) compared to those on emergent rock (*Patella vulgata*), an experiment was carried out on two dates in both winter 2004 and summer 2005. Five similar sized limpets of each species were enclosed, using fences, in their respective environments (pools and open rocks). The fences were circular (perimeter: 2m) made of folded chicken wire (diameter 13mm) fixed on the rock with screws and washers. Ten wax discs were deployed in each fenced area for 15 days in 6 replicate rockpools, for *Patella ulyssiponensis*, and 6 replicate areas of emergent rock for *Patella vulgata*. Limpet grazing marks were counted in the laboratory to estimate grazing intensity.

Species specific grazing intensity was compared using a one-way ANOVA with a fixed factor, species (*Patella ulyssiponensis*, *Patella vulgata*), for each trial date.

3.2.2.2 Grazer movements and spatial foraging distribution

Direct observation by snorkelling: Observations were made to test if there was any movement of limpets between the emergent surrounding rock and rockpools when the pools were submerged at high tide that could cause greater consumer pressure in rockpools than on emergent rock. Positions of the limpet *Patella vulgata*, relative to the edges of the pool, were recorded. At the beginning of September 2003, six rockpools at high shore level (3-4m above LAT) were selected and examined by snorkelling during high neap tides. At this level, rockpool communities were dominated by encrusting algae *Phymatolithon* spp. with small patches of *Corallina* spp. and *Chondrus crispus*, while barnacles dominated the open rock. Herbivores were mostly *Patella ulyssiponensis*, *P. vulgata*, *P. depressa*, *Gibbula* spp., *Osilinus lineatus* and *Littorina* spp. At the beginning of the experiment, the density of grazers was recorded in three replicate quadrats of 20x20cm in each rockpool and on surrounding emergent rock to ensure herbivore homogeneity across the replicate pools. A total of 89 *P. vulgata* situated at the edges of the rockpools on the emergent rock were tagged with coloured letters and numbers (Helagrip PVC cable markers, HellermannTyton) pasted on their shells with Subcoat S epoxy (Veneziani). Coding allowed the limpets to be identified and recording of their home scar positions using their distance from the border of the pools. The border of the pools was defined as the limit of the encrusting *Phymatolithon* spp. Positions of limpets at high tide and the following low tide were studied on four dates. Two distance categories were defined in relation to the limpet's original home scar position: limpets situated between 0 and 3.5 cm (Close) from the border of the pools (54 limpets tagged for this category) and limpets between 3.6 and 25 cm (Far) (35 limpets tagged for this category). For each tidal observation, the positions of the limpets were recorded by measuring the minimum distance from the center of their shell to the *Phymatolithon* spp. limit. Positive values were attributed to limpets that remained on emergent rock and negative values for the ones that entered the rockpool. Limpets were classified in three activity states: not moving (Inactive), active on emergent rock (Active) and active entering the pool (Entering). The percentages of each activity state per rockpool were calculated for each tidal observation.

Data on the percentage of limpets entering pools, recorded by snorkelling, were analysed using a two-way ANOVA with two fixed and orthogonal factors: tide (High tide and Low tide), and distance from the pool border (Close and Far).

Indirect wax disc approach: In order to test if observed movement of limpets from the emergent surrounding substrate to the rockpools was sufficient to increase the grazing intensity in those rockpools, and to quantify it, six rockpools of similar size and community composition were randomly selected at three shore levels: high (3-4m above LAT), mid (1-3m above LAT) and low (0.5-1m above LAT). At each of the three shore levels, three of these pools were fenced to block any movement of limpets between the emergent rock and the pools, and three others were left open. Field observations had shown that fencing had little or no effect on movements of non-patellid herbivores (trochids and littorinids). Therefore, it was anticipated that fenced and non-fenced treatments would have similar abundances of non-patellid herbivores. No attempt was made to control for fence effects on herbivores as the aim was to block their activities. Twenty wax discs were deployed in each pool at the beginning of November 2003 and left for fifteen days. Grazer density was recorded in each pool in three replicate quadrats of 20x20 cm. All discs were returned to the laboratory and the grazing marks of limpets and topshells were counted separately.

Grazing intensity and herbivore density recorded when grazer movements were observed, were analysed using a two-way ANOVA with two fixed and orthogonal factors: shore level (High, Mid, Low shore), and fence (Open and Fenced pool).

Microhabitat preferences: In order to confirm that limpets entering pools do so to graze, *P. vulgata* of similar biomass situated at natural densities on the edges of six rockpools were fenced. The fences covered an area which was half in the rockpool and half on the emergent rock. In each habitat (rockpool or emergent rock) and in each fenced area, an array of nine wax discs was deployed during 15 days for three replicate dates in June and July 2005 on two shores, Wembury and Downderry. The percentage of grazing was estimated by counting the grazing marks on the wax discs in the laboratory.

Microhabitat feeding preference was compared using a one-way ANOVA with one fixed factor: habitat (Rockpool and Emergent rock).

3.3 Results

3.3.1 Grazing patterns in rockpools and on emergent rock

The density of grazers (*Patella vulgata*, *Patella ulyssiponensis*, *Patella depressa*, *Gibbula umbilicalis*, *Osilinus lineatus*, *Littorina littorea* and *Littorina saxatilis*) differed significantly between pools and emergent substrata. In all seasons except summer, there was a general greater density of grazers outside the pools (table 3.1). This difference, however, was not consistent across all shore heights, indicated by the significant Habitat × Level interaction at all four sampling dates. Examination of figure 3.1 shows a similar pattern of grazer distribution for the autumn and winter sampling dates with similar grazer density in the two habitats at the low shore level and a lower density in high and mid shore rockpools. This pattern was reversed, however, in the spring with a clear difference between the two habitats on the low and mid shore, but similar density on the high shore.

In contrast to grazer density, grazing intensity was higher inside rockpools than on emergent rock (fig. 3.2). Grazing intensity differed significantly between rockpools and emergent rock during all four seasons with higher grazing pressure inside rockpools (table 3.2). Grazing pressure was twice as high in rockpools with an annual average of 83% ±3 SE compared to emergent rock with 42% ±4 SE. This pattern was consistent across all three tidal heights indicated by the lack of any interaction between the shore height and habitats. Seasonal differences were observed with consumer pressure being higher in summer and lower in winter (fig. 3.2). No relationship was detected between grazer density and grazing intensity in rockpools or on emergent rock at each shore level in any season (correlation, rockpools: r=0.22, p>0.05; emergent rock: r=-0.06, p>0.05).

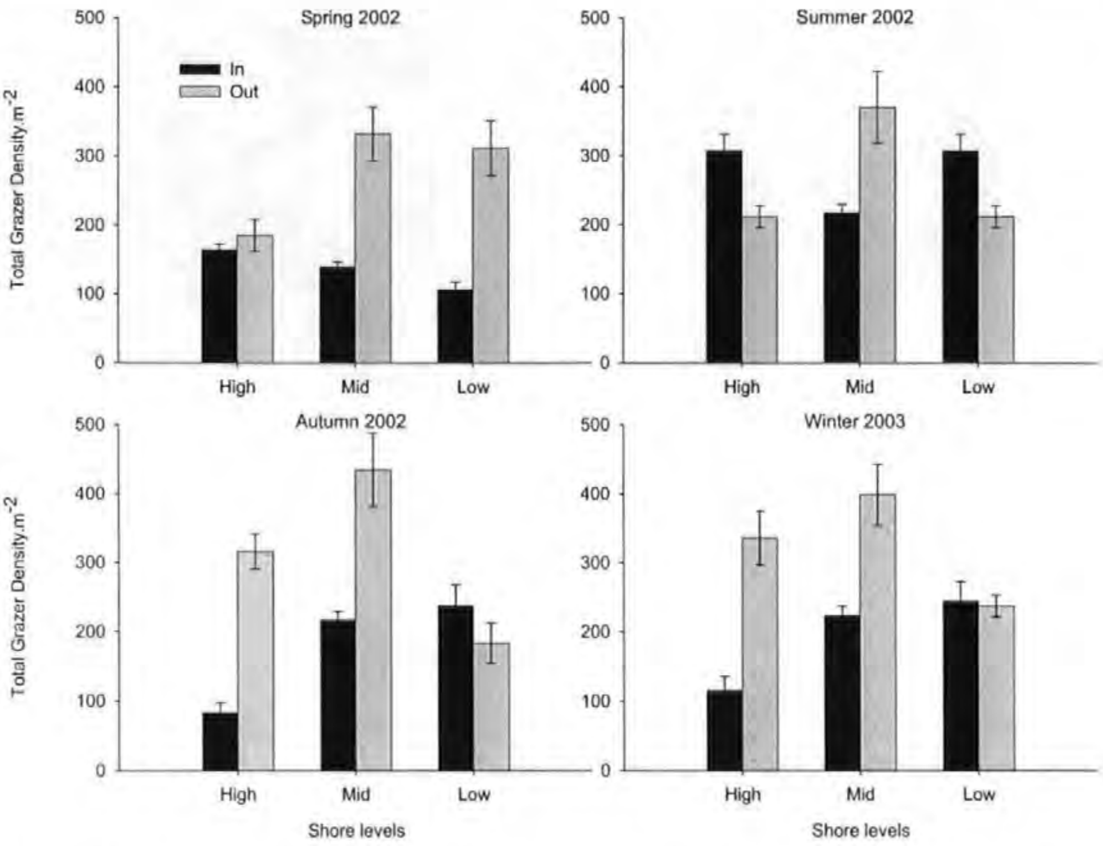

Figure 3.1: Total grazer density in rockpools (In) and on emergent substrate (Out) at the four seasons (Spring, Summer, Autumn, Winter) and the three shore levels (High, Mid, Low). Data are mean of grazer count (±SE) in three replicate 20×20cm quadrats averaged per plot (n=6).

Table 3.1: 2-way Anova of total grazer density counted in two habitats (Ha: inside pool (In) and emergent rock(Out)) at the three shore levels (Le: High, Mid, Low) in each of the 4 seasons. (n=6). Data were (ln+1) transformed. (Cochran's test non significant for all seasons except for autumn). ns: non significant; * * *: $P<0.001$; **: $P<0.01$; *: $P<0.05$. SNK: "=": factor levels of the same group, "<" or ">": factor levels with significant differences according to their rank order.

		Spring			Summer			Autumn			Winter		
	DF	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Habitat (Ha)	1	3.95	63.13	* * *	0.06	1.44	ns	3.45	23.52	* * *	2.77	31.92	* * *
Level (Le)	2	0.16	2.56	ns	0.03	0.71	ns	1.44	9.84	* * *	0.62	7.14	*
Ha×Le	2	0.78	12.53	* * *	0.74	16.27	* * *	2.23	15.21	* * *	0.93	10.81	**
RES	30	0.06			0.04			0.15			0.09		
SNK (Ha×Le)		High:	In=Out		High:	In>Out		High:	In<Out		High:	In<Out	
		Mid:	In<Out		Mid:	In<Out		Mid:	In<Out		Mid:	In<Out	
		Low:	In<Out		Low:	In>Out		Low:	In=Out		Low:	In=Out	

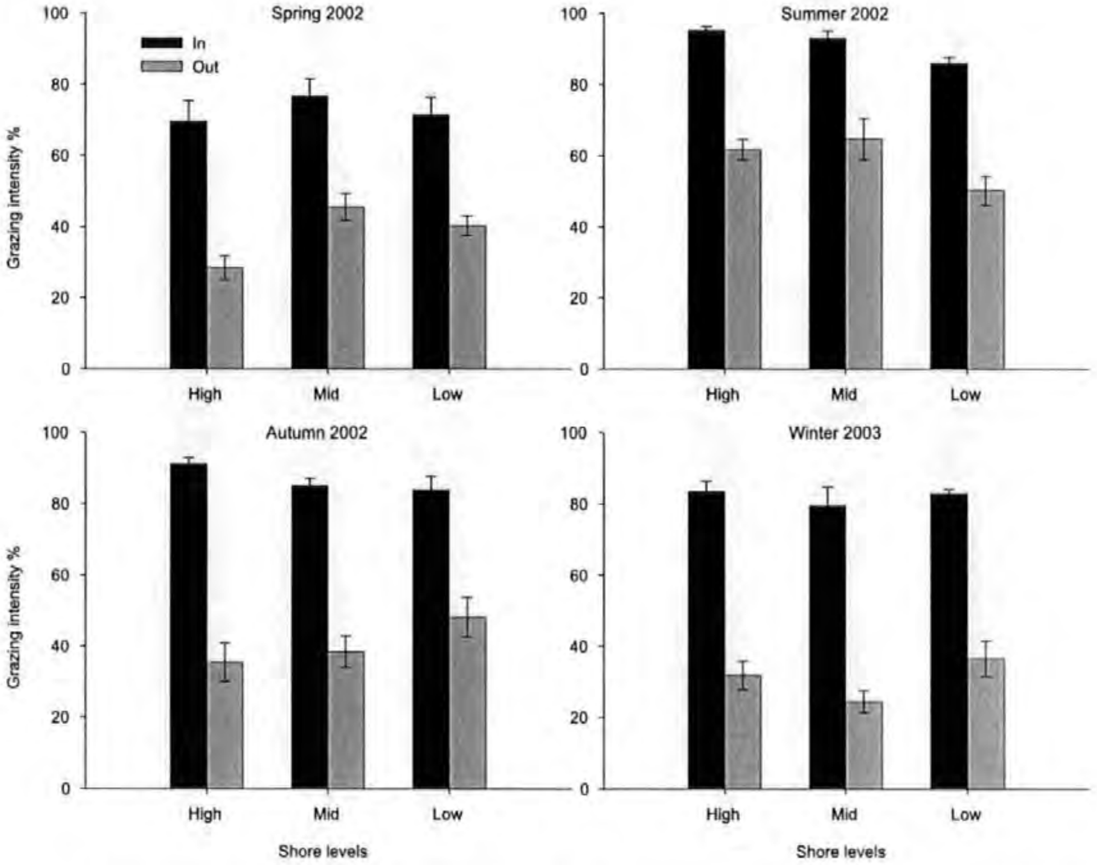

Figure 3.2: Grazing intensity percentage in rockpools (In) and on emergent substrate (Out) at the three shore levels (High, Mid, Low) in each of four seasons. Data are mean percentage of surface scraped (±SE) of nine replicate discs averaged per plot (n=6).

Table 3.2: 2-way Anova for percentage of grazing intensity found in two habitats (Ha: inside pools and emergent rock) (n=6) at the three shore levels (Le: High, Mid, Low) at each of the 4 seasons. Data were ARCSIN transformed. (Cochran's test non significant for all season). ns: non significant; ∗∗∗: $P<0.001$; ∗∗: $P<0.01$; ∗: $P<0.05$. SNK: "=": factor levels of the same group, "<": factor levels with significant differences according to their rank order.

		Spring			Summer			Autumn			Winter		
	DF	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Habitat (Ha)	1	3994.3	84.0	∗∗∗	4979.9	152.5	∗∗∗	8012.4	178.4	∗∗∗	9073.4	243.5	∗∗∗
Level (Le)	2	172.6	3.6	∗	264.1	8.1	∗∗	23.5	0.5	ns	73.7	2.0	ns
Ha×Le	2	35.8	0.8	ns	14.7	0.5	ns	143.3	3.2	ns	25.3	0.7	ns
Residual	30	47.6			32.6			45.0			37.3		
SNK (Level)		High<Mid			Low<Mid=High								

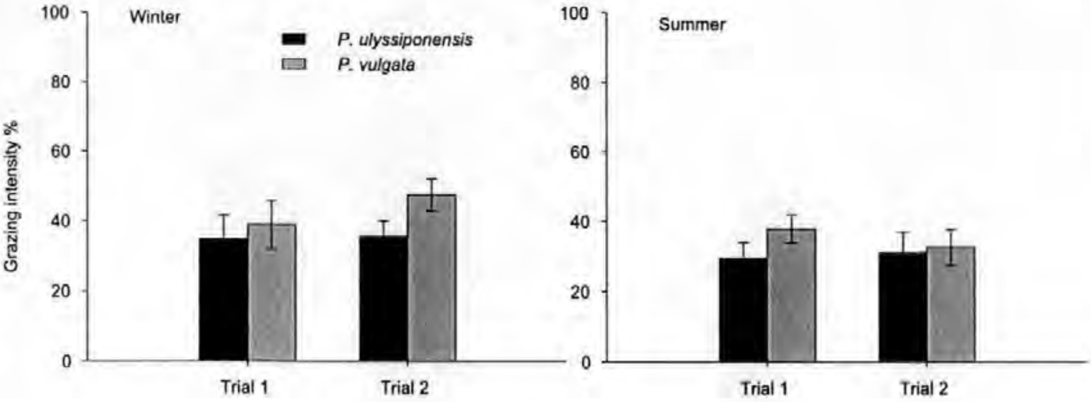

Figure 3.3: Grazing intensity percentage of *Patella vulgata* on emergent rock and *Patella ulyssiponensis* in rockpool for 2 replicate trial dates in Winter and Summer at high level shore. Data are mean of percentage of scraped area (± SE) of 10 wax discs for each plot (n=6).

3.3.2 Causes of greater grazing intensity in rockpools

3.3.2.1 Influence of species specific environment on grazing intensity

Constant immersion of *Patella ulyssiponensis* did not increase its grazing rate compared to *P. vulgata* under intertidal conditions in winter and summer and for all trial dates (table 3.3). Grazing pressure of *P. vulgata* was actually slightly higher than *P. ulyssiponensis* although not significantly different (fig. 3.3).

Table 3.3: Anova for percentage of grazing activity of the 2 species (Sp) *Patella vulgata* on emergent rock and *Patella ulyssiponensis* in rockpools for 2 replicate trials (Tr) in Winter and Summer (Seasons: Se) at high shore level. Wax discs were deployed in enclosures of 5 limpets in 6 replicate pools and emergent rock (n=6). (Cochran's test non significant for all dates). ns: non significant.

	DF	MS	*F*	*P*
Species (Sp)	1	505.05	2.92	ns
Seasons (Se)	1	502.75	2.91	ns
Trials (Tr)	1	23.60	0.14	ns
Sp×Se	1	26.55	0.15	ns
Sp×Tr	1	0.42	0.01	ns
Se×Tr	1	123.06	0.71	ns
Sp×Se×Tr	1	160.24	0.93	ns
Residual	40	172.77		

3.3.2.2 Grazer movements and spatial foraging distribution

Direct observation by snorkelling: For those limpets that did not enter pools, the percentage of *Patella vulgata* away from their home scar (active) was similar at high tide, with 32% ±4 SE, and low tide, with 30% ±4 SE (fig. 3.4). For those limpets that entered pools, significant differences were found between high and low tide, with none of the *Patella vulgata* entering pools at low tide. However, at high tide, an average of 10% ±2 SE entered the pools (table 3.4). The distance between limpets home scar and the border of the pool (Close or Far) only mattered for the last sampling date with a greater percentage of limpets closest to the pool entering at high tide. This was highlighted by the significant interaction between the factors: tidal state and distance (table 3.4).

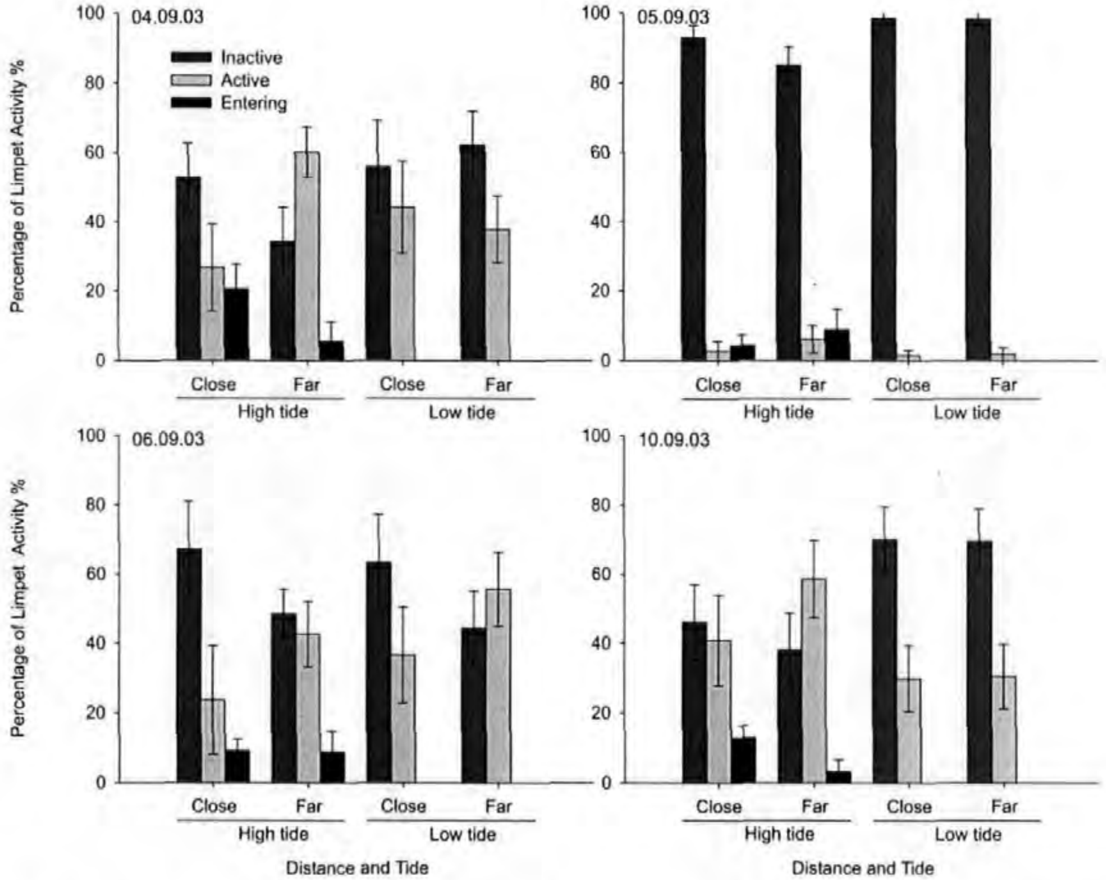

Figure 3.4: *Patella vulgata* activity at rockpool edges and inside high shore pools during consecutive high and low tide on 4 dates. Limpets were classified in three categories: not moving (Inactive), active on emergent rock (Active), active and entering in the rockpool (Entering). Data are mean of percentage (± SE) of limpet estimated activity (n=6). Close: limpet home scar position from the edge of the pool between 0-3.5cm; Far: limpet home scar position from the edge of the pool between 3.6-25cm.

Table 3.4: Anova for percentage of *Patella vulgata* recorded entering the rockpool at the two tidal conditions (Tide: Ti) when the pool was submersed during high tide (High) or when the pool was uncovered by the sea during low tide (Low) considering their home scare distance (Di) from the edge of the pool (Di: Close or Far) at 4 dates (Da). Data were ARCSIN transformed. (Cochran's test was significant after transformation). ns: non significant; ∗: $P<0.05$.

	DF	MS	*F*	*P*
Tide (Ti)	1	3939.84	18.34	*
Distance (Di)	1	677.34	3.35	ns
Date (Da)	3	241.84	1.70	ns
Ti×Di	1	677.34	3.35	ns
Ti×Da	3	214.84	1.70	ns
Di×Da	3	202.34	*1.60*	*ns*
Ti×Di×Da	3	202.34	1.60	ns
Residual	80	126.09		

Indirect wax disc approach: Limpet grazing intensity was significantly higher in unfenced rockpools compared to fenced ones (fig. 3.5 and table 3.5, see grazing, limpet). However, no differences in limpet density were measured between fenced treatments (Fenced, Open) during low water periods (table 3.5, see density, limpet). This result was in agreement with direct observations when snorkelling at high tide, indicating movement of limpets from the emergent substrata into the pools. This significantly increased the consumer pressure by more than 25% in upper pools, 8% in mid shore pools and 50% in lower rockpools compared to emergent rock grazing intensity (fig. 3.5). Overall grazing intensity from limpets was higher on the mid and lower shore compared to the upper shore (table 3.5, SNK). As predicted, fences did not block any topshell movements, hence topshells were present in fenced and unfenced pools at the same density (fig. 3.5) and it was unclear if there were differences in their grazing intensity owing to fenced treatments (table 3.5). The density of topshells and limpets did not differ between fenced and open rockpools (table 3.5).

Variation in herbivore density was observed between shore levels (table 3.5). Limpet density was higher at the mid shore level and topshell density was higher at mid and high shore level (table 3.5, SNK).

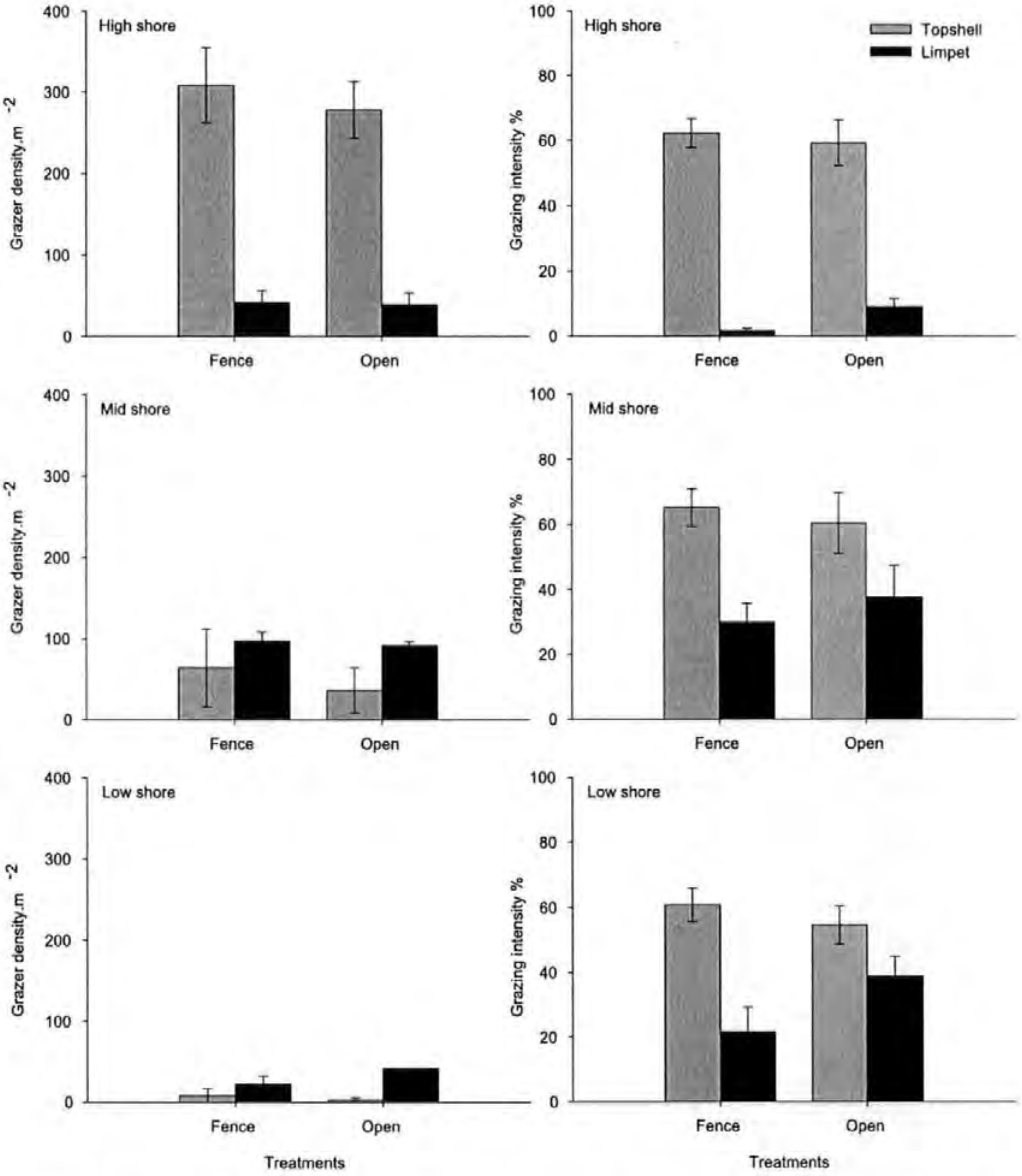

Figure 3.5: Grazer density and grazing intensity percentage in fenced (Fence) and non-fenced (Open) rockpools at the three shore levels (High, Mid, Low). Data are mean of density and percentage of scraped wax disc area (± SE) of six replicate pools.

Table 3.5: 2-way Anova for percentage of grazing activity and grazer density in rockpools fenced or open (treatment:Fe) to control grazer movement at three shore levels (High, Mid, Low). (Cochran's test non significant for all date). ns: non significant; $***$: $P<0.001$; $**$: $P<0.01$; $*$: $P<0.05$. SNK: factor levels of the same group are represented with: =, factor levels with significant differences are represented with < or > according to their rank order.

		Grazing						Density					
		Topshell			Limpet			Topshell			Limpet		
	DF	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Level (Le)	2	38.59	0.31	ns	1444.46	12.63	$***$	143707.56	43.98	$***$	6909.72	20.59	$***$
Fence (Fe)	1	99.14	0.79	ns	518.15	4.53	$*$	2040.89	0.62	ns	61.72	0.18	ns
Le×Fe	2	3.85	0.03	ns	46.58	0.41	ns	281.63	0.09	ns	281.63	0.84	ns
Residual	12	125.28			114.40			3267.74			335.64		
SNK (Level):					Low=Mid>High			Low<Mid=High			Low=High<Mid		

Microhabitat preferences: Clarification of the grazing activity of limpets that entered the pools from emergent rock resulted in different observations at each of the two sites. At both Wembury and Downderry, *Patella vulgata* at the edge of the pools showed some grazing inside rockpools (fig. 3.6). However there was a difference between shores in the extent to which they grazed in pools. At Wembury, there was a general trend for limpets at pool edges to preferentially graze inside rockpools (table 3.6, SNK). At Downderry, limpets showed a significant preference for grazing on the emergent substrata (table 3.6, SNK).

Table 3.6: Anova for percentage of grazing activity of *Patella vulgata* in pools and on emergent rock habitats (ha) at rockpool edges at high shore level at the two sites (Si): Wembury and Downderry. Wax discs were deployed within fences at the edge of the pool covering half the immersed part of the pool and half of the emergent rock at 3 replicate trials (Tr). (Cochran's test non significant). ns: non significant; $***$: $P<0.001$; $**$: $P<0.01$.

	DF	MS	*F*	*P*
Site (Si)	1	1310.07	11.21	$**$
Habitat (Ha)	1	181.24	1.55	ns
Trial (Tr)	2	28.36	0.24	ns
Si×Ha	1	2414.72	20.66	$***$
Si×Tr	2	42.28	0.36	ns
Ha×Tr	2	45.84	0.39	ns
Si×Ha×Tr	2	67.91	0.58	ns
Residual	60	116.86		
SNK: Ha(Si)			Downderry: In<Out Wembury: In>Out	

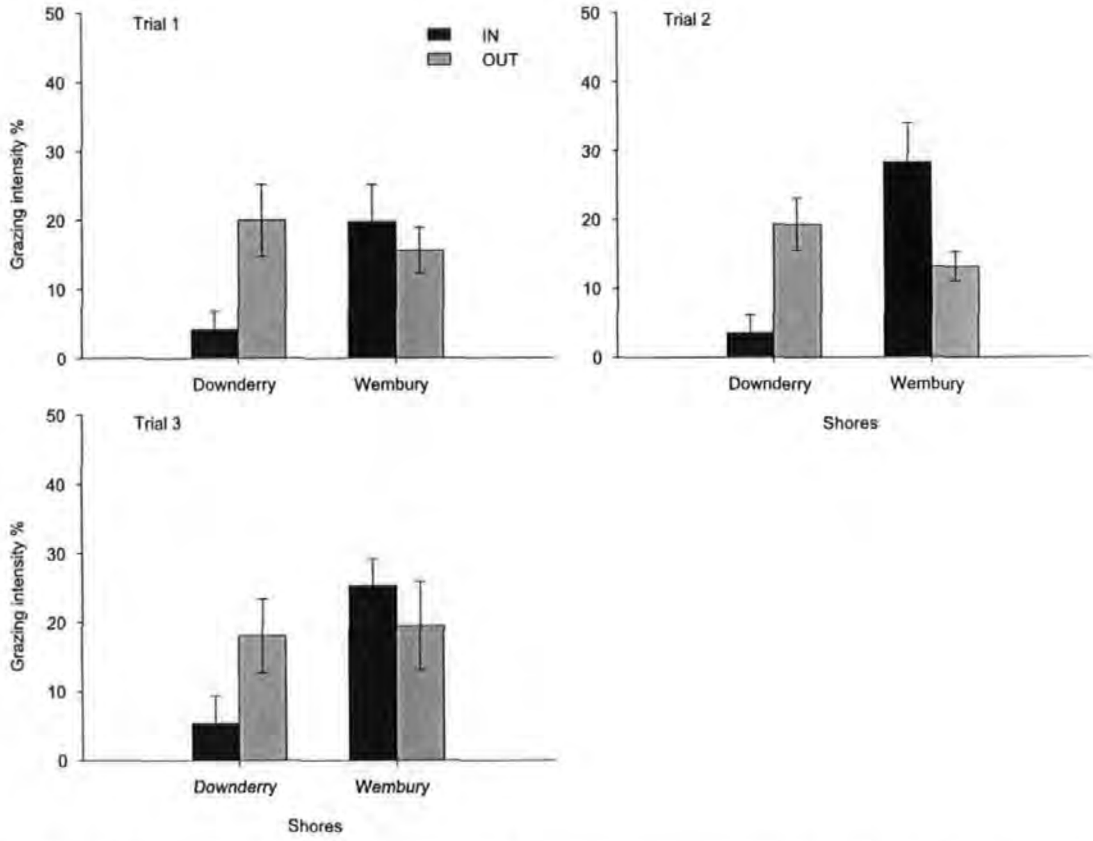

Figure 3.6: Grazing intensity percentage of *Patella vulgata* situated at the edge of high shore level rockpools showing grazing preferences either in pools (In) or on emergent rock (Out). Data are mean of percentage of scraped wax disc area (± SE) of 9 wax discs deployed in fences at the edge of the pool: in half immersed in pools and half on emergent rock (n=6).

3.4 Discussion

Grazing intensity in rockpools was twice that recorded on emergent substrata, despite a lower density of herbivores in pools. These observations confirm the speculations of Lubchenco (1982) and Dethier (1982) regarding the balance of grazing pressure between the two habitats, but contrast with the conclusions of Lubchenco (1982) and Forrest *et al.* (2001) of a relationship between the density of grazers, and grazing intensity, both inside pools and on emergent rock.

The greater grazing intensity in rockpools, despite the low herbivore density, can be ascribed to several causes. Constant immersion of grazers in rockpools might positively influence their ability to forage compared to those on emergent rock (Dethier, 1982). However, the present study did not support this hypothesis, with no detected differences in grazing pressure between limpets fenced in their natural environments of either rockpools or emergent rock. However, this test was confounded by species identity since *Patella ulyssiponensis* were used in their natural environment, in pools, and *Patella vulgata* on emergent rock. It is still true to say that given the natural distribution of limpet species, enhanced grazing in pools cannot be explained solely on the basis of lower stress (i.e. constant immersion) in rockpools.

Secondly, limpet movement from the edges of the pools into the pools themselves at high tide could increase consumer pressure. Grazing pressure in rockpools with similar limpet densities was greater where pools were left open to grazer movement than in fenced pools. This indicates migration of limpets from emergent rock into pools during high tide. Observations by snorkelling also showed movement of *Patella vulgata* from the edges of high shore level rockpools during high tide, regardless of their distance from the pool borders, and supported these results. Maximum foraging activity was recorded during daytime high tide as previously observed in Plymouth by Orton (1929), and at other locations (Hartnoll and Wright, 1977). Limpet migration into pools at high tide, although only observed in small proportion at each sampling occasion, was sufficient to increase consumer pressure in unfenced rockpools and explain why the grazing intensity was twice as much in rockpools than on emergent rock. Other cases of grazer movement have been described, with highly active grazers feeding at high tide outside the zone they occupied at low tide (see Chelazzi *et al.*, 1983, for review). Many animals have been found aggregating in clusters at low tide (Moulton, 1962; Moran, 1985; Chapman and Underwood, 1996), and in the tropics some grazers find protection against physical stress at pool edges and in crevices (Williams and Morritt, 1995). At Wembury, aggregations of the limpet *Patella vulgata*, observed at the edges of the pools rather than in the pool itself (pers. observ.), could be the result of physiological factors or competition. All *Patella vulgata* recorded in rockpools at high tide, during the snorkelling observations, returned to emergent rock on the falling tide. Although *Patella vulgata* can tolerate continual immersion, Delany *et al.* (1998) showed that they migrate outside pools when they become adults. Thus, *Patella vulgata* migration on emergent rock environment at low tide could be explained by a competition with *Patella ulyssiponensis* or a low tolerance to low tide conditions in rockpools.

Another explanation for limpet movement into the rockpools could be due to the greater availability of food resources. The rockpool environment could allow a better development of microalgae because of protection against higher air temperatures and insolation, which are likely to have a negative effect on microalgae (Jenkins *et al.*, 2001; Thompson *et al.*, 2004) and high-density areas of microalgae were found attract limpets (Mackay and Underwood, 1977). At Wembury, *Patella vulgata* showed a preference for foraging in high shore level rockpools, but this behaviour was not consistent between shores, and an opposite trend was observed at Downderry. The contrasting results at Downderry could be explained by differences in wave exposure, or in biofilm abundances. The Downderry shore was more exposed than Wembury and this might have influenced grazing behaviour. In addition, Jenkins and Hartnoll (2001) reported a higher grazing intensity on exposed shores although food resources were lower on the emergent rock of the Isle of Man. Further investigations need to measure microalgal abundance in rockpools and on adjacent emergent rock.

A different distribution of limpet species exists between rockpools and emergent substrate. *Patella ulyssiponensis* inhabits rockpools or damp areas whereas the other species of limpets observed on Irish coasts, *P. vulgata* and *P. depressa* can be found in both pools and on emergent rock (Delany *et al.*, 1998). Different grazing patterns have been observed for different species (Parker and Chapman, 1994; Hawkins and Hartnoll, 1983b) and this could affect algal recruitment. Parker and Chapman (1994) found that littorinids and amphipods grazed preferentially on adult algal fronds, whereas patellids reduced germling recruitment by grazing the biofilm on bedrock surface . Moreover, *Patella ulyssiponensis* might graze more deeply than *Patella vulgata* owing to its radula structure (Hawkins and Hartnoll, 1983b; Hawkins *et al.*, 1989b) and exert a greater consumer pressure than *Patella vulgata*. While attempts were made in tidal tanks in the laboratory to directly compare the grazing intensity of immersed *Patella ulyssiponensis* and *Patella vulgata*, these experiments were limited by limpet mortality. Thus, no direct determination of the grazing intensity of the two species under the same conditions was made. However, indirect evidence suggests that enhanced grazing in pools was not caused by the greater ability of *Patella ulyssiponensis* to graze. Observations made during the snorkelling experiment showed that *Patella ulyssiponensis*, on the whole, did not graze during low water periods and hence, their apparent time advantage for foraging in pools was not important. Given that no differences in overall grazing pressure were observed in pools with *Patella ulyssiponensis* or on emergent rock with similar densities of *Patella vulgata*, this implies that there was little if any differences in grazing activity

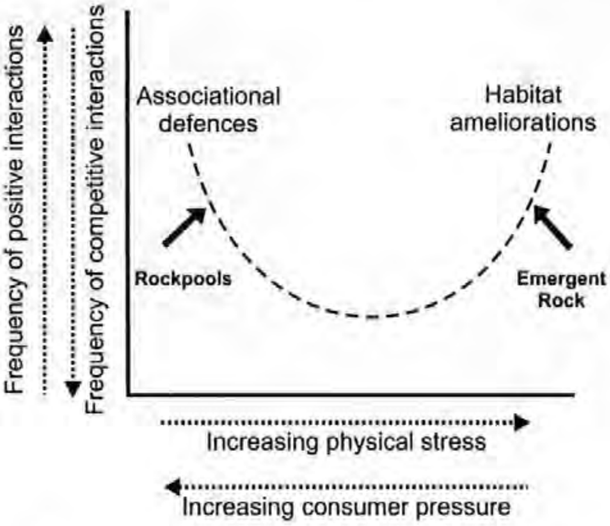

Figure 3.7: Bertness and Callaway model (1994) with its consumer pressure gradient related with grazing pressure found in rockpool and emergent rock environment at Wembury

between the two species.

Seasonal changes in herbivore density and intensity were observed during the experiments. Temporal variability was observed between sampling made at each season for herbivore density, but no clear seasonal trend was apparent. However, a seasonal pattern with greater grazing activity in summer than in winter was detected, but with no relationship to the temporal patterns of grazer density. Similar results were found by Jenkins *et al.* (2001) at a European scale and were attributed to temperature (Newell *et al.*, 1971; Boyden and Zeldis, 1979) and gonad development effects (Orton *et al.*, 1956) on grazing activity. No clear trends were found in grazing activity in relation to shore height. On the contrary, density in rockpools was highest at mid shore level for limpets and at high and mid shore level for topshells as found previously by Underwood (1973).

During the fencing experiment, given that the design was not meant to stop them, topshells invaded fenced pools, resulting in no differences between fenced and unfenced pools in their grazing intensity after a 15 day period. This result raises questions about the efficiency of herbivore exclusions either by fencing or hand removal. However, numerous investigations as well as experiment conducted in Chapter 2, using these methods showed significant effects on macroalgae from the grazer manipulations (Lubchenco, 1982; Benedetti-Cecchi and Cinelli, 1996; van Tamelen, 1987; Hawkins, 1981). Therefore herbivore exclusions, manual or with fences seem to be more efficient in excluding limpets than topshells, and this may suggest that limpets play a greater role in observed algae development than topshells.

In summary, consumer pressure was higher in rockpools, despite a lower herbivore density. High grazing activity in rockpools was caused by limpet movement from the pool edges into the rockpools to forage, rather than constant herbivore immersion, or different feeding mechanisms between *Patella ulyssiponensis* and *P. vulgata*. The observations made thus far about the grazing patterns, in pools versus emergent rock, can be placed into the context of the Bertness and Callaway model (1994). As the grazing intensity in rockpools is double than on the emergent substrate, the two habitats can be situated on the model with rockpools in the higher part of the consumer pressure gradient, and emergent substrate in the lower part (fig. 3.7). Organisms living in rockpools are therefore under a very high consumer stress although they can escape environmental stress such as desiccation. Such an herbivore pressure can induce switches in the nature of interactions between species which usually would be competitors in benign environment and at lower consumer stress to positive relationships (Bertness and Callaway, 1994). Associational defences, for instance when a palatable algae benefit from a barrier protection against grazer by growing among less palatable ones (Pfister and Hay, 1988; Bertness and Callaway, 1994), can be expected rockpools. The influence of herbivore foraging on rockpool community composition can be an even more predominant structuring force than on emergent rocky shores. The effect of this grazing intensity gradient on species interactions during algal succession in rockpools and on emergent rock was examined in chapter 4.

Chapter 4

Species interactions during succession

4.1 Introduction

The term succession, first coined by Clement (1916), is currently defined as species replacement occurring during recolonization following a disturbance (Clement, 1928, 1936; Connell and Slatyer, 1977; Sousa and Connell, 1992) and is generally driven by complex species interactions. Disturbance on rocky shores may be due to stochastic physical events, such as wave action (Dethier, 1984), scouring by sand (Airoldi, 1998), heat stress (Underwood and Jernakoff, 1984) or wave driven logs or rocks (Clement, 1916; Dayton, 1971; Lubchenco, 1983; Dethier, 1984; Benedetti-Cecchi and Cinelli, 1996). Primary succession is the colonisation of completely virgin (e.g. following volcanic activity) or totally denuded substrata (e.g. after ice scour, ice-melt or shifts in sediments covering rock). Secondary succession in contrast occurs on substrata which may be partially occupied and can occur following relaxation of grazer, predator activity or removal of canopy shading.

Disturbance plays a major role in structuring community assemblages, preventing monopolization of a single species by creating a mosaic of patches (Sousa, 1979b; Dethier, 1984). Early colonists occurring after a disturbance are usually ephemeral diatoms, filamentous and foliose algae that rapidly monopolise the cleared substrata, then turf forming species or sessile invertebrates (e.g. *Corallina* spp., *Gelidium* spp., barnacles) and finally late colonists which often include slow growing perennial species with more complex morphologies such as dominant canopy forming fucoids, *Sargassum muticum* or large macroinvertabrates such as mussels (Pyefinch, 1943; Lubchenco and Menge, 1978; Sousa, 1979b; Hawkins, 1981; Lubchenco, 1983;

Underwood *et al.*, 1983; Underwood and Jernakoff, 1984; Dethier, 1984; van Tamelen, 1987; Kim, 1997; Benedetti-Cecchi, 2000a).

Patterns of recolonization following disturbance show high levels of spatial and temporal variability (Benedetti-Cecchi and Cinelli, 1996; Benedetti-Cecchi, 2000b). Such variability is caused by numerous factors. For instance, the distance between the source of colonists and site of recruitment dictates the pattern of succession (Menge *et al.*, 1993; Reed *et al.*, 2000). Colonists of new open space may arrive from the border or surrounding area either by vegetative reproduction or propagule arrival (Dethier, 1984) and in the case of mobile animals, migration (Underwood, 1977). Recruitment relies on the local pool of propagules (Gaines and Roughgarden, 1985; Dethier, 1984; Sousa, 1984b, 1985; Benedetti-Cecchi and Cinelli, 1993) especially for species with short range dispersal (Dayton, 1973; Paine, 1979). In addition, there is considerable temporal variability in succession. The time of clearance affects the trajectory of succession depending on the seasonality of species reproduction and hence propagule availability (Paine, 1971; Foster, 1975; Emerson and Zedler, 1978; Sousa, 1979b, 1985; Hawkins, 1981; Turner, 1983; Dayton *et al.*, 1984; Breitburg, 1985; Benedetti-Cecchi and Cinelli, 1993, 1996; Benedetti-Cecchi, 2000b). Propagules available at the time of clearance recruit first to the open space (Egler, 1954; Dean and Hurd, 1980; Robinson and Dickerson, 1987; Benedetti-Cecchi and Cinelli, 1996; Benedetti-Cecchi, 2000b) and can become dominant in succession by a priority effect (Benedetti-Cecchi, 2000b). The outcome of competition between newly settled early colonizers may vary depending on the relative size and density of the organisms. Large species have an inhibiting effect by overgrowing, shading or bulldozing other species (Connell, 1961b; Dayton, 1971, 1975; Paine, 1977; Hawkins, 1983; Goldberg, 1987). In addition to size, the outcome of competition depends on the life stage of the organisms involved. Species might only be dominant when recruiting during their main reproductive period (Drake, 1991; Benedetti-Cecchi and Cinelli, 1996). Moreover, high density of a given species, even for organisms of small size, may pre-empt space inducing non-hierarchical competition (Hruby and Norton, 1979; Hawkins, 1981; Sousa *et al.*, 1981; Lubchenco, 1983; Reed and Foster, 1984; Benedetti-Cecchi and Cinelli, 1996; Benedetti-Cecchi, 2000b).

Connell and Slatyer (1977) classified species interactions during succession into various models which have been tested in many subsequent studies (Clement, 1916; Connell and Slatyer, 1977; Sousa, 1979b; Sousa *et al.*, 1981; Lubchenco, 1983; Underwood *et al.*, 1983; van Tamelen, 1987; Farrell, 1991) (see Pickett and White, 1987; Sousa and Connell, 1992, for reviews). The three major patterns in the course of succession are tolerance, inhibition and facilitation (Connell and Slatyer, 1977) and these are often observed to occur together along successional trajectories (Hawkins, 1981; Farrell, 1991). Early work had viewed facilitation as the dominant model during succession (Clement, 1928) but later experimental studies showed that negative interactions such as competition were also important (see Benedetti-Cecchi and Cinelli, 1996; Benedetti-Cecchi, 2000b). Thus, inhibition was subsequently considered to be the dominant successional model (Connell and Slatyer, 1977; Sousa, 1979b; Breitburg, 1985; Sousa and Connell, 1992) and positive interactions, such as facilitation, have tended to be neglected (Bertness and Callaway, 1994). One possible positive interaction is habitat amelioration, where a species alters the environment and consequently allows other species to establish (Bertness and Callaway, 1994). Whilst, these interactions can be direct, there are many examples of indirect interactions when a species affects another through mediation of a third species (Dungan, 1986; van Tamelen, 1987; Farrell, 1991; Strauss, 1991; Kim, 1997; Benedetti-Cecchi, 2000a). In addition, historical abiotic and biotic events can also affect the successional trajectories. Berlow (1997) classified these sequences as "canalized succession" when trajectories are predictable and convergent, contrasting to "contingent succession" where colonisation processes are more variable and divergent owing to physical and biological influences.

The effects of herbivores on the course of succession have been shown to be crucial (see Sousa and Connell, 1992, for review). Herbivores can affect succession in different ways (Farrell, 1991): grazers may remove most of the settling organisms (Dethier, 1984) depending on the foraging intensity. The effect of consumers in mediating the interaction between early and late colonisers was predicted by Farrell (1991) in his modification of the Connell and Slatyer (1977) model. Seasonality in herbivore abundance and feeding rate can also influence the successional trajectory (Hawkins, 1981; Breitburg, 1985; Jenkins *et al.*, 2001). Moreover, gastropods and other grazers feed preferentially on ephemeral algal species, potentially preventing early coloniser inhibition at later stages (Sousa, 1979b; Littler and Littler, 1980; Underwood *et al.*, 1983; van Tamelen, 1987). In addition, some seaweeds such as encrusting algae are better adapted to resist consumer pressure (Lubchenco and Cubit, 1980; Dethier, 1981; Steneck, 1982; Steneck and Watling, 1982), whilst others escape grazing by rapid growth and attaining a size related refuge (Lubchenco, 1983; Chapman, 1990a) or through chemical defence (Padilla and Allen, 2000; Hay and Fenical, 1992). Another way of protecting themselves from consumers are associational defences (Bertness and Callaway, 1994). These occur when palatable species find protection by growing between less palatable species (Hay, 1986). Recently, Benedetti-Cecchi (2000a) developed successional models integrating the role of consumer pressure and behaviour, indirect and direct interspecific interactions between early and later successional stages and the life history traits of species involved.

Succession on emergent intertidal rock is well documented, but fewer studies have been made in the rockpool environment (but see Dethier, 1984; Benedetti-Cecchi and Cinelli, 1996; Benedetti-Cecchi, 2000b). The effect of tidal height has also been neglected even though it could have a strong influence due to the gradient in physical stress and disturbance regimes: high shore levels are subject to more heat stress and lower shore levels are subject to greater wave action on some shores (Dethier, 1984; Underwood and Jernakoff, 1984; Hawkins, 1983). In addition, previous work has shown that more investigations are needed to determine the influence of herbivores on succession (Underwood and Jernakoff, 1984; Sousa and Connell, 1992).

The overall aim of this chapter was to test species interactions during succession over physical stress and consumer pressure gradients as described in the Bertness and Callaway (1994) model. To investigate the effect of physical stress gradient, both rockpools and emergent rock were used over the vertical gradient of the shore. Experiments were replicated spatially, temporally and in relation to consumer pressure in order to investigate in detail species interactions during colonisation and examine them in relation to previous successional models (Bertness and Callaway, 1994; Benedetti-Cecchi, 2000b). With increasing tidal height emergent rock is subject to increasing desiccation stress, whilst rockpools are subject to more extreme conditions of pH, salinity and temperature fluctuations as disconnection time from the sea increases (Dethier, 1984). In addition, I created a consumer pressure gradient using differences in grazing intensity between rockpools and emergent rock found in Chapter 3 and manipulating the herbivore density in those two habitats. According to Bertness and Callaway (1994) conceptual model, positive interaction increases with physical stress (i.e. shore elevation or between rockpool and emergent rock). Therefore, in rockpools which are subjected to low physical stress and high consumer pressure (see Chapter 3), associational defences were expected between early and later colonists. Conversely, on emergent rock which experience high physical stress when consumer pressure was suppressed, habitat ameliorations were predicted from early colonists. In benign environments at medium consumer pressure, Bertness and Callaway (1994) predicted competition so inhibition was expected between early and later colonists. Multifactorial experiments were carried out over these two gradients to test: (1) if physical stress and consumer pressure were influencing species recruitment and interactions, and hence, driving different successional sequences; (2) if succession initiated at different times of the year had divergent successional trajectories owing to differences in recruitment according to species life history; (3) if interactions between ephemeral and perennial species were always following an inhibition model or whether there was any positive effect on each other owing to physical stress and consumer pressure with particular attention to the status of the invasive species, *Sargassum muticum*, and the role of barnacles during colonisation sequences.

Table 4.1: Summary of experiments setup to study the influence of consumer pressure and physical stress on succession in rockpools and emergent rock

Experiments	Purpose	Experimental design	Null Hypotheses
Exp1 General Pattern of Succession	Succession	Grazer (+G,-G), Shore heights (High, Mid, Low), Habitats (Rockpools, Emergent rock)	Removal of herbivores, shore heights and habitat locations make no differences to successional species occurrence
	Control for grazer removal	Grazer (+G,-G), Shore height (Mid) Habitats (Rockpools, Emergent rock)	Removal of grazers make no differences to grazing intensity and grazer density
Exp2 Timing of initiation	Succession	Grazer (-G), Shore heights (High, Mid, Low), Habitats (Rockpools, Emergent rock), Initiation (Aug02, Feb03)	Timing of initiation make no differences to species recruitment and therefore succession
Exp3 Ephemeral and Perennial manipulations	Control for manipulation	Grazer (+G), Mid Shore Habitats (Rockpools), Manipulation	Removal manipulation make no differences to assemblages
	Ephemeral manipulation	Grazer (+G,-G), Shore heights (High, Mid, Low), Habitats (Rockpools, Emergent rock), Ephemeral (Presence, Absence)	Ephemeral species removal make no differences to perennial ones during succession
	Perennial manipulation	Grazer (+G,-G), Shore heights (High, Mid, Low), Habitats (Rockpools, Emergent rock), Perennial (Presence, Absence)	Perennial species removal make no differences to ephemeral ones during succession
	Sargassum	Grazer (+G,-G), Shore heights (High, Mid, Low), Habitats (Rockpools) Community (Scraped, Mature)	Consumers removal and plot clearances make no differences to *Sargassum* recruitment and establishment
	Barnacle	Grazer (+G,-G), Shore heights (High, Mid, Low), Habitats (Emergent rock) Barnacle (Scraped, Mature)	Consumers and barnacles removal make no differences to recruitment and establishment of algae

4.2 Material and methods

4.2.1 Experiment 1. General patterns of succession: the role of herbivores and physical stress

The hypothesis that physical stress and herbivore pressure will influence species distribution and recruitment, and therefore, the interspecific interactions occurring during succession thereby leading to different pathways was tested. An experimental manipulation (hereafter named: Exp 1. General Pattern of Succession) was carried out in order to study species interactions during succession using rockpools and emergent rock habitats distributed over the vertical height of the shore to generate gradients of environmental stress. Over these gradients, experimental plots were maintained at natural and reduced grazer density to control consumer pressure.

A total of 48 experimental plots were distributed in medium-sized rockpools (depth 8-15 cm, area 0.35-1 m^2) and emergent rock with similar initial community composition (fig. 4.1). Their distribution was over three shore levels (high level shore between 3-4m above LAT; mid level shore between 1-3 m above LAT and low level shore between 0.5-1m above LAT) at Wembury Point over a 1km stretch of shore. After selection, rockpool and emergent rock heights were determined by recording their time of emersion on replicate dates and referring to a tide level prediction program (Poltips3, Proudman Oceanographic Laboratory, NERC, Liverpool, UK). High shore rockpools dominated by *Ulva* spp. were not used due to their differing assemblages. In order to investigate the effect of herbivores on species interactions, grazers were removed from half the plots (reduced grazer density: -G) and these were compared to the other plots left at natural grazer density (controls: +G). The two grazer treatments (+G and -G) were randomly allocated to these plots and grazers were manually removed every month from August 2002 to the end of the experiment in November 2004. All detectable herbivores were removed inside the whole rockpool, and from an area of one meter around the pool and emergent rock plots to minimise grazer recolonization from the borders. For each treatments, four replicate plots composed of two subsample quadrats of 20×20cm were cleared with a paint scraper and a wire brush to remove all existing biota in the rockpool and on emergent rock in August 2002. The two quadrats were used as subsamples to generate a percentage cover estimate for each plot. A buffer zone of two centimeters was scraped around the edges of the delimited quadrats to minimise border effects (e.g. Sousa, 1985; Farrell, 1989). Special care was taken to remove any encrusting seaweed to give 100% bare rock. The corners of each quadrat were marked by four screws inside the pool and by two screws on emergent rock quadrats. The size choosen for the quadrats was within the range of natural disturbance (e.g. Benedetti-Cecchi, 2000b,a).

The plots were sampled every three months from the start of the experiment until November 2004. The percentage cover of macroalgae forming primary and secondary layers was estimated at intersection points in the centre of the 20×20cm quadrat, to minimise edge effects, using a 15×15cm grid of 64 points. A grid with two layers of lines was used to avoid parallax errors in sighting (Hawkins and Jones, 1992). Primary cover was assessed by moving aside the canopy species forming the secondary cover. Organisms present in the plots but not recorded by this method were also assessed and a value of 1% was assigned to them. Seaweeds were identified in the field to species level when possible, but in case of doubt, samples were collected for further identification in the laboratory using various identification keys (Hiscock, 1979, 1986; Irvine, 1983; Irvine and Chamberlain, 1991; Burrows, 1991; Dixon and Irvine, 1977; Fletcher, 1987; Maggs and Hommersand, 1993).

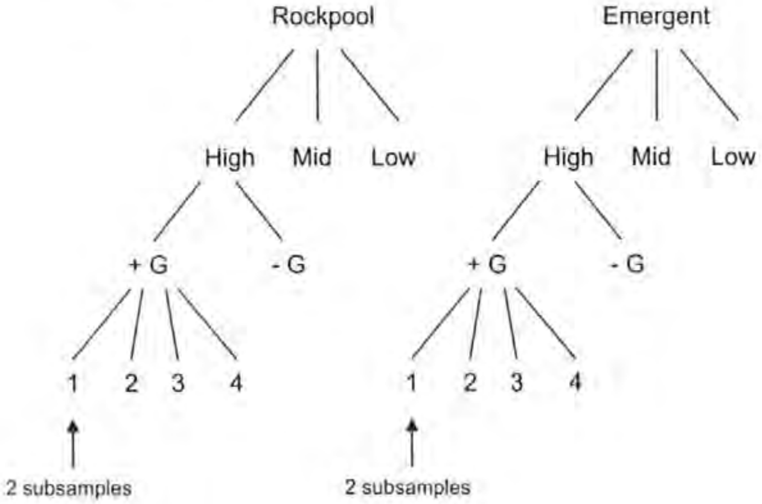

Figure 4.1: Schematic diagram of the experimental design for the general pattern of succession (Experiment 1) testing the role of physical stress in rockpools and emergent rock (Habitat) over the high, mid and low shore (Level) at natural (+G) and reduced grazer density (-G). n=4.

Multifactorial ANOVAs (Underwood, 1997) were used to compare growth rate over time of particular species such as *Phymatolithon* spp., *Corallina* spp. and *Sargassum muticum* between the factors: (1) shore levels (High, Mid, Low); (2) herbivore treatments (natural (+G) and reduced (-G) grazer density). Cochran's test was used to test for the assumption of homogeneity of variances

(Winer, 1971). When this assumption was not verified, data were logarithmicaly transformed to achieve homogeneity of variance. When required, *post hoc* multiple comparisons of the means were made using Student-Newman-Keuls's test (SNK) (Underwood, 1997). These analyses were carried out using WinGmav5 (Underwood and Chapman 1997). Pearson correlation coefficient was also calculated to test for a relationship between *Corallina* spp. and *Sargassum muticum* abundances.

Succession in rockpools and emergent rock was analyzed separately for clarity of the results. Multivariate analysis was performed on the average cover of the 2 subsample quadrats of each experimental plot. The species assemblages of the general patterns of succession experiment (experiment 1) were compared by PERMANOVA (Anderson, 2001; McArdle and Anderson, 2001) between the factors: (1) shore levels (High, Mid, Low) and (2) herbivore treatments (natural (+G) and reduced (-G) grazer density). PERMANOVA was performed in order to test for interactions between factors which ANOSIM does not test for (Anderson, 2001; McArdle and Anderson, 2001). When applicable, pairwise *a posteriori* comparisons were tested among levels of each factor. All factors were fixed and orthogonal with n=4 replicates in each factor level. Analysis was performed within each sampling date and not between dates in order to avoid any problems of non-independence that could arise when observations are repeated in the same plots over time (Underwood and Anderson, 1994; Anderson and Underwood, 1997). Analysis was performed using the PERMANOVA program (Anderson, 2001; McArdle and Anderson, 2001). Individual species percentage contributions to the differences between groups of samples were calculated when appropriate using average Bray-Curtis dissimilarities between each pair of samples given by SIMPER (PRIMER-E v6.1.5). Species contributing the most to the differences between groups were plotted as a function of time.

Matrices of similarities were calculated between each pair of samples using the Bray-Curtis similarity coefficient (Bray and Curtis, 1957) on fourth-root transformed data for each sampling date. The fourth-root transformation downweights the effect of fluctuating contributions between common and rare species (Clarke and Warwick, 2001). From these matrices, non-metric multidimensional scaling (nMDS) 2-dimensional ordination maps of the samples were produced for the first and last sampling date (November 2002 and November 2004) to illustrate the difference in the general pattern of succession between shore levels and grazer treatments. In addition, nMDS of the algal community over the time was represented in order to illustrate succession trajectories. nMDS were considered interpretable with stress <0.20 (Underwood and Anderson, 1994; Anderson and Underwood, 1997; Clarke and Warwick, 2001). The stress value measures how closely the distances in the nMDS match the Bray-Curtis rank order similarities (Kruskal, 1964). Analyses were performed using PRIMER-E v6.1.5 (Clarke and Warwick, 2001).

In addition, an experiment was set up in August 2004, to test the efficiency of the grazer removal, and hence, the reduction of grazing intensity. To measure grazing activity, ten wax discs were deployed in 4 replicate plots in rockpools and on emergent rock at natural and reduced grazer density at the mid shore level in August 2004 in 2 periods of 15 days over 1 month (see Thompson *et al.* (1997); Forrest *et al.* (2001) for methods). The wax discs were deployed between 2 grazer removal dates (separated by 1 month) allowing grazer recolonisation and grazing pressure to be recorded. At the start of each deployment, grazer density was counted in three replicate quadrats of 20×20 cm in each plot. The wax discs were returned and analysed in the laboratory (see Chapter 3 for methods). ANOVAs were used to test hypotheses about grazing intensity and grazer density in the control for grazing reduction experiment (n=4).

4.2.2 Experiment 2. Succession: role of timing of initiation

Different species were expected to recruit at different times of the year according to their reproductive phenology. The hypothesis that succession initiated at different times of the year would have different species colonisation patterns because of variability in the timing of species reproduction and recruitment was tested with a multifactorial experiment. Twenty four experimental plots (with 2 subsample quadrats each) were cleared in February 2003 (hereafter named Feb03 plots) in rockpools and emergent rock at three shore levels (High, Mid, Low) and were all kept at reduced grazer density to ensure algal growth via recruitment of species reproducing during winter. Observed successional sequences were compared with those in the General Patterns of Succession experiment (Exp 1), which were kept at reduced grazer density (-G) (24 plots) and set up in August 2002 (hereafter named Aug02 plots). Sampling and grazer removal regimes were similar and simultaneously to the previous experiment (Exp 1. General Pattern of Succession)- i.e. every three months for the sampling and every month for the manual grazer removal from the start of the experiment until November 2004.

The effect of time of initiation of succession on assemblages was compared by PERMANOVA among the factors: (1) shore levels (High, Mid, Low) and (2) initiation times (August 2002 and February 2003). To determine the effect of different initiation times on the successional trajectory, analyses were done at 3, 9, 15 and 21 months after the clearance of the plots. The results might be confounded by seasonal effects due to the comparison between data collected at two different seasons. For example, at the third month after the initiation (started in August 2002 and February 2003), data from November 2002 were compared with data from May 2003. This should not affect the conclusions about the hypothesis regarding the assemblage trajectory. According to the null hypothesis, if the communities were found to be the same at the end of the experiment (after 21 months) including with seasonal patterns then time of initiation was not affecting the outcome of the colonisation. In addition, particular attention was given to perennial species present throughout the year rather than annual species which fluctuate in abundance with seasons. However, to test for this confounding effect, an additional PERMANOVA analyses were done to compare the successional trajectories (Aug02 and Feb03) at the same seasons but with different length of time (e.g. in May 2003, succession would have run for 9 months for the Aug02 plots and 3 months for the Feb03 plots). Analyses were done for the sampling dates of May 2003, November 2003, May 2004 and November 2004. These analyses were compared to the previous ones (same length of time but different seasons) in order to investigate the influence of initiation time on the successional trajectories end state.

4.2.3 Experiment 3. Role of ephemeral and perennial species in later stages of succession

Three hypotheses were tested: (1) reciprocal inhibition between early ephemeral and later perennial colonists was the major interaction occurring under mild physical stress and low consumer pressure in both rockpools and emergent rock; (2) associational defences occurred between perennial non palatable species and ephemeral colonists at high consumer pressure and low physical stress (i.e. in rockpools); and (3) habitat ameliorations occurred under high physical stress and low consumer pressure (i.e. emergent rock at reduced grazer density). In order to study interactions of ephemeral and perennial species during late succession, an additional 96 experimental plots (with two subsample quadrats each) were cleared in rockpools and emergent rock simultaneously with those set up in August 2002 (Exp 1. General Pattern of Succession). These plots were haphazardly distributed over the three shore levels (High, Mid, Low) of Wembury point and grazer reduction was applied to half of them following the same regime as in the previous experiments (i.e. monthly removal). Ephemeral species including epiphytes were carefully removed every 3 months leaving perennial species in 48 plots from August 2003. Erect perennial species (excluding barnacles) were removed every three months from the 48 other plots from November 2003. Removal was done during the later stages of succession to ensure correct identification of the species manipulated. The sampling and removal regime was established every three months simultaneously with the initial experiment (Exp 1. General Pattern of Succession) until November 2004. In order to investigate the effect of ephemeral removal on the development of perennial species during succession, percentage cover of perennial species was compared with the percentage cover of perennial species of the experiment 1 (Exp 1. General Pattern of Succession). Percentage cover of ephemeral species was compared with the percentage cover of ephemeral species of the first experiment (Exp 1. General Pattern of Succession) to determine the effect of perennial removal on the development of ephemeral species during succession.

Interactions during later successional stages were analysed by PERMANOVA between the factors: (1) shore levels (High, Mid, Low), (2) herbivore treatments (natural (+G) and reduced (-G) grazer density) and (3) removal treatments (presence or absence of perennial species) for the ephemeral species assemblages or (presence or absence of ephemeral species) for the perennial species assemblages.

4.2.3.1 Procedural control for removal manipulation

Algae were carefully removed using a razor blade and forceps to avoid damaging or scraping the remaining organisms. However, the manipulation of both ephemeral and perennial algae could have created artifacts by accidental removal. In order to investigate the effect of manipulation, 8 quadrats of 20×20cm were marked in identical mature rockpool communities at mid shore level in February 2005. The manipulation treatment, was mimicked in half the plots (randomly selected by pinching the algae and bedrock with forceps and razor blade during 15 min without removal). This treatment, as in the removal experiments, was made every 3 months during one year. The quadrats were sampled using the same methods as in the previous experiments in February 2006 and percentage cover was compared between manipulated and unmanipulated quadrats. An analysis of similarity (one-way ANOSIM, PRIMER-E v6.1.5) was calculated from the similarity matrix in order to test for the null hypothesis that experimental removal of ephemeral and perennial species had no effect on the surrounding community.

4.2.3.2 *Sargassum muticum* invasibility in rockpools

Sargassum muticum was found to be an highly invasive species which took advantage of any opportunity of free space to colonise the shore (Fernandez, 1999). In order to investigate if the recruitment of *Sargassum muticum* was higher in open space and influenced by grazing pressure, the number of individuals of *S. muticum* including adults and germlings were counted in two quadrats of 10×10cm in each of the 48 plots haphazardly distributed within the mature community and in plots cleared in August 2002 at the three shore levels (High, Mid, Low) in rockpools at natural (+G) and reduced grazer density (-G). The plots were sampled in September 2003 to allow substantial development of *Sargassum muticum* plants that recruited in summer 2002 (adults holdfast) and in summer 2003 (germlings). ANOVA was used to test the hypothesis about recruitment of *Sargassum muticum* between the factors: (1) shore levels (High, Mid, Low); (2) herbivore treatments (natural (+G) and reduced (-G) grazer density) and (3) community treatment (mature and cleared) (n=4).

4.2.3.3 Role of barnacles during succession on emergent rock

In order to assess if barnacles were facilitating the development of algae during succession by reducing consumer pressure, plots with no erect algae which were originally barnacle dominated (>70% cover) were cleared in August 2002. The colonisation in those plots was then were compared to a mature barnacle dominated community (>70% cover) in August 2003 and August 2004. Twenty four plots were sampled by using two quadrats of 20×20cm each at natural (+G) and reduced grazer density (-G) on emergent rock at the three shore levels (High, Mid, Low).

In addition, in order to investigate the role of barnacles on grazing intensity, 10 wax discs were deployed in 16 plots without erect algae at natural grazer density with high barnacle cover ($> 80\%$) and with low barnacle cover ($< 10\%$) at mid shore level during 2 trials of 15 days periods (see Thompson *et al.* (1997); Forrest *et al.* (2001) for method). At the time of each deployment, grazer density was counted in three replicate quadrats of 20×20cm in each plot. The quadrat size was chosen in order to fit natural areas of low barnacle cover. The wax discs were returned and analysed in the laboratory (see chapter 3 for methods).

ANOVA was used to test for differences in grazer density and grazing intensity between high *vs* low barnacle cover (n=8). Direct and indirect effects of barnacles on algal assemblages were analysed on emergent rock by PERMANOVA among the factors: (1) shore levels (High, Mid, Low), (2) herbivore treatments (natural (+G) and reduced (-G) grazer density) and (3) barnacle treatments (mature with high barnacle cover and cleared from barnacles).

4.3 Results

4.3.1 Experiment 1. General patterns of succession: the role of herbivores and physical stress

4.3.1.1 Grazing reduction

Monthly removal of grazers was sufficient to reduce consumer pressure and grazer density in the appropriate plots (-G) (fig. 4.2). Limpet grazing pressure and density were significantly reduced throughout the month during which the experiment was conducted, (fig. 4.2 and Anova, tables 4.2 and 4.3) compared to the control plots left at natural grazer density (+G). Topshell grazing and density were reduced in rockpools and on emergent rock only over the first 15 days after grazer removal but this effect was significant only for densities (fig. 4.2 and Anova, tables 4.2 and 4.3, SNK). A gradient of grazing pressure was maintained with highest total consumer pressure in rockpools at natural grazer density (+G) with 65.5% ±3.55 SE, lowering in rockpools at reduced grazer density (-G) to 48% ±7 SE, reducing to 45% ±5.3 SE on emergent rock at natural grazer density (+G) and finally with lowest grazing pressure of 30% ±3.1 SE on emergent rock at reduced grazer density (-G) (fig. 4.2).

Table 4.2: 3-way Anova comparing percentage of grazing activity of topshells and limpets in rockpool and emergent rock (Habitat: Ha) over one month (Time (Ti): 15 days, 30 days) in habitats left at natural grazer density and after manual grazer removal (Grazer (Gr): Control (+G), -Grazer (-G)) at mid shore level. Data were ARCSIN transformed. (Cochran's test non significant for topshell). ns: non significant; * * *: P<0.001.

		Topshell			Limpet		
	DF	MS	F	P	MS	F	P
Habitat (Ha)	1	13.47.53	19.71	* * *	51.67	1.36	ns
Grazer (Gr)	1	89.74	1.31	ns	2042.09	53.75	* * *
Time (Ti)	1	114.77	1.68	ns	28.22	0.74	ns
Ha×Gr	1	37.64	0.55	ns	12.20	0.32	ns
Ha×Ti	1	46.25	0.68	ns	100.31	2.64	ns
Gr×Ti	1	114.98	1.68	ns	12.97	0.34	ns
Ha×Gr×Ti	1	98.06	1.43	ns	81.41	2.14	ns
Residual	24	68.37			37.99		

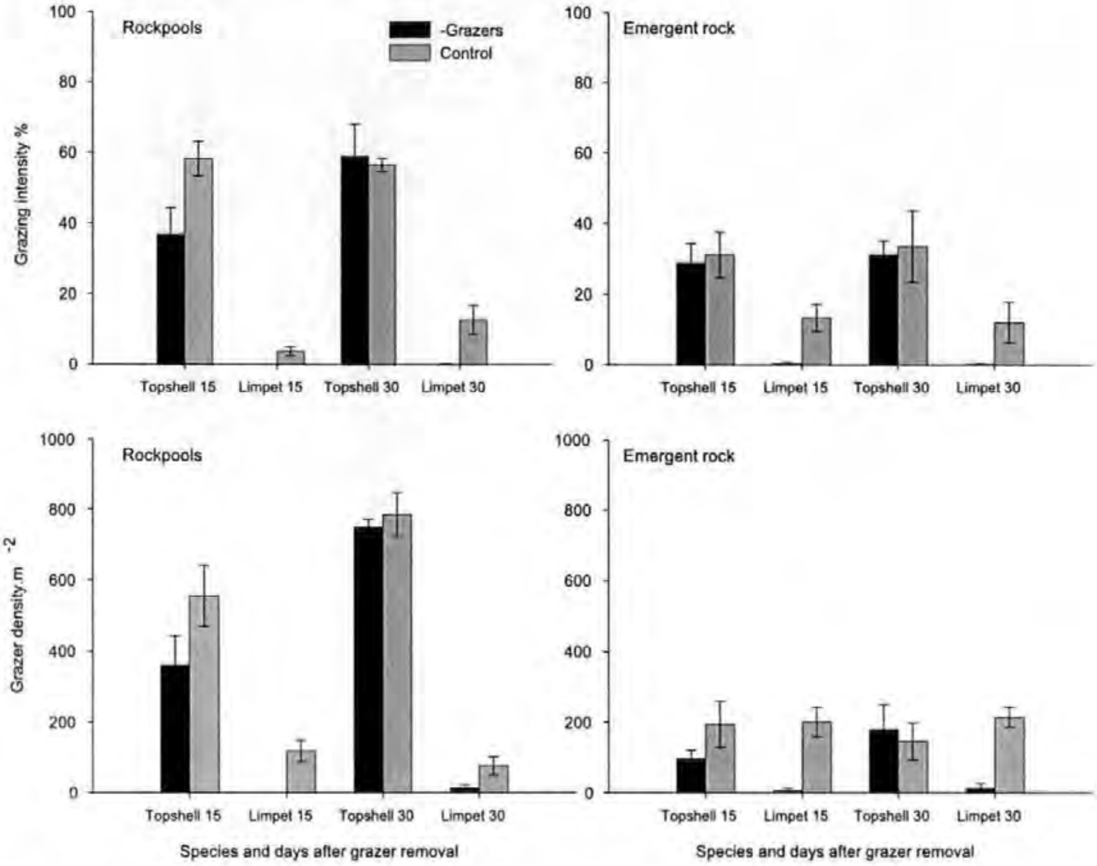

Figure 4.2: Grazing intensity percentage and grazer density in rockpools and on emergent substrate habitats over one month after manual removal of topshells and limpets (-Grazers (-G)) compared to habitat left at natural grazer density (Control(+G)) at mid shore level in August 2004. Data are mean of percentage of surface grazed (±SE) of ten replicate wax discs averaged per plots and grazer count (±SE) in three replicate 20×20cm quadrats averaged per plots measured after 15 days and 30 days (n=4).

Table 4.3: 3-way Anova comparing grazer density of topshells and limpets in rockpool and emergent rock (Habitat: Ha) over one month (Time (Ti): 15 days, 30 days) in habitats left at natural grazer density and after manual grazer removal (Grazer (Gr): Control, -Grazer) at mid shore level. (Cochran's test non significant in all case). ns: non significant; $***$: $P<0.001$; $**$: $P<0.01$.

		Topshell			Limpet		
	DF	MS	*F*	*P*	MS	*F*	*P*
Habitat (Ha)	1	1680555.55	107.67	***	26258.68	11.71	**
Grazer (Gr)	1	42534.72	2.73	ns	166112.08	74.08	***
Time (Ti)	1	213059.41	13.65	**	24.11	0.01	ns
Ha×Gr	1	13888.89	0.89	ns	23172.26	10.33	**
Ha×Ti	1	170138.89	10.90	**	1181.52	0.53	ns
Gr×Ti	1	42534.72	2.73	ns	1158.52	0.53	ns
Ha×Gr×Ti	1	385.80	0.02	ns	1953.13	0.87	ns
Residual	24	15608.92			2242.48		
SNK		In: 15 days < 30 days Out: 15 days = 30 days			+G: Out > In -G: Out = In		

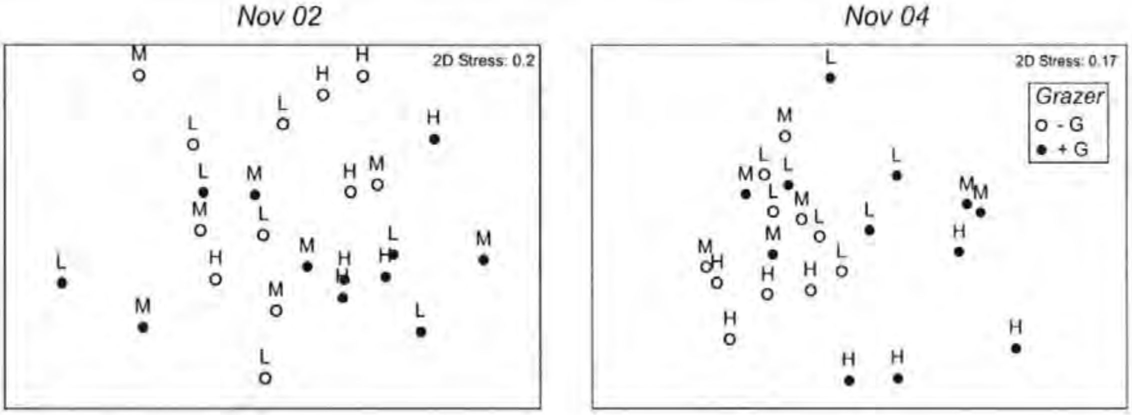

Figure 4.3: nMDS ordination of the algal percentage cover assemblages in rockpools at natural (+G) and reduced (-G) grazer density at each of three shore levels (High, Mid, Low) at the beginning and the end of the experiment in November 2002 and 2004 (n=4). High shore rockpools were toward the bottom and low shore rockpool toward the top of the nMDS. Reduced grazer density community were grouped toward the left and natural herbivores density community on the right of the nMDS.

4.3.1.2 Succession: general patterns in rockpools

The successional trajectory was significantly different in rockpools between natural (+G) and reduced grazing density (-G) from the beginning of recolonisation until the end of the experiment (PERMANOVA, table 4.4, November 2002 to November 2004). Species contributing the most to the dissimilarities between grazer treatments (-G and +G) were highlighted by the SIMPER procedure (appendix, table E.1). Calcareous species such as *Corallina* spp., *Lithophyllum incrustans* and *Phymatolithon* spp. were positively enhanced by the presence of grazers in rockpools at natural herbivore density (+G) (appendix, fig. D.1 and see SIMPER, appendix, table E.1). The canopy alga *Himanthalia elongata* also had a higher percentage cover in low shore rockpools left at natural grazer density (+G) (appendix, fig. D.2 and SIMPER, appendix, table E.1). *Sargassum muticum* also proliferated in those pools (+G) but in lower abundance than in rockpools where herbivores were manipulated (-G) (appendix, fig. D.2). On the other hand, ephemeral species such as *Ulva intestinalis*, *Ceramium* spp., *Scytosiphon lomentaria*, the encrusting species *Ralfsia* spp. (appendix, fig. D.3) and canopy species, such as fucoids (*Fucus serratus*, *Fucus vesiculosus*, *Fucus spiralis*), *Sargassum muticum* (appendix, fig. D.2) colonised and grew in higher abundances in rockpools where herbivores were reduced (-G) (SIMPER, appendix, table E.1). Sand and stones tended to accumulate in rockpools with higher abundances of erect ephemeral and canopy algae where grazers were reduced (-G) in August and November 2003 (appendix, fig. D.1). Differences in species assemblage between the two grazer treatments

Table 4.4: PERMANOVA and Pair-wise *a posteriori* comparisons based on Bray-Curtis dissimilarity comparing assemblages during succession in rockpool habitat comparing differences between shore levels (Le: High, Mid, Low) and herbivore treatment (Gr: natural (+G) and reduced grazer (-G) density) at each sampling dates . Data were fourth-root transformed. ns: non significant; * * *: $P<0.001$; **: $P<0.01$; *: $P<0.05$.

		Nov 02			Feb 03			May 03			Aug 03			Nov 03		
Source	df	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Le	2	1109.52	1.13	ns	1318.46	1.15	ns	2145.40	1.90	ns	1967.51	1.56	ns	2460.46	2.17	*
Gr	1	2530.57	2.57	*	5391.76	4.71	* * *	7985.49	7.08	* * *	5512.21	4.36	* * *	6291.46	5.55	* * *
Le×Gr	2	382.55	0.39	ns	798.79	0.70	ns	1150.57	1.02	ns	1177.28	0.93	ns	1185.39	1.05	ns
Residual	18	985.51			1145.59			1127.57			1263.02			1133.06		

		Feb 04			May 04			Aug 04			Nov 04		
Source	df	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Le	2	2580.73	2.38	**	2019.99	1.52	ns	2306.36	1.87	*	2150.92	1.85	*
Gr	1	5354.97	4.94	* * *	1478.35	1.11	ns	5247.92	4.26	* * *	6093.30	5.23	* * *
Le×Gr	2	1080.93	1.00	ns	2619.83	1.97	*	1202.00	0.98	ns	1043.38	0.90	ns
Residual	18	1083.08			1329.66			1232.51			1164.53		

Pair-wise *a posteriori* comparisons

Nov 03			Feb 04			May 04								Aug 04			Nov 04		
Le			Le			Le (Gr)			Gr (Le)					Le			Le		
Groups	*t*	*P*	Groups	*t*	*P*	Levels	*t*	*P*	Groups	-G *t*	*P*	+G *t*	*P*	Groups	*t*	*P*	Groups	*t*	*P*
(High,Low)	1.68	*	(High,Low)	1.80	**	High	1.37	ns	(High,Low)	0.94	ns	1.77	*	(High,Low)	1.70	**	(High,Low)	1.63	*
(High,Mid)	1.15	ns	(High,Mid)	1.14	ns	Mid	0.30	*	(High,Mid)	0.11	ns	1.55	*	(High,Mid)	1.10	ns	(High,Mid)	1.10	ns
(Low,Mid)	1.05	ns	(Low,Mid)	1.25	ns	Low	1.24	ns	(Low,Mid)	0.19	ns	1.26	ns	(Low,Mid)	0.93	ns	(Low,Mid)	0.86	ns

(-G and +G) were also detected in the nMDS (fig. 4.3, Nov 04).

Species recruitment and distribution were significantly different between shore levels from November 2003 (PERMANOVA, table 4.4) particularly between the high and the low shore rockpools (see pairwise comparisons, table 4.4), with the mid shore pools having mixed transitory assemblages. Species contributing the most to the dissimilarities between shore levels (High, Mid, Low) were highlighted by the SIMPER procedure (appendix, table E.2). The calcareous species *Phymatolithon* spp. was more abundant in the high shore (fig. 4.5) and decreased in rockpools when going towards the low shore; whereas *Corallina* spp. percentage cover increased to become one of the dominant algae in the low shore rockpools (fig. 4.5 and SIMPER, appendix, table E.2). *Lithophyllum incrustans* was most abundant in low shore pools (appendix, fig. D.1 and SIMPER, appendix, table E.2). Similarly, fucoids, mainly *Fucus serratus*, were more abundant in the high shore rockpools, whereas the percentage cover of *Sargassum muticum* was highest in low shore pools (appendix, fig. D.2 and SIMPER, appendix, table E.2). The differences in algal community between the high and the low shore rockpools was also highlighted by the nMDS (see for example, fig. 4.3 for the last sampling date of November 2004).

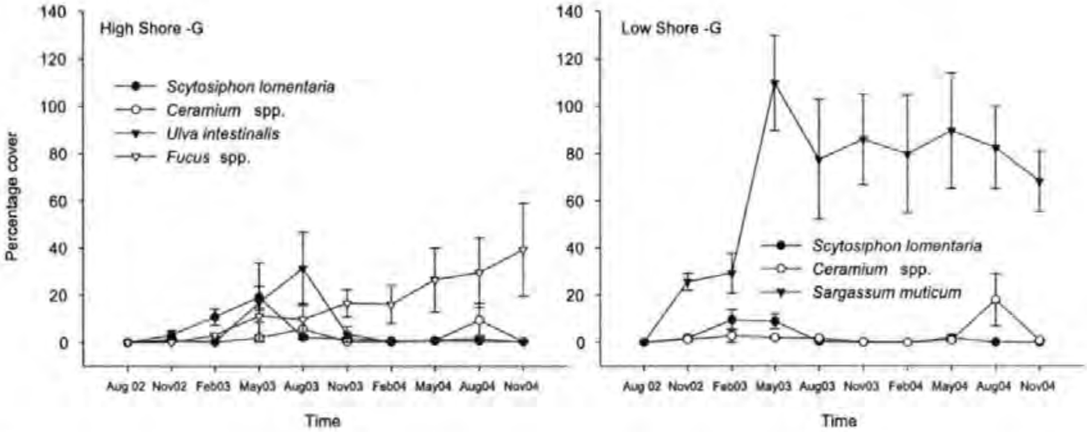

Figure 4.4: Exp 1: Succession in rockpools. Percentage cover of *Scytosiphon lomentaria*, *Ceramium* spp., *Ulva intestinalis* and *Fucus* spp. at the high shore level and *Scytosiphon lomentaria*, *Ceramium* spp. and *Sargassum muticum* at the low shore level during succession started in Summer 2002 in rockpools at reduced grazer density (-G). Data are mean of percentage cover (±SE) of 2 replicate 20×20cm quadrats averaged for each of the 4 replicate pools (n=4).

In rockpools at reduced grazer density (-G), ephemeral species colonised and grew in the cleared plots during the first months of the succession with a peak in spring 2003 (May 03) for *Scytosiphon lomentaria* and in summer 2003 (Aug 03) for *Ulva intestinalis* and *Ceramium* spp. (fig. 4.4). During the second spring and summer 2004, however, a peak in abundance was observed only for *Ceramium* spp. in August, with higher percentage cover than for the first summer peak (fig. 4.4). Remarkably, the invasive species *Sargassum muticum* recruited and developed from the start of the succession as an early coloniser in stark contrast to the other later coloniser canopy species, reaching a maxima of 40% cover from May 2003 in rockpools of the mid and 110% in those of the low shore at reduced herbivore density (-G) (fig. 4.4 and appendix, fig. D.2). During those first 9 months, its cover (increasing of 12.2% per months ±2.2 SE) was significantly higher in the low shore at reduced grazer density (-G) (fig. 4.4) as shown by significant Grazer×Shore level interaction (Anova, F=3.84, P<0.05; SNK). Percentage cover of perennial species, such as fucoids (*Fucus serratus*, *Fucus vesiculosus*, *Fucus spiralis*), *Sargassum muticum* (fig. 4.4, but see appendix, fig. D.2), *Ralfsia* spp. (appendix, fig. D.3), *Corallina* spp., *Lithophyllum incrustans* and *Phymatolithon* spp. (fig. 4.5, but see appendix fig. D.1) increased through time and became well established from November 2003.

During the first year (until August 2003), the exponential growth of *Phymatholiton* spp. (around 6.5% per months ±0.6 SE) was promoted by the presence of herbivores (Anova, F=31.09, P<0.001) and was higher in high shore pools (Anova, F=8.64, P<0.01) before reaching a plateau

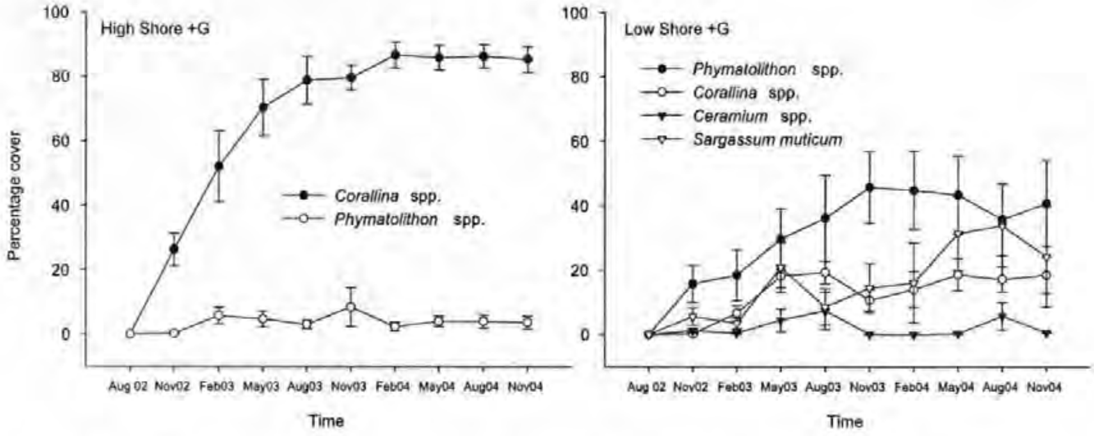

Figure 4.5: Exp 1: Succession in rockpools. Percentage cover of *Phymatolithon* spp. and *Corallina* spp. at the high shore level and *Phymatolithon* spp., *Corallina* spp., *Ceramium* spp. and *Sargassum muticum* at the low shore during succession started in Summer 2002 in rockpools at natural grazer density (+G). Data are mean of percentage cover (±SE) of 2 replicate 20×20cm quadrats averaged for each of the 4 replicate pools (n=4).

(fig. 4.5). Meanwhile, *Corallina* spp. cover (increasing of 1.6% per months ±0.3 SE) was significantly greater in the presence of herbivores (+G) in the low shore pools and highlighted by the interaction between Grazer×Shore level (Anova, F=6.33, P<0.01; SNK); it continued to increase steadily until the end of the experiment (fig. 4.5). In addition, the increase in abundance of *Sargassum muticum* had a significant positive relationship with increase of *Corallina* spp. in rockpools at natural herbivore density (Correlation: r=0.40, P<0.001) (fig. 4.5). The stabilisation of the assemblages in rockpools also appeared on the nMDS trajectories (fig. 4.6) from the 9^{th} month with seasonal patterns highlighted by the two groups formed by the spring and summer sampling dates and by the autumn and winter sampling dates.

In summary, herbivores promoted the establishment of grazer resistant species such as *Phymatholiton* spp. in the high shore rockpools, *Corallina* spp. and *Himanthalia elongata* in the low shore rockpools but prevented the establishment of *Ralfsia verrucosa*. The absence of consumers was beneficial to *Fucus serratus* in the high shore rockpools, *Sagassum muticum* in the low shore pools and to ephemeral species at all shore heights. In rockpools at reduced grazer pressure, early successional species were ephemeral species and *Sargassum muticum* and later colonists were the canopy species *Fucus* spp. and *Sargassum muticum*. However, in rockpools at natural herbivore density, there was no clear difference between early and later colonisers, such as *Phymatolithon* spp., *Corallina* spp., *Lithophyllum incrustans*, *Sargassum muticum* and *Himanthalia elongata*.

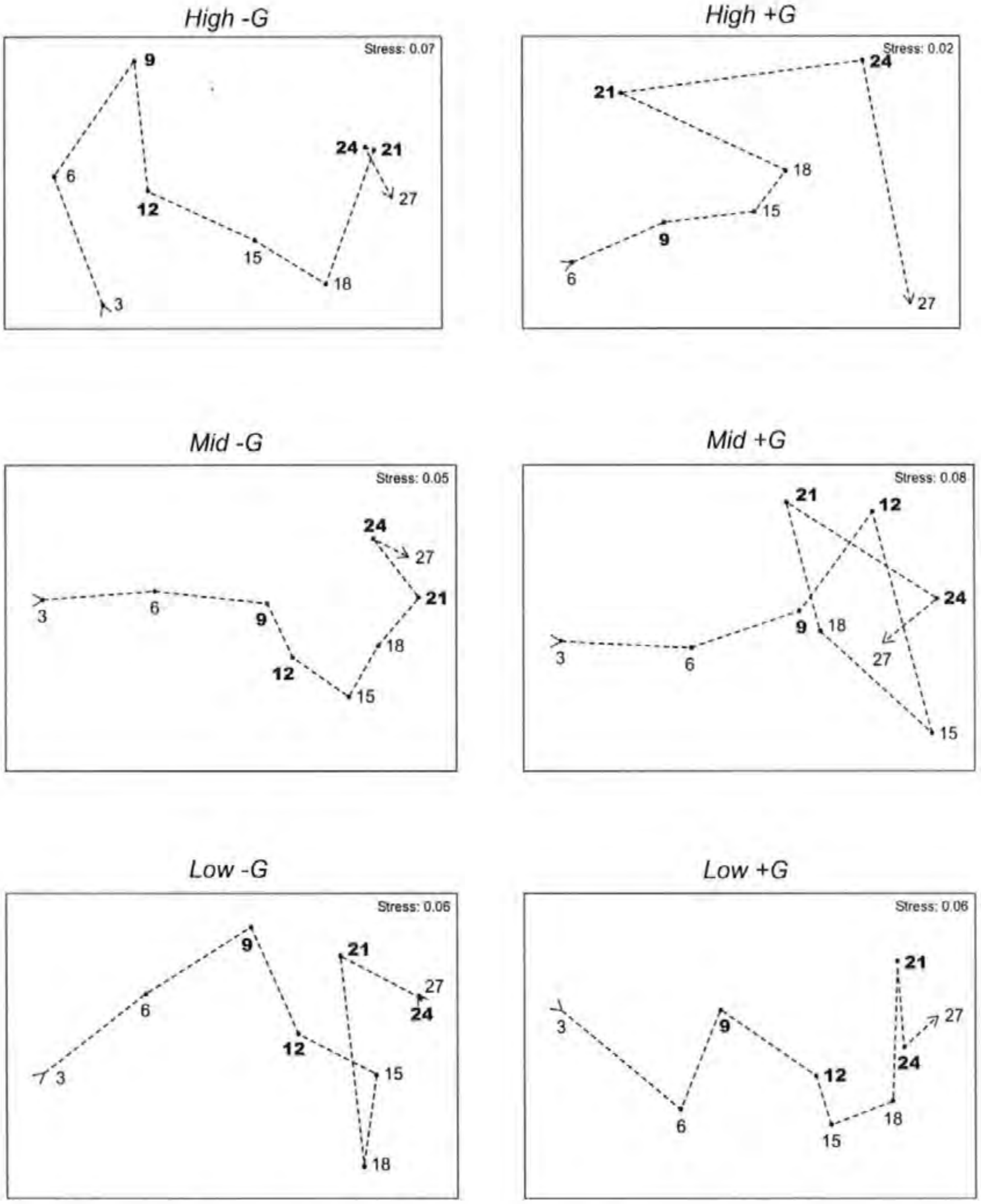

Figure 4.6: nMDS ordination of the algal percentage cover assemblages in rockpools for each factor: grazer (natural (+G) and reduced (-G) grazer density) and shore level at each of three shore levels (High, Mid, Low) as a function of time (n=4). Fictive time trajectories were overlaid between the sampling months of the experiment. Seasonality was observed with 2 groups corresponding to the autumn and winter months (3, 6, 15, 18, 27 months) and to the spring and summer months (9, 12, 21, 24 months in bold). High shore +G: outlier sampling dates of 3^{rd} and 12^{th} months were omitted for clarity of the results.

4.3.1.3 Succession: general patterns on emergent rock

Colonisation on emergent rock was significantly different between plots at natural (+G) and reduced (-G) grazer density from February 2003 until the end of the experiment in November 2004 (PERMANOVA, table 4.5). There was virtually no algal growth in the areas with grazers at all shore levels (appendix, fig. D.4, fig. D.5). Species contributing the most to the dissimilarities between grazer treatments (-G and +G) were highlighted by the SIMPER procedure (appendix, table E.4). Ephemeral species, such as *Ulva intestinalis*, *Porphyra* spp., the encrusting algae *Ralfsia verrucosa* (appendix, fig. D.4) and the fucoids, such as *Fucus serratus*, *Fucus vesiculosus*, *Fucus spiralis* (appendix, fig. D.5) were all found in higher abundances within plots where herbivores were removed (-G) (SIMPER, appendix, table E.4). In contrast, barnacle species, such as *Chthamalus* spp., *Semibalanus balanoides* and the lichen *Verrucaria* spp. had higher abundances in the plots left at natural grazer density (+G) (appendix, fig. D.6; SIMPER, appendix, table E.4). Differences in species assemblage between the two grazer treatments (-G and +G) were also detected in the nMDS (see for example, fig. 4.7 for the last sampling date of November 2004).

Table 4.5: PERMANOVA and Pair-wise *a posteriori* comparisons based on Bray-Curtis dissimilarity comparing assemblages during succession on emergent rock habitat comparing differences between shore levels (Le: High, Mid, Low) and herbivore treatment (Gr: natural (+G) and reduced (-G) grazer density) at each sampling dates. Data were fourth-root transformed. ns: non significant; * * *: $P<0.001$; **: $P<0.01$; *: $P<0.05$.

		Nov 02			Feb 03			May 03			Aug 03			Nov 03		
Source	df	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Le	2	198.60	1.10	ns	88.19	0.17	ns	1216.29	2.34	ns	1840.14	2.61	*	1430.56	2.54	*
Gr	1	10.51	0.06	ns	7742.55	15.10	* * *	12790.89	24.63	* * *	4927.71	6.99	* * *	6312.64	11.20	* * *
Le×Gr	2	67.64	0.37	ns	460.92	0.90	ns	1235.25	2.38	ns	1272.81	1.80	ns	967.88	1.72	ns
Residual	18	180.52			512.84			519.27			705.44		563.68			

		Feb 04			May 04			Aug 04			Nov 04		
Source	df	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Le	2	3237.40	3.70	* * *	1618.60	1.76	ns	2210.30	3.44	**	2481.79	2.97	**
Gr	1	6413.43	7.33	* * *	8665.35	9.44	* * *	5943.29	9.25	* * *	6141.78	7.34	* * *
Le×Gr	2	1165.75	1.33	ns	1406.50	1.53	ns	1676.93	2.61	*	976.49	1.17	ns
Residual	18	875.52			918.30			642.53			836.88		

Pair-wise *a posteriori* comparisons

Aug 03			Nov 03			Feb 04			Aug 04								Nov 04		
Le			Le			Le			Le (Gr)			Gr (Le)					Le		
Groups	*t*	*P*	Groups	*t*	*P*	Groups	*t*	*P*	Levels	*t*	*P*	Groups	-G *t*	*P*	+G *t*	*P*	Groups	*t*	*P*
(High,Low)	1.77	*	(High,Low)	1.48	ns	(High,Low)	1.50	ns	High	1.93	ns	(High,Low)	2.68	*	0.74	ns	(High,Low)	2.07	**
(High,Mid)	1.07	ns	(High,Mid)	0.67	ns	(High,Mid)	1.43	ns	Mid	0.98	*	(High,Mid)	0.95	ns	0.29	ns	(High,Mid)	1.04	ns
(Low,Mid)	1.20	ns	(Low,Mid)	1.34	ns	(Low,Mid)	1.95	**	Low	2.92	ns	(Low,Mid)	1.85	ns	1.03	ns	(Low,Mid)	1.18	ns

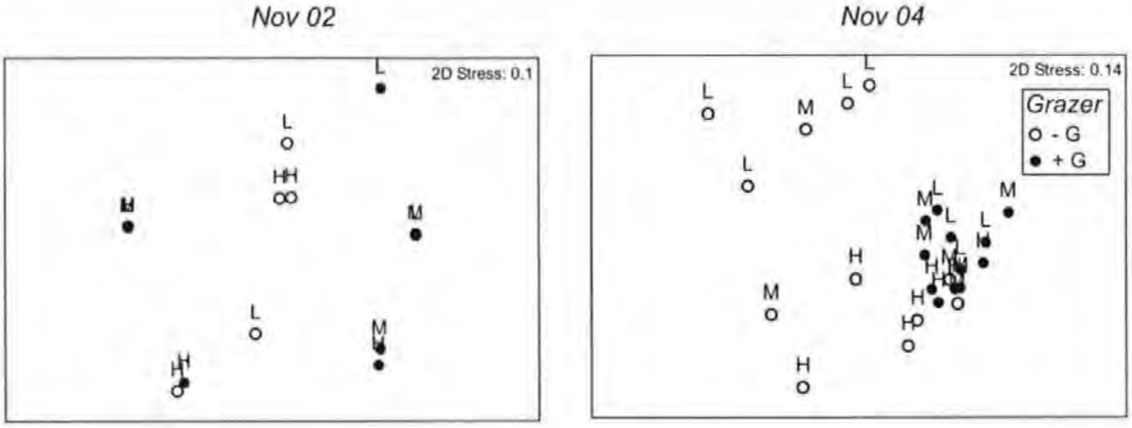

Figure 4.7: nMDS ordination of the algal percentage cover assemblages on emergent rock at natural (+G) and reduced (-G) grazer density at each of three shore levels (High, Mid, Low) at the beginning and the end of the experiment in November 2002 and 2004 (n=4). High shore plots were toward the bottom and low shore plots toward the top of the nMDS. Reduced grazer density community were grouped toward the left and natural herbivores density community on the right of the nMDS.

Trajectories of succession varied between shore levels essentially differing between the high and low shores (PERMANOVA, table 4.5) at the sampling dates of August 2003, August 2004 and November 2004 and also between mid and low shore in February 2004 (pairwise comparisons, table 4.5). In the high shore plots, the most abundant species were: *Verrucaria* spp. (appendix, fig. D.6; SIMPER, appendix, table E.3), *Fucus vesiculosus* and *Fucus spiralis* (appendix, fig. D.5; SIMPER, appendix, table E.3). Species that had their highest percentage cover in low shore plots were encrusting algae, such as *Ralfsia verrucosa* , *Hildenbrandia rubra*, *Phymatolithon* spp., the ephemeral algae *Ulva intestinalis* (appendix, fig. D.4), the fucoid *Fucus serratus* (appendix, fig. D.5) and *Semibalanus balanoides* (appendix, fig. D.6) (SIMPER, appendix, table E.3). The differences in algal community between the high and the low shore was also highlighted in the nMDS (see for example, fig. 4.7 for the last sampling date of November 2004). *Chthamalus* spp., however, occurred in similar abundances at all shore heights (appendix, fig. D.6).

In plots at reduced herbivore density (-G), colonisation started with ephemeral species such as *Ulva intestinalis* and *Porphyra* spp. which reached a first peak in spring-summer 2003 (fig. 4.8). Following the appearance of ephemeral algae, fucoids developed in plots where grazers were removed (-G) (fig. 4.8). It is worth noting, that *Fucus spiralis* appeared on mid shore in plots at reduced grazer density (-G) which was lower on the shore than its natural occurrence (appendix, fig. D.5) showing the opportunistic character of this species. During the second spring-summer in

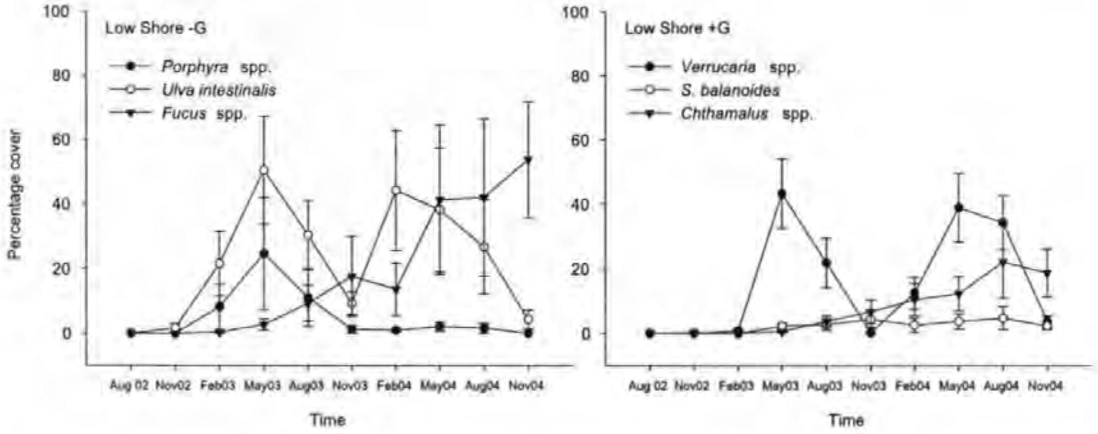

Figure 4.8: Exp 1: Succession on emergent rock. Percentage cover of *Ulva intestinalis* and *Porphyra spp.* and the total cover of *Fucus* spp. at reduced grazer density (-G) and *Semibalanus balanoides*, *Chthamalus* spp. and *Verrucaria spp.* at natural grazer density (+G) during succession started in Summer 2002 on emergent rock at low shore level. Data are mean of percentage cover (±SE) of 2 replicate 20×20cm quadrats averaged for each of the 4 replicate plots (n=4).

2004, the ephemeral peak was only composed of *Ulva intestinalis* (fig. 4.8).

In plots left at natural density (+G), *Verrucaria* spp. varied seasonally with peaks from the end of the winter to the end of the summer for both years 2003 and 2004 with higher abundances in 2004 (fig. 4.8). Barnacle recruitment occurred for *Chthamalus* spp. between May and August 2003 and again between May and August 2004 (fig. 4.8). *Semibalanus balanoides* recruited in early spring 2003, but showed a low recruitment in spring 2004 (fig. 4.8). The nMDS trajectories also showed seasonal patterns on emergent rock (fig. 4.9) from the 9^{th} month of succession, with patterns being highlighted by the two groups formed from spring and summer sampling dates and by the autumn and winter sampling dates.

In summary, herbivores prevented the establishment of all algae on emergent rock. Only *Verrucaria* spp. and barnacles settled, with *Chthamalus* spp. at all shore levels and *Semibalanus balanoides* at mid and low shore. The removal of consumers promoted ephemeral species, such as *Ulva intestinalis* and *Porphyra* spp. which showed higher abundances in the low shore. Abundance of *Fucus* spp. reflected zonation patterns: *Fucus vesiculosus* (high shore), *Fucus spiralis* (high and mid shore) and *Fucus serratus* (low shore). No differences were observed during succession in areas where herbivores were present between early and later colonisers. However, in the absence of consumer pressure, ephemeral species recruited as early colonisers and fucoids recruited as later successional species.

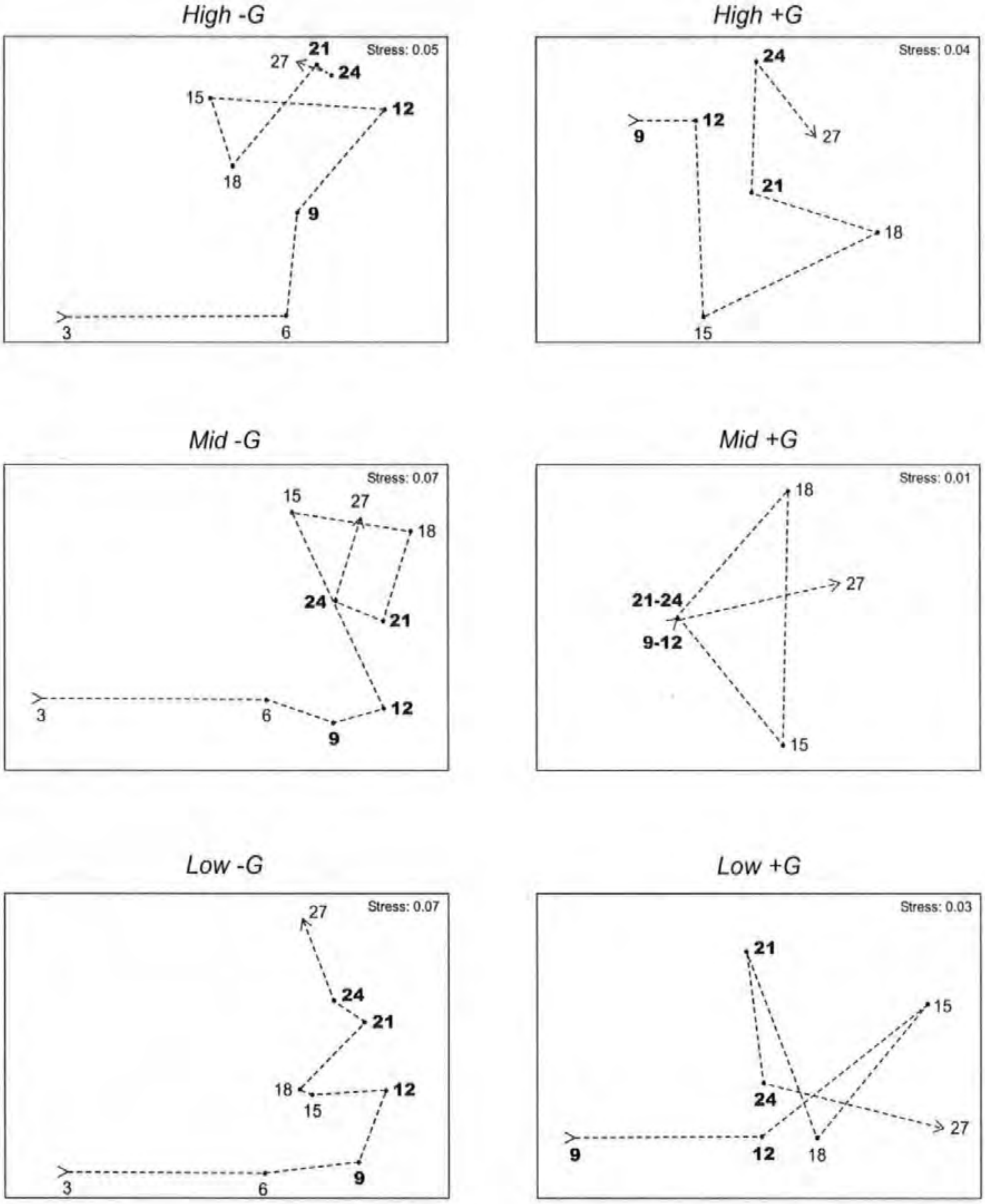

Figure 4.9: nMDS ordination of the algal percentage cover assemblages on emergent rock for each factor: grazer (natural (+G) and reduced (-G) grazer density) and shore level at each of three shore levels (High, Mid, Low) as a function of time (n=4). Fictive time trajectories were overlaid between the sampling months of the experiments. Seasonality was observed with 2 groups corresponding to the autumn and winter months (3, 6, 15, 18, 27 months) and to the spring and summer months (9, 12, 21, 24 months in bold in subset). +G: sampling date of the 3^{rd} and 6^{th} months were relatively close but distant from other dates and were omitted for clarity of the results.

4.3.2 Experiment 2. Succession: role of timing of initiation

4.3.2.1 Effect of timing of initiation on succession in rockpools

Communities created at different time of the year (Aug 2002 and Feb 2003)- in order to investigate differences in succession owing to differences in timing of species recruitment - were significantly different from the beginning until the 21^{st} month of succession when assemblages from Aug02 and Feb03 plots converged (PERMANOVA, table 4.6). After 3 months of succession, early colonisers, which were mostly ephemeral species were higher in abundance in plots initiated in Feb03 (appendix, table E.5). This was the result of the ephemeral spring bloom, since the third month of succession corresponded with the sampling date of May 2003, compared to plots cleared in Aug02 sampled in November 2002 when ephemeral species were usually at their lowest abundance (appendix, fig. D.7 A). Therefore, SIMPER results were only considered for perennial species. However, when the analysis was done between sampling dates, assemblages from Aug02 and Feb03 also converged from the second year of the experiment (from May 2004, PERMANOVA, table 4.7) excluding any confounding effect between timing and seasons on the successional trajectories.

After 3 months, most of the perennial species, such as *Sargassum muticum* (appendix, fig. D.7 B), *Phymatholiton* spp., *Petrocelis*, *Ralfsia verrucosa* (appendix, fig. D.8 B) recruited during

Table 4.6: PERMANOVA and Pair-wise *a posteriori* comparisons based on Bray-Curtis dissimilarity comparing assemblages during succession in rockpool habitat between shore levels (Le: High, Mid, Low) and initiation times (In: succession initiated in August 2002 and February 2003) after 3, 9, 15, 21 months from the start of the colonization. Data were fourth-root transformed. ns: non significant; $***$: $P<0.001$; $**$: $P<0.01$; $*$: $P<0.05$.

		3 months			9 months			15 months			21 months		
Source	df	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Le	2	1035.35	0.85	ns	2195.25	2.12	**	2348.99	2.44	***	2218.75	1.28	ns
In	1	13542.22	11.15	***	4454.26	4.29	***	4082.69	4.24	***	3261.17	1.88	ns
Le×In	2	1520.94	1.25	ns	1027.45	0.99	ns	1092.41	1.13	ns	1066.86	0.62	ns
Residual	18	1214.34			1037.84			963.78			1733.48		

Pair-wise *a posteriori* comparisons:
test among level of the factor Le

9 months			15 months		
Le			Le		
Groups	*t*	*P*	Groups	*t*	*P*
(High,Low)	1.68	**	(High,Low)	1.99	***
(High,Mid)	1.03	ns	(High,Mid)	0.98	ns
(Low,Mid)	1.28	ns	(Low,Mid)	1.18	ns

Table 4.7: PERMANOVA and Pair-wise *a posteriori* comparisons based on Bray-Curtis dissimilarity comparing assemblages during succession in rockpool habitat between shore levels (Le: High, Mid, Low) and initiation times (In: succession initiated in August 2002 and February 2003) for the sampling dates of May and November 2003 and 2004. Data were fourth-root transformed. ns: non significant; ∗∗∗: $P<0.001$; ∗∗: $P<0.01$; ∗: $P<0.05$.

		May 03			Nov 03			May 04			Nov 04		
Source	df	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Le	2	1723.05	1.35	ns	2682.71	2.39	∗∗	2083.53	1.98	∗∗	1558.72	1.37	ns
In	1	16242.25	12.73	∗∗∗	4029.43	3.59	∗∗∗	1753.37	1.67	ns	869.44	0.77	ns
Le×In	2	1765.80	1.38	ns	996.27	0.89	ns	930.57	0.89	ns	618.21	0.54	ns
Residual	18	1275.83			1122.98			1050.17			1134.53		

Pair-wise *a posteriori* comparisons:
test among level of the factor Le

Nov 03			May 04		
Le			Le		
Groups	*t*	*P*	Groups	*t*	*P*
(High,Low)	1.92	∗∗∗	(High,Low)	1.78	∗∗∗
(High,Mid)	1.08	ns	(High,Mid)	1.08	ns
(Low,Mid)	1.27	ns	(Low,Mid)	1.25	ns

summer 2002 and were in higher abundance in plots cleared in Aug02 compared to the ones cleared in Feb03 except for *Lithophyllum incrustans* (SIMPER, appendix, table E.5).

After 9 months, both of the plots, cleared in Aug 02 and Feb 03, had gone through one summer. Some of the perennial species, such as *Corallina* spp., *Lithophyllum incrustans* and *Petrocelis* (appendix, fig. D.8) had equal abundances in plots cleared at different times (Aug02 and Feb03) (SIMPER, appendix, table E.5). Other perennial algal abundances, such as *Ralfsia verrucosa*, *Phymatolithon* spp. (appendix, fig. D.8 B) were higher in plots cleared in Feb03 (SIMPER, appendix, table E.5). Finally, some perennial species were still in higher proportion in plots initiated in Aug02 (e.g. *Sargassum muticum*, *Fucus serratus* (appendix, fig. D.7 B), *Gelidium* spp., *Palmaria palmata*, *Chondrus crispus*; SIMPER, appendix, table E.5).

After 15 months, an increasing number of perennial species had equal abundances such as *Sargassum muticum* (appendix, fig. D.7 B), *Phymatolithon* spp., *Corallina* spp. (appendix, fig. D.8) (SIMPER, appendix, table E.5). However, several species had higher abundances in plots cleared in Feb03 than in Aug02, such as *Ralfsia verrucosa*, *Petrocelis*, *Lithophyllum incrustans* (appendix, fig. D.8), *Fucus vesiculosus*, *Fucus serratus* (appendix, fig. D.7 B) (SIMPER, appendix, table E.5). In contrast, *Fucus spiralis*, *Mesophyllum liquenoides*, and *Gelidium* spp. all had a higher percentage cover in plots cleared in Aug02 (SIMPER, appendix, table E.5).

At the end of the experiment after 21 months, the majority of the perennial species had similar

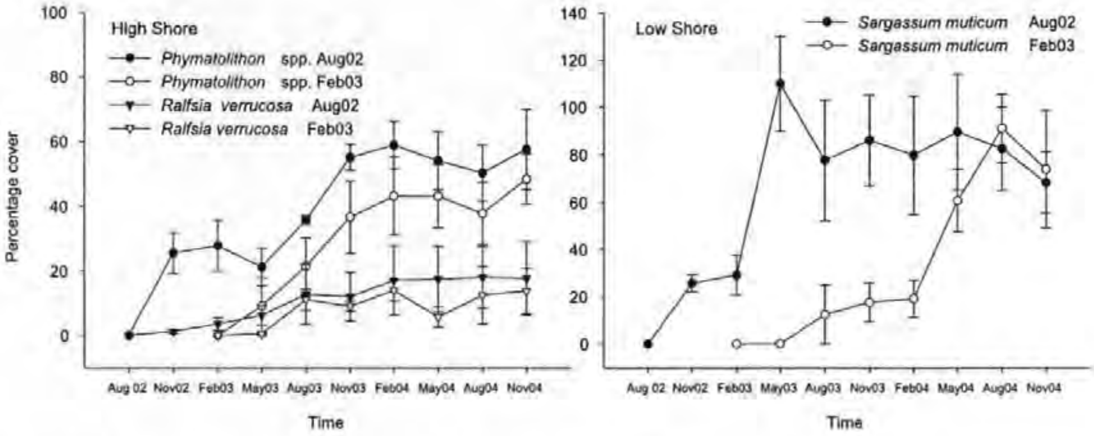

Figure 4.10: Exp2. Initiation timing in rockpools. Percentage cover of *Ralfsia verrucosa* and *Phymatolithon* spp. at the high shore level and *Sargassum muticum* at the low shore level during succession started in August 2002 (black symbols) and February 2003 (white symbols) in rockpools. All plots were at reduced grazer density. Data are mean of percentage cover (±SE) of 2 replicate 20×20cm quadrats averaged for each of the 4 replicate pools (n=4).

abundances regardless of the time of clearance such as *Sargassum muticum* (appendix, fig. D.7 B), *Ralfsia verrucosa*, *Phymatolithon* spp., *Corallina* spp., *Lithophyllum incrustans* (appendix, fig. D.8), *Gelidium* spp., *Mesophyllum liquenoides*, *Chondrus crispus* (SIMPER, appendix, table E.5). Only *Fucus vesiculosus* and *Osmundea pinnatifida* had higher proportions in plots cleared in Feb03 (SIMPER, appendix, table E.5). *Fucus spiralis* was only present in plots cleared in Aug02 (SIMPER, appendix, table E.5) and *Petrocelis*, *Himanthalia elongata* and Fucus serratus were also found with a higher percentage cover (SIMPER, appendix, table E.5) in those plots.

Trajectories of succession initiated in August 2002 and February 2003, converged after 21 months (PERMANOVA, 21 months, table 4.6). Despite differences in timing of recruitment of new individuals and proliferation of existing plants, abundance of *Sargassum muticum* became similar by the end of the experiment (21 months), (fig. 4.10). In the plots cleared in February 2003, the recruitment of *Sargassum muticum* juveniles occurred in the second summer of the succession in 2003 and adult development in summer 2004 (fig. 4.10). However, in August 2002 plots, *Sargassum muticum* had slightly lower abundances than the plots cleared in February 2003 (fig. 4.10). This was also the case for *Corallina* spp. (appendix, fig. D.8 A), *Phymatolithon* spp., *Ralfsia verrucosa* (fig. 4.10) by the end of the experiment in November 2004. After a delay due to the different clearance times (Aug02 and Feb03), their abundances were similar towards the end of the experiment and were only a little lower in plots initiated in February 2003 (fig. 4.10).

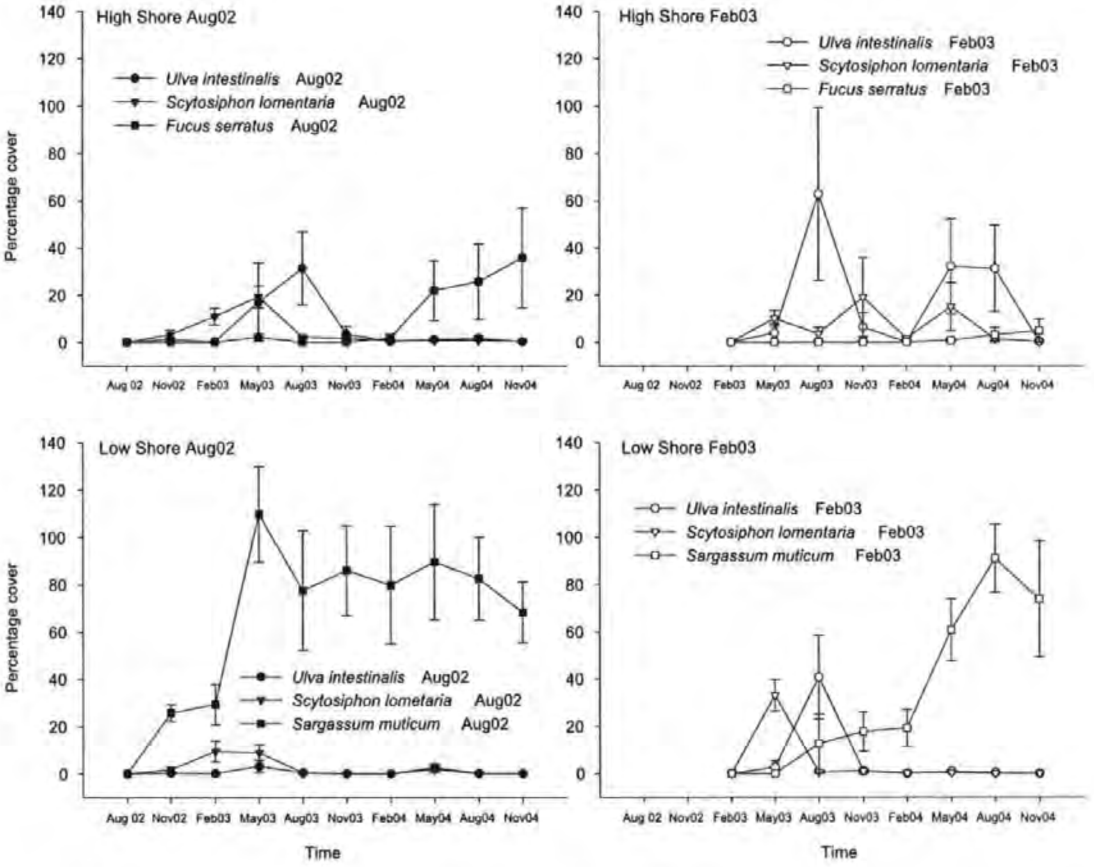

Figure 4.11: Exp2. Initiation timing in rockpools. Percentage cover of ephemeral species: *Ulva intestinalis*, *Scytosiphon lomentaria* and canopy species: *Fucus serratus* and *Sargassum muticum* during succession started in August 2002 (black symbols) and February 2003 (white symbols) in rockpools at high and low shore levels. All plots were at reduced grazer density. Data are mean of percentage cover (±SE) of 2 replicate 20×20cm quadrats averaged for each of the 4 replicate pools (n=4).

Ephemeral species showed seasonal patterns with peaks in spring-summer for both trajectories (Aug02 and Feb03) with higher abundance in plots where succession was initiated in February 2003 (fig. 4.11). Two particular cases appeared with *Scytosiphon lomentaria* and *Ulva intestinalis*: in the high shore rockpools, during the second summer, a peak of these species was observed in plots cleared in Feb03 (fig. 4.11 A) from where *Fucus serratus* was in low abundance (fig. 4.11 B; SIMPER, appendix, table E.5). On the contrary, the peak of *Scytosiphon lomentaria* and *Ulva intestinalis* was not recorded at the same time of year in plots cleared in Aug02 (fig. 4.11), while *Fucus serratus* was one of the dominant canopy species at this shore level (fig. 4.11). In the low shore rockpools, during the first spring-summer 2003, a peak of *Scytosiphon lomentaria* and *Ulva intestinalis* was observed in plots cleared in Feb03 while *Sargassum muticum* was only in a juvenile stage (fig. 4.11); this did not occur in plots cleared in Aug02 where *Sargassum muticum* was already at its adult stage (fig. 4.11). However, during the second spring-summer 2004, no peak of *Scytosiphon lomentaria* and *Ulva intestinalis* was recorded in both plots cleared in Feb03 and Aug02, where *Sargassum muticum* had reached its adult stage (fig. 4.11).

Species distribution differed significantly between high and low shore rockpools (PERMANOVA, table 4.6) as found in Experiment 1 (see General Pattern of Succession in rockpools for details).

4.3.2.2 Effect of timing of initiation on succession on emergent rock

Species distributions differed significantly between high and low shore emergent rock plots through the whole succession; differences were also apparent between the mid and low shore levels after 15 months of succession (PERMANOVA, table 4.8) as in Exp1. (General Patterns of Succession on emergent rock).

As in rockpools, algal assemblages on emergent rock were significantly different in plots cleared in Aug02 and Feb03 until the 21^{st} month of succession where they converged (PERMANOVA, table 4.8). The abundance of early colonising ephemeral species were influenced by seasonal patterns throughout the shore. For example, blooms of *Ulva intestinalis* and *Scytosiphon lomentaria* were observed in spring and summer (fig. 4.12, A); seasonal variation of *Verrucaria* spp. with low abundances during autumn were recorded (appendix, fig. D.9, B). Analysis done between time since succession was initiated (3, 9, 15, 21 months) instead of sampling dates, this implied comparison between assemblages sampled in autumn with assemblages sampled in spring (see material and methods). Therefore, comparing ephemeral spring blooms with autumn die off (e.g. analysis at 3 months after clearance compared the November 2002 sampling date (Aug02 plots) with May 2003 sampling date (Feb03 plots)) which resulted in high differences in abundances between plots initiated in Aug02 and Feb03 (SIMPER, appendix, table E.6 and fig. 4.12, A). Thus, only perennial species were considered in the results of the SIMPER analysis. Additional analyses were done between sampling dates and comparing the same seasons but with different length of time since the initiation of the succession. Convergence of the successional trajectories (Aug02 and Feb03) was also evidenced from May 2004 (PERMANOVA, table 4.9) excluding any confounding effect between time and season.

After 9 months, perennial species, such as *Ralfsia verrucosa* (appendix, fig. D.9 B), *Fucus*

Table 4.8: PERMANOVA and Pair-wise *a posteriori* comparisons based on Bray-Curtis dissimilarity comparing assemblages during succession on emergent rock habitat between shore levels (Le: High, Mid, Low) and initiation times (In: succession initiated in August 2002 (Aug02) and February 2003 (Feb03)) after 3, 9, 15, 21 months from the start of the colonization. Data were fourth-root transformed. ns: non significant; * * *: $P<0.001$; **: $P<0.01$; *: $P<0.05$.

		3 months			9 months			15 months			21 months		
Source	df	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Le	2	1735.14	5.38	**	3031.69	4.33	**	4380.37	4.31	***	3737.60	2.84	**
In	1	8940.69	27.71	***	7640.83	10.92	***	5163.32	5.09	**	2730.99	2.08	ns
Le×In	2	1701.60	5.27	**	964.28	1.38	ns	476.87	0.47	ns	628.24	0.48	ns
Residual	18	322.67			699.53			1015.17			1314.74		

Pair-wise *a posteriori* comparisons: test among the interaction Le×In and the level of the factor Le

3 months								9 months			15 months			21 months		
Le (In)			In (Le)					Le			Le			Le		
Levels	*t*	*P*	Groups	Aug02 *t*	*P*	Feb03 *t*	*P*	Groups	*t*	*P*	Groups	*t*	*P*	Groups	*t*	*P*
High	3.94	**	(High,Low)	1.11	ns	4.27	*	(High,Low)	2.45	***	(High,Low)	2.26	**	(High,Low)	2.40	***
Mid	2.54	*	(High,Mid)	0.29	ns	0.65	ns	(High,Mid)	0.72	ns	(High,Mid)	1.05	ns	(High,Mid)	0.77	ns
Low	4.63	*	(Low,Mid)	0.50	ns	2.60	ns	(Low,Mid)	1.70	ns	(Low, Mid)	2.09	**	(Low,Mid)	1.58	*

Table 4.9: PERMANOVA and Pair-wise *a posteriori* comparisons based on Bray-Curtis dissimilarity comparing assemblages during succession on emergent rock habitat between shore levels (Le: High, Mid, Low) and initiation times (In: succession initiated in August 2002 (Aug02) and February 2003 (Feb03)) for the sampling dates of May and November 2003 and 2004. Data were fourth-root transformed. ns: non significant; * * *: $P<0.001$; **: $P<0.01$; *: $P<0.05$.

		May 03			Nov 03			May 04			Nov 04		
Source	df	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Le	2	5651.84	8.01	***	3690.85	5.44	***	4475.99	3.14	*	4592.00	4.03	**
In	1	3759.47	5.32	*	4004.78	5.90	**	1317.88	0.93	ns	694.27	0.61	ns
Le×In	2	-15.45	-0.02	ns	393.37	0.58	ns	1264.05	0.89	ns	375.52	0.33	ns
Residual	18	678.35			678.35			1424.02			1140.33		

Pair-wise *a posteriori* comparisons: test among the level of the factor Le

May 03			Nov 03			May 04			Nov 04		
Groups	*t*	*P*	Groups	*t*	*P*	Groups	*t*	*P*	Groups	*t*	*P*
(High,Low)	4.02	**	(High,Low)	2.81	***	(High,Low)	2.44	**	(High,Low)	2.83	***
(High,Mid)	0.96	ns	(High,Mid)	1.12	ns	(High,Mid)	0.80	ns	(High,Mid)	0.55	ns
(Low,Mid)	2.59	*	(Low,Mid)	2.18	**	(Low, Mid)	1.71	*	(Low,Mid)	2.26	**

spp. (too young to be identified, fig. 4.12 B) and adults of *Chthamalus* spp. (appendix, fig. D.9 A) - that had recruited during the spring and summer 2003 - were in higher abundances in plots cleared in Feb03 than in Aug02 (SIMPER, appendix, table E.6). At this time, Feb03 plots had already experienced a high period of recruitment (spring and summer 2003) unlike the Aug02 cleared plots.

After 15 months, perennial species that had higher abundances in the plots cleared in Feb03

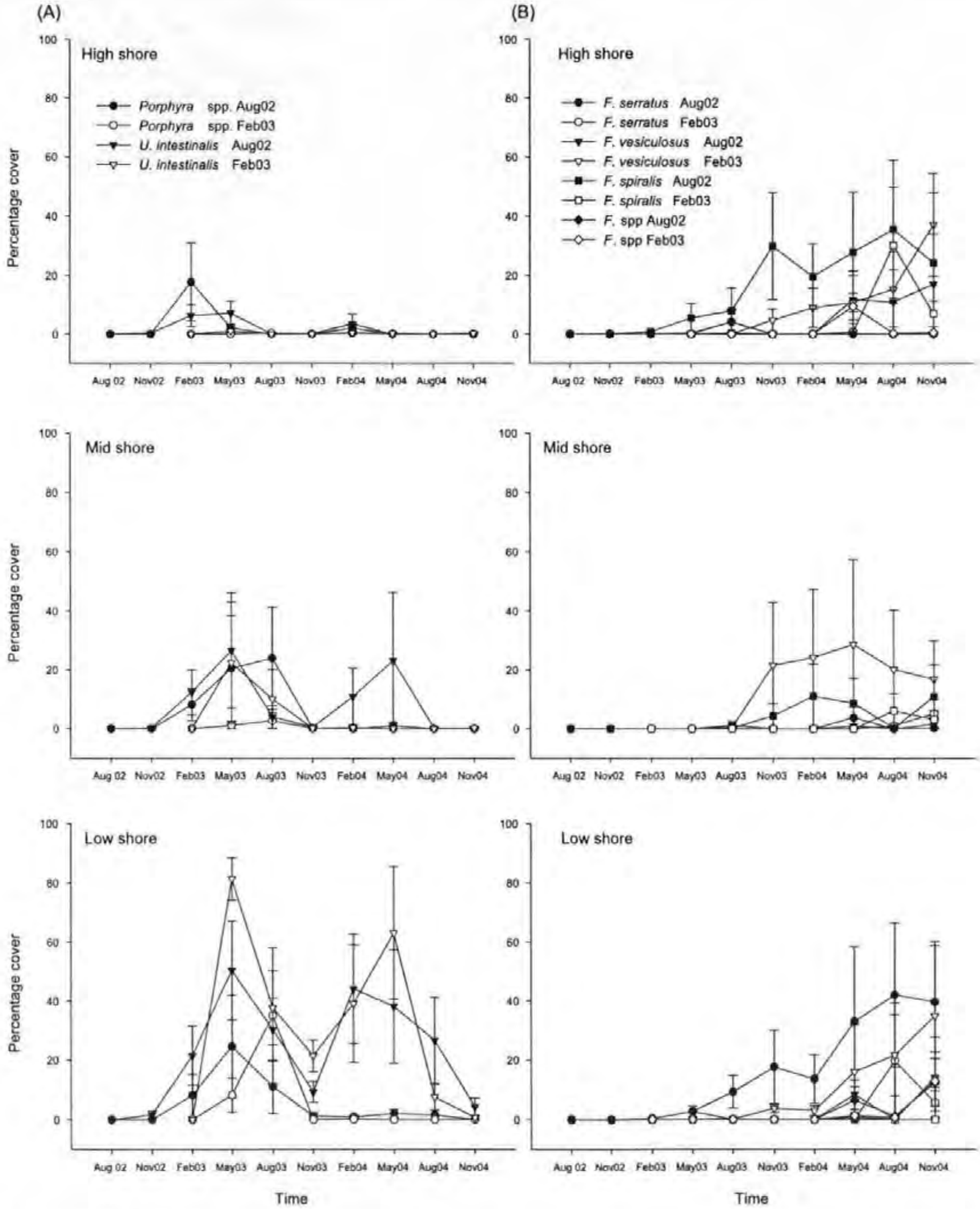

Figure 4.12: Exp2. Initiation timing on emergent rock. Percentage cover of ephemeral (A): Porphyra spp., Ulva intestinalis and canopy species (B): *Fucus serratus*, *Fucus vesiculosus*, *Fucus spiralis* during succession started in August 2002 (black symbols) and February 2003 (white symbols) on emergent rock at each of three shore levels: High, Mid and Low shore. All plots were at reduced grazer density. Data are mean of percentage cover (±SE) of 2 replicate 20×20cm quadrats averaged for each of the 4 replicate plots (n=4).

than Aug02 were: *Chthamalus* spp. juveniles, which were recruiting at the time (15 months for Feb03 plots corresponding at May 2004), young *Fucus* spp. and *Fucus vesiculosus* (fig. 4.12 B) (SIMPER, appendix, table E.6). Whereas, in plots cleared in Aug02, *Ralfsia verrucosa* (appendix, fig. D.9 B), *Fucus spiralis* and *Chthamalus* spp. adults (from summer 2003 colonisation, appendix, fig. D.9 A) were more abundant (SIMPER, appendix, table E.6).

After 21 months of succession, some perennial species had similar abundances, such as *Ralfsia verrucosa*, *Chthamalus* spp. juveniles, *Semibalanus balanoides* and also similar bare rock (appendix, fig. D.9, SIMPER, appendix, table E.6). However, for some species there was a higher percentage cover in plots cleared in Aug02 (e.g. *Fucus serratus*, *Fucus spiralis*, fig. 4.12 B) whilst others had higher abundances in plots cleared in Feb03 (e.g. *Chthamalus* spp. adults, appendix, fig. D.9 A and *Fucus vesiculosus*, fig. 4.12 B) (see SIMPER, appendix, table E.6).

The general trajectory and pattern of succession were similar in plots initiated in Aug02 and Feb03 on emergent rock for the barnacles. For example, *Chthamalus* spp. recruited in both plots (Aug02 and Feb03) in May 2003 and 2004 to reach similar abundances at the end of the experiment in November 2004 (fig. 4.13). Similar trajectories were also found for the lichens *Verrucaria* spp., showing the same seasonality irrespective of whether cleared in Aug02 or Feb03 (fig. 4.13). For *Ralfsia verrucosa*, although colonisation only occurred from November 2003 in the plots initiated in Feb03, its abundance was similar to the plots cleared in Aug02 by November 2004 (appendix, fig. D.9 B).

Markedly different trends in ephemeral species between the two initiation times (Aug02 and Feb03) were apparent at the different shore levels. In plots cleared in Aug02, at all shore levels, a *Porphyra* spp. peak was only recorded during the first spring-summer 2003 but not in the second one in 2004 (fig. 4.12 A) by which time fucoid canopy was well developed (fig. 4.12 B). In contrast, in plots cleared in Feb03, a *Porphyra* spp. peak was also observed during the first spring-summer 2003, but only on the low shore and with a higher percentage cover than in Aug02 plots (fig. 4.12 A). On the high shore, *Ulva intestinalis* was recorded in low abundance during the first spring-summer 2003 only in Aug02 plots (fig. 4.12 A) where *Fucus spiralis* canopy cover had became dominant from the winter 2003 (fig. 4.12 B). On the mid shore, a peak of *Ulva intestinalis* was observed during both spring-summer 2003 and 2004 (fig. 4.12 A) in Aug02 plots. However, no peak was recorded in spring-summer 2004 in the Feb03 plots where *Fucus vesiculosus* had become well established (fig. 4.12 B) since the previous autumn (November 2003). In the low shore, *Ulva intestinalis* peaks were observed in both spring-summer 2003 and 2004 for both set of plots (Aug02 and Feb03), with higher abundances in the Feb03 plots (fig. 4.12 A). Meanwhile, *Fucus serratus* established only in Aug02 plots on the low shore to reach its highest percentage cover in spring-summer 2004 (fig. 4.12 B).

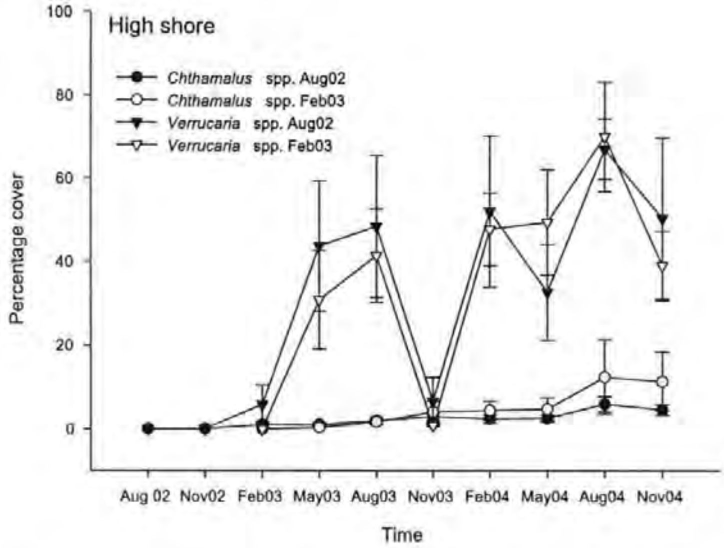

Figure 4.13: Exp2. Initiation timing on emergent rock. Percentage cover of *Chthamalus* spp. and the lichens *Verrucaria* spp. during succession started in August 2002 (black symbols) and February 2003 (white symbols) on emergent rock at the high shore level at reduced grazer density (-G). Data are mean of percentage cover (±SE) of 2 replicate 20×20cm quadrats averaged for each of the 4 replicate plots (n=4).

4.3.3 Experiment 3. Role of ephemeral and perennial species in later stages of succession

4.3.3.1 Procedural control for manipulation

The removal of ephemeral and perennial species using forceps and scalpel did not have any effect on macroalgal assemblages as no differences were found between plots unmanipulated and plots where algae being manipulated in order to mimic removal after one year (ANOSIM: *R*=-0.032, p>5%).

4.3.3.2 Role of ephemeral species during late succession in rockpools

Table 4.10: PERMANOVA and Pair-wise *a posteriori* comparisons based on Bray-Curtis dissimilarity comparing assemblages of perennial species during succession in rockpools between shore levels (Le: High, Mid, Low), herbivore treatments (Gr: natural (+G) and reduced (-G) grazer density) and manipulation treatments (Tr: removal of annual species (-A) and unmanipulated control plots (C)). Data were fourth-root transformed. ns: non significant; $***$: $P<0.001$; $**$: $P<0.01$; $*$: $P<0.05$.

		Aug 03			Nov 03			Feb 04		
Source	df	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Le	2	2301.55	2.85	***	2664.31	3.14	**	3163.79	3.77	***
Gr	1	6769.24	8.39	***	8723.15	10.28	***	8074.45	9.62	***
Tr	1	1577.38	1.96	ns	731.72	0.86	ns	869.03	1.04	ns
Le×Gr	2	935.66	1.19	ns	458.23	0.54	ns	1006.17	1.20	ns
Le×Tr	2	582.76	0.72	ns	488.23	0.58	ns	564.35	0.67	ns
Gr×Tr	1	432.85	0.54	ns	102.39	0.12	ns	395.33	0.47	ns
Le×Gr×Tr	2	286.02	0.35	ns	576.99	0.68	ns	236.32	0.28	ns
Residual	36	806.70			848.51			839.12		

		May 04			Aug 04			Nov 04		
Source	df	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Le	2	2858.43	3.31	***	3002.38	3.48	***	1655.19	1.99	*
Gr	1	10438.23	12.08	***	747.58	0.87	ns	1806.64	2.17	*
Tr	1	606.12	0.70	ns	662.21	0.77	ns	405.16	0.49	ns
Le×Gr	2	910.83	1.05	ns	935.01	1.09	ns	3424.55	4.12	***
Le×Tr	2	437.01	0.51	ns	1544.08	1.79	ns	2171.62	2.61	**
Gr×Tr	1	134.26	0.16	ns	9180.97	10.65	***	3059.93	3.68	**
Le×Gr×Tr	2	345.47	0.40	ns	1584.61	1.84	ns	931.23	1.12	ns
Residual	36	864.34			861.69			832.19		

Pair-wise *a posteriori* comparisons:
test among levels of the factor Tr

Aug 04			Nov 04		
Gr (Tr)			Le (Tr)		
Grazer	*t*	*P*	Levels	*t*	*P*
-G	1.79	*	High	1.33	ns
+G	2.50	***	Mid	0.29	ns
			Low	1.63	*

The removal of ephemeral species had little effect on perennial species in rockpools. An interaction between grazer treatments (rockpools at natural (+G) and reduced (-G) grazer density) and removal manipulation treatments (removal of ephemeral species (manip) and unmanipulated plots (control)) was found only for the last two sampling dates of August and November 2004 (PERMANOVA, table 4.10). However, no clear discriminating perennial species were identified by the SIMPER procedure (SIMPER, appendix, table E.7) to distinguish between manipulation treatments in the presence or absence of ephemeral algae .

For example, the successional trajectories of *Lithophyllum incrustans*, *Phymatolithon* spp., *Ralfsia verrucosa* (appendix, fig. D.10), *Corallina* spp., *Gelidium* spp. (appendix, fig. D.11), *Sargassum muticum*, *Fucus serratus* and *Fucus spiralis* (appendix, fig.D.12) did not show different trends in presence (control) or absence (manip) of ephemeral species.

4.3.3.3 Role of ephemeral species during late succession on emergent rock

The absence of ephemeral algae enhanced some perennial species; this was particularly the case in plots with reduced herbivore density (-G) and in mid and low shore plots (PERMANOVA and pairwise comparisons, table 4.11) corresponding to plots where ephemeral algae were found in higher abundance (see Exp 1. General Pattern of Succession on emergent rock, appendix, fig. D.4). For example, *Chthamalus* spp., which had a similar percentage cover at the start of the

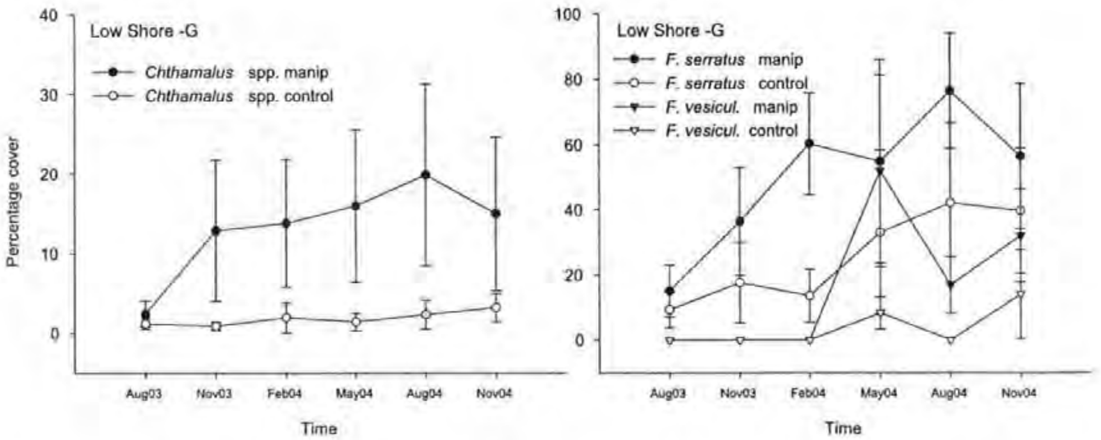

Figure 4.14: Exp3. Ephemeral removal on emergent rock. Percentage cover of *Chthamalus* spp., *Fucus serratus* and *Fucus vesiculosus* in manipulated plot where ephemerals were removed (manip: black symbols) and in unmanipulated plots (control: white symbols) during succession started in Summer 2002 at the low shore level on emergent rock at reduced grazer density (-G). Data are mean of percentage cover (±SE) of 2 replicate 20×20cm quadrats averaged for each of the 4 replicate plots (n=4).

experiment in August 2003, was positively affected by the removal of ephemeral species in plots of the low shore at reduced grazing pressure (-G) during later succession from November 2003 (fig. 4.14 and SIMPER, appendix, table E.7). Fucoids also developed better in the absence of ephemeral algae. Higher percentage cover of *Fucus spiralis*, *Fucus vesiculosus* and *Fucus serratus* were observed from the first spring bloom since the start of the manipulation in May 2004 in the mid and low shore plots with reduced consumer pressure (-G) (e.g. fig. 4.14, SIMPER, appendix, table E.7) where and when ephemeral algae were at their higher levels (see Exp 1. General Pattern of Succession on emergent rock, appendix, fig. D.4). However, some perennial species, such as *Ralfsia verrucosa* and *Semibalanus balanoides* were not affected by the presence of ephemeral species (appendix, fig. D.15 and fig. D.13, SIMPER, appendix, table E.7).

Table 4.11: PERMANOVA and Pair-wise *a posteriori* comparisons based on Bray-Curtis dissimilarity comparing assemblages of perennial species during succession on emergent rock between shore levels (Le: High, Mid, Low), herbivore treatments (Gr: natural (+G) and reduced (-G) grazer density) and manipulation treatments (Tr: removal of annual species (-A) and unmanipulated control plots (C)). Data were fourth-root transformed. ns: non significant; * * *: $P<0.001$; **: $P<0.01$; *: $P<0.05$.

		Aug 03			Nov 03			Feb 04		
Source	df	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Le	2	2226.87	3.25	**	2053.73	5.01	* * *	2757.29	3.17	**
Gr	1	6394.21	9.34	* * *	9033.38	22.04	* * *	11711.23	13.48	* * *
Tr	1	223.80	0.33	ns	3228.58	7.88	* * *	1984.90	2.28	ns
Le×Gr	2	926.40	1.35	ns	1078.51	2.63	*	1194.91	1.38	ns
Le×Tr	2	310.65	0.45	ns	313.30	0.76	ns	1440.77	1.66	ns
Gr×Tr	1	159.13	0.23	ns	3229.59	7.88	* * *	2624.74	3.02	*
Le×Gr×Tr	2	152.98	0.22	ns	229.48	0.56	ns	347.37	0.40	ns
Residual	36	684.97			409.94			868.72		

		May 04			Aug 04			Nov 04		
Source	df	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Le	2	667.77	0.84	ns	2257.21	2.39	*	1494.28	1.39	ns
Gr	1	972.69	1.22	ns	3808.51	4.04	**	1371.21	1.28	ns
Tr	1	689.68	0.87	ns	151.29	0.16	ns	49.81	0.05	ns
Le×Gr	2	2091.81	2.63	**	6609.57	7.01	* * *	1839.01	1.71	ns
Le×Tr	2	1516.64	1.91	ns	1494.10	1.58	ns	1779.17	1.66	ns
Gr×Tr	1	9763.73	12.27	* * *	261.26	0.28	ns	925.52	0.86	ns
Le×Gr×Tr	2	2732.98	3.43	**	925.87	0.98	ns	2627.15	2.44	*
Residual	36	795.94			943.10			1074.80		

Pair-wise *a posteriori* comparisons: test among levels of the factor Tr

Nov 03			Feb 04			May 04 Le×Gr (Tr)									Nov 04 Le×Gr (Tr)								
Gr (Tr)			Gr (Tr)			High			Mid			Low			High			Mid			Low		
Gr	*t*	*P*	Gr	*t*	*P*	Gr	*t*	*P*	Gr	*t*	*P*	Gr	*t*	*P*	Gr	*t*	*P*	Gr	*t*	*P*	Gr	*t*	*P*
-G	2.78	* * *	-G	1.73	*	-G	0.80	ns	-G	2.66	*	-G	1.53	ns	-G	0.80	ns	-G	1.55	ns	-G	1.53	ns
+G	0.98	ns	+G	0.68	ns	+G	1.50	ns	+G	2.00	*	+G	3.31	*	+G	1.50	ns	+G	1.46	ns	+G	0.48	ns

Table 4.12: PERMANOVA and Pair-wise *a posteriori* comparisons based on Bray-Curtis dissimilarity comparing assemblages of ephemeral species during succession in rockpools between shore levels (Le: High, Mid, Low), herbivore treatments (Gr: natural (+G) and reduced (-G) grazer density) and manipulation treatments (Tr: removal of perennial species (-B) and unmanipulated control plots (C)). Data were fourth-root transformed. ns: non significant; * * *: $P<0.001$; **: $P<0.01$; *: $P<0.05$.

		Nov 03			Feb 04			May 04			Aug 04			Nov 04		
Source	df	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Le	2	3047.35	3.49	* * *	3509.28	4.98	* * *	2353.78	3.04	**	3335.95	4.26	* * *	4417.81	6.26	* * *
Gr	1	3502.97	4.02	**	3424.92	4.86	* * *	5502.55	7.12	* * *	3688.26	4.71	* * *	4101.89	5.81	* * *
Tr	1	9121.66	10.46	* * *	10221.28	14.50	* * *	9979.30	12.91	* * *	8951.51	11.43	* * *	10776.85	15.27	* * *
Le×Gr	2	1103.71	1.27	ns	813.52	1.15	ns	521.24	0.67	ns	474.31	0.61	ns	676.20	0.96	ns
Le×Tr	2	1066.61	1.22	ns	600.87	0.85	ns	977.93	1.27	ns	332.16	0.42	ns	225.81	0.32	ns
Gr×Tr	1	343.38	0.39	ns	2022.96	2.87	*	1457.70	1.89	ns	2205.14	2.81	*	729.42	1.03	ns
Le×Gr×Tr	2	729.44	0.84	ns	523.25	0.74	ns	1409.23	1.82	ns	1817.38	2.32	*	1638.63	2.32	*
Residual	36	872.26			705.01			773.06			783.41			705.96		

Pair-wise *a posteriori* comparisons: test among levels of the factor Tr

Feb 04			Aug 04 Le×Gr (Tr)									Nov 04 Le×Gr (Tr)								
Gr (Tr)			High			Mid			Low			High			Mid			Low		
Gr	*t*	*P*	Gr	*t*	*P*	Gr	*t*	*P*	Gr	*t*	*P*	Gr	*t*	*P*	Gr	*t*	*P*	Gr	*t*	*P*
-G	2.83	* * *	-G	1.97	*	-G	1.39	ns	-G	2.87	*	-G	1.62	*	-G	1.72	ns	-G	1.61	ns
+G	2.57	* * *	+G	1.42	ns	+G	1.79	ns	+G	1.73	*	+G	1.65	ns	+G	2.05	ns	+G	3.03	*

4.3.3.4 Role of perennial species during late succession in rockpools

Perennial species had significant, but contrary effects on the same ephemeral algal species depending on the presence or absence of grazers (PERMANOVA, table 4.12). These opposing trends were dependent on the species distribution between shore levels and driven by the presence (+G) or absence (-G) of herbivores. This was highlighted by interactions in February 2004 between manipulation and grazer treatments and in August and November 2004 between shore levels, manipulation and grazer treatments (PERMANOVA and pairwise comparisons, table 4.12).

A first trend was observed in rockpools at reduced grazing pressure (-G) where most of the ephemeral algae were positively affected by the removal of perennial species (SIMPER, appendix, table E.9). For example, green ephemeral algae such as *Ulva intestinalis* (fig. 4.15), other *Ulva* spp., *Cladophora* spp. were found in much higher proportions in the absence of perennial algae and herbivores (but see appendix, fig. D.16 and SIMPER, appendix, table E.9). This was also confirmed by a significant interaction between grazer and perennial manipulation treatments for *Ulva intestinalis* abundances during their May 2004 peak (Anova, Gr×Tr: F=7.77, P<0.01; SNK: -G: +perennial<-perennial and +G: +perennial=-perennial). The same pattern was found for the brown seaweeds, *Scytosiphon lomentaria* (fig. 4.15), *Colpomenia peregrina*, *Sphacelaria* spp.

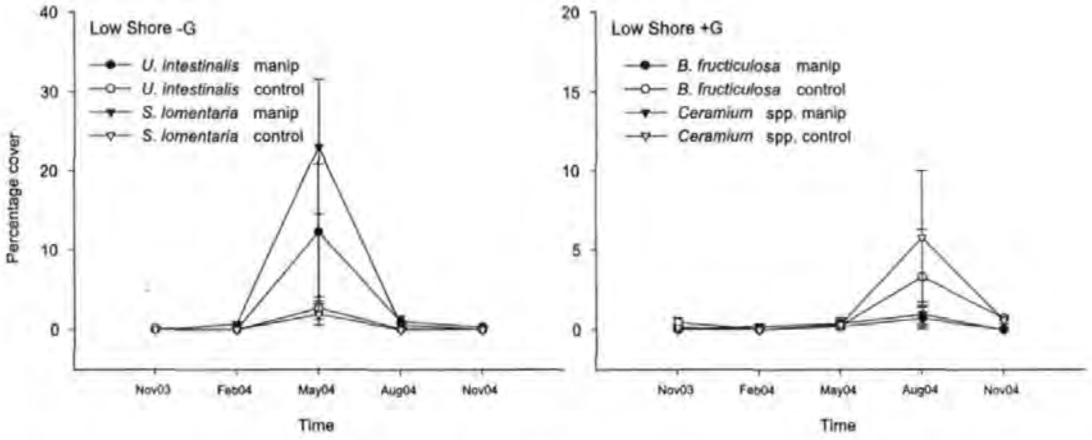

Figure 4.15: Exp3. Perennial removal in rockpool. Percentage cover of ephemeral species: *Ulva intestinalis*, *Scytosiphon lomentaria* spp. in pools at reduced grazer density (-G) and *Ceramium* spp., *Boergeseniella fructiculosa* in pools at natural grazer density (+G) in manipulated plot where perennials were removed (manip: black symbols) and in unmanipulated plots (control: white symbols) during succession started in Summer 2002 at the low shore level. Data are mean of percentage cover (±SE) of 2 replicate 20×20cm quadrats averaged for each of the 4 replicate pools (n=4).

and *Ectocarpus* spp. (appendix, fig. D.17 and/or SIMPER, appendix, table E.9). Likewise, the red ephemeral algae *Ceramium* spp., *Polysiphonia* spp. and *Dumontia contorta* were enhanced by the absence of perennial species in May 2004 or had similar abundances with unmanipulated plots in August and November 2004 in the case of *Ceramium* spp. (appendix, fig. D.18 and/or SIMPER, appendix, table E.9). *Boergeseniella fructiculosa* had a higher percentage cover among low shore rockpools where perennial algae were removed (appendix, fig. D.18) but it was the only algae with an average abundance over the three shore levels (High, Mid and Low) which was higher in unmanipulated plots (SIMPER, appendix, table E.9).

An opposite trend to this ephemeral inhibition by perennial species in pools at reduced grazer density was recorded in rockpools at natural grazer density (+G). Ephemeral algae were higher in abundance in unmanipulated plots (control) where the perennial species at were present. For example, green ephemeral algae such as *Ulva intestinalis*, other *Ulva* spp. and *Cladophora* spp. were found in higher or similar abundances in unmanipulated plots compared to manipulated ones (SIMPER, appendix, table E.9) (appendix, fig. D.16). This was also the case for the red algae *Ceramium* spp. and *Boergeseniella fructiculosa* (fig. 4.15), *Dumontia contorta*, *Polysiphonia* spp., *Aglaothamnion* spp., *Champia parvula*, *Chylocladia verticillata* (SIMPER, appendix, table E.9) and the brown algae *Sphacelaria* spp., *Ectocarpus* spp. and *Colpomenia peregrina* (SIMPER, appendix, table E.9) (appendix, fig. D.17).

In addition, there was no significant effect of perennials on the encrusting algae *Phymatolithon spp.* and *Lithophyllum incrustans* (SIMPER, appendix, table E.9 and appendix, fig. D.19). However, a slight increase of *Phymatolithon spp.* appeared at natural grazer density where perennial species were removed (appendix, fig. D.19).

Finally, Sand and stone tended to accumulate where erect perennial species were present (SIMPER, appendix, table E.9).

4.3.3.5 Role of perennial species during late succession on emergent rock

Although *Ulva intestinalis*, *Porphyra* spp. and *Drachiella* spp. (fig. 4.16) were observed in higher abundances in plots at reduced grazer density (-G) where perennial species were removed at the mid and low shore levels, no significant differences in ephemeral assemblages were found (PERMANOVA, table 4.13). In plots left at natural grazer density (+G), *Calothrix crustacea* (appendix, fig. D.21) and *Verrucaria* spp. (appendix, fig. D.20) were not affected by the presence or absence of perennial algae. Barnacle species *Chthamalus* spp. and *Semibalanus balanoides* established independently of the presence or absence of perennial algae (appendix, fig. D.22). Differences detected by PERMANOVA (table 4.13) between shore levels and grazer treatments were similar to those presented in the general pattern of succession on emergent rock (Exp 1. General Pattern of Succession).

Table 4.13: PERMANOVA comparisons based on Bray-Curtis dissimilarity comparing assemblages of ephemeral species during succession on emergent rock between shore levels (Le: High, Mid, Low), herbivore treatments (Gr: natural (+G) and reduced (-G) grazer density) and manipulation treatments (Tr: removal of perennial species (-P) and unmanipulated control plots (C)). Data were fourth-root transformed. ns: non significant; $***$: $P<0.001$; $**$: $P<0.01$; $*$: $P<0.05$.

		Nov 03			Feb 04			May 04			Aug 04			Nov 04		
Source	df	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Le	2	6795.71	4.71	**	4741.25	2.16	ns	13412.78	9.81	* * *	9213.97	13.64	* * *	6997.24	4.95	**
Gr	1	35918.94	24.89	* * *	42455.89	19.32	* * *	31375.68	22.96	* * *	26586.69	39.35	* * *	16096.40	11.39	* * *
Tr	1	1273.47	0.88	ns	795.21	0.36	ns	3235.26	2.37	ns	971.10	1.44	ns	1467.47	1.04	ns
Le×Gr	2	5088.96	3.53	*	2669.86	1.22	ns	3617.59	2.65	ns	9213.97	13.64	* * *	3974.75	2.81	*
Le×Tr	2	828.71	0.57	ns	2050.09	0.93	ns	2087.92	1.53	ns	926.80	1.37	ns	1393.49	0.99	ns
Gr×Tr	1	1193.31	0.83	ns	3661.07	1.67	ns	1664.73	1.22	ns	971.10	1.44	ns	2782.05	1.97	ns
Le×Gr×Tr	2	868.79	0.60	ns	1397.37	0.64	ns	2428.22	1.78	ns	926.80	1.37	ns	968.96	0.69	ns
Residual	36	1442.90			2197.43			1366.83			675.59			1413.26		

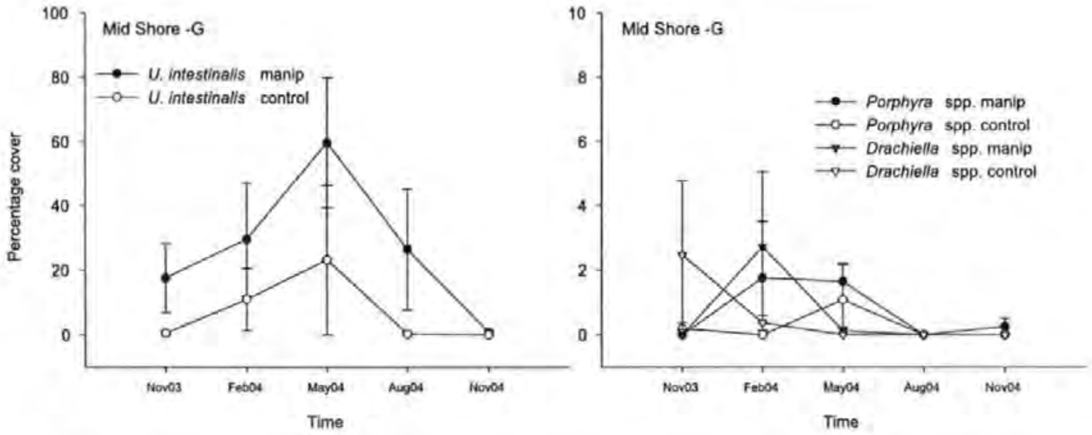

Figure 4.16: Exp3. Perennial removal on emergent rock. Percentage cover of ephemeral species: *Ulva intestinalis*, *Porphyra* spp. and *Drachiella* spp. in manipulated plot where perennials were removed (manip: black symbols) and in unmanipulated plots (control: white symbols) during succession started in Summer 2002 at the mid shore levels shore on emergent rock at reduced grazer density (-G). Data are mean of percentage cover (±SE) of 2 replicate 20×20cm quadrats averaged for each of the 4 replicate plots (n=4).

4.3.3.6 *Sargassum muticum* invasibility

Recruitment of the invasive species *Sargassum muticum* was significantly greater in rockpools at reduced grazing pressure (-G) in open space created the previous year by clearance (scraped) compared to mature communities; there was a decreasing number of individuals higher on the shore (ANOVA, SNK, table 4.14 and fig. 4.17). This was highlighted by the interactions between shore levels (High, Mid, Low) and grazer treatments (natural (+G) and reduced (-G) grazer density), shore levels and plots treatments (mature and scraped) and between grazer and plots treatments (ANOVA, SNK, table 4.14). In mature plots, *Sargassum muticum* was observed in higher proportion in low shore rockpools at reduced grazer density compare to natural density ones (ANOVA, SNK, table 4.14 and fig. 4.17).

In rockpools at natural herbivore densities (+G), *Sargassum muticum* had similar individual numbers in mature and cleared plots at mid and low shore (SNK, table 4.14) compared to high shore rockpools where a lower number of plants of *Sargassum muticum* was recorded only in mature plots (ANOVA, SNK, table 4.14 and fig. 4.17).

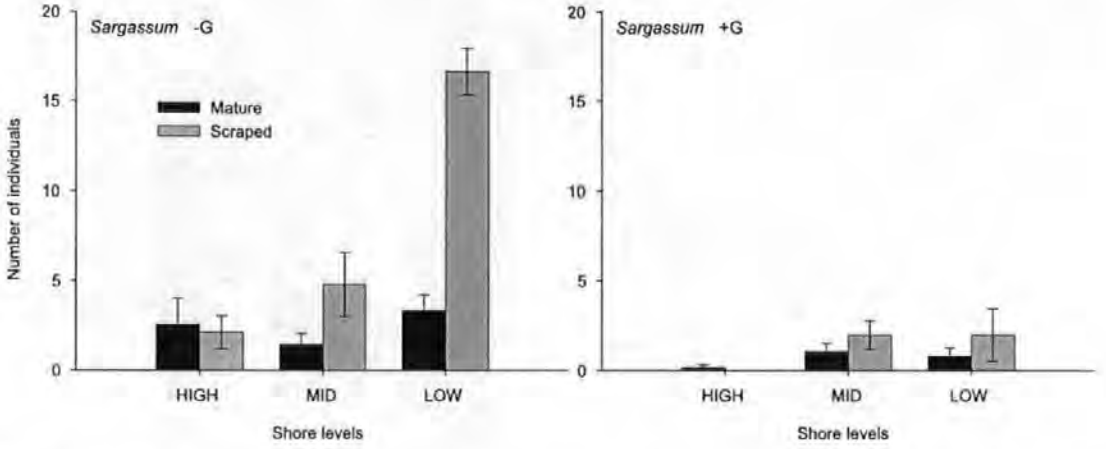

Figure 4.17: Exp3. *Sargassum muticum* invasibility. *Sargassum muticum* individual numbers in September 2003 in mature and scraped plots in August 2002 at each of three shore levels: High, Mid and Low shore in rockpools at reduced grazer density (-G) and natural grazer density (+G). Data are mean of individual numbers (±SE) of 2 replicate 10×10cm quadrats averaged for each of the 8 replicate plots (n=8).

Table 4.14: ANOVA and SNK *a posteriori* comparisons comparing individual number of *Sargassum muticum* in mature and scraped plots (Tr: Mature, Scraped) in rockpools between shore levels (Le: High, Mid, Low), herbivore treatments (Gr: natural (+G) and reduced (-G) grazer density). Data were (ln+1) transformed. Cochran's test non significant. ns: non significant; $***$: $P<0.001$; $**$: $P<0.01$; $*$: $P<0.05$. SNK: factor levels of the same group are represented with: =, factor levels with significant differences are represented with < or > according to their rank order.

Source	DF	SS	MS	*F*	*P*
Level (Le)	2	10.92	5.46	13.79	***
Grazer (Gr)	1	20.91	20.91	52.83	***
Treatment (Tr)	1	4.54	4.54	11.47	***
Le×Gr	2	6.09	3.04	7.69	***
Le×Tr	2	3.46	1.73	4.38	*
Gr×Tr	1	2.41	2.41	6.08	*
Le×Gr×Tr	2	1.36	0.68	1.72	ns
Residual	84	33.25	0.40		

SNK

Le×Gr		Le×Tr		Gr×Tr	
Le(Gr)	Gr(Le)	Le(Tr)	Tr(Le)	Gr(Tr)	Tr(Gr)
-G: High = Mid<Low	High: -G>+G	Mature: High = Mid = Low	High: Mature = Scraped	Mature: -G>+G	-G: Mature<Scraped
+G High<Mid = Low	Mid: -G = +G	Scraped: High<Mid<Low	Mid: Mature<Scraped	Scraped: -G>+G	+G: Mature = Scraped
	Low: -G>+G		Low: Mature<Scraped		

4.3.3.7 Role of barnacles during succession

Grazing intensity There were no significant differences in limpet grazing intensity between emergent rock with high barnacle cover (Barnacle: > 80%) and rock with low cover (Rock: < 10% barnacle cover) (fig. 4.18, table 4.15). However, during the trial 2, where limpet grazing intensity was recorded to be higher in plots with high barnacle cover (fig. 4.18, table 4.15). Topshell grazing

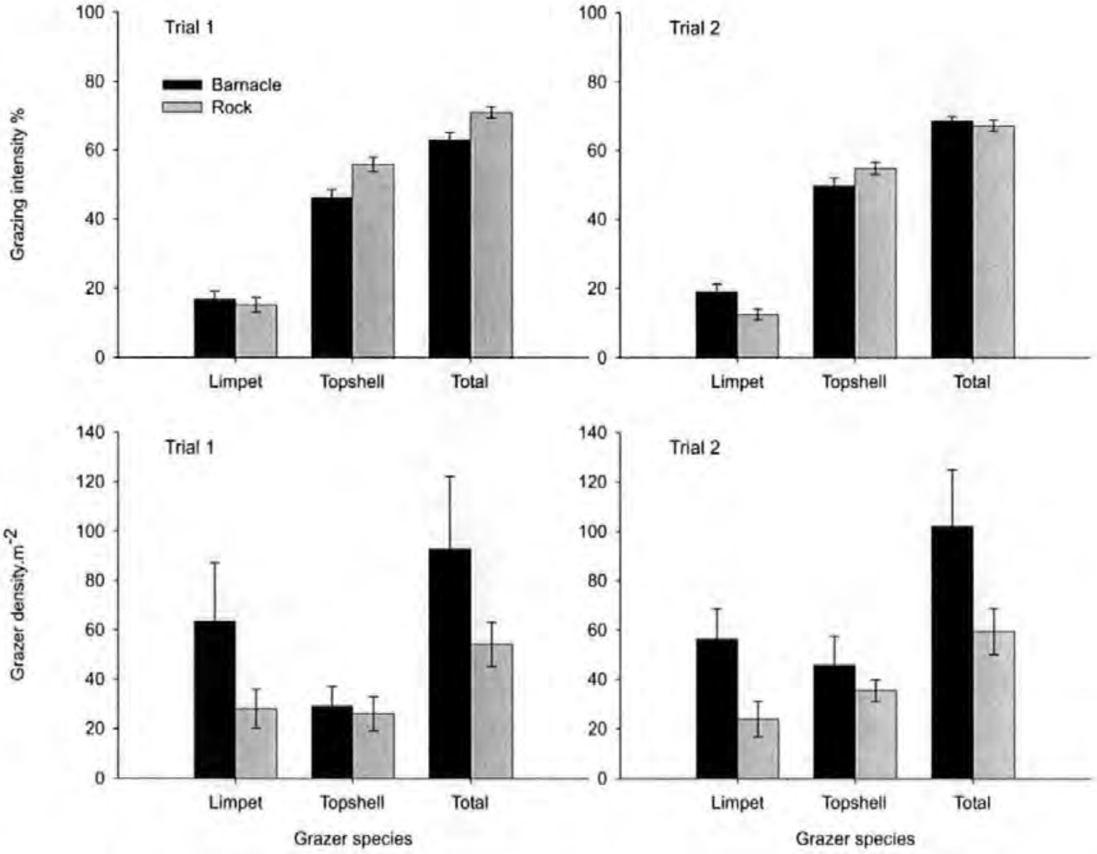

Figure 4.18: Exp3. Role of barnacles. Grazing intensity percentage and grazer density in plots with high barnacle cover (Barnacle: > 80%) and with low cover (Rock: < 10% barnacle cover) on emergent rock at mid shore level at naturel grazer density for 2 consecutive 15 days periods (trial 1, trial 2) in August 2004. Data are mean of percentage of surface grazed (±SE) of ten replicate wax discs averaged per plot for each of the 8 replicate plots and grazer count (±SE) in three replicate 20×20cm quadrats averaged per plots (n=8).

Table 4.15: 2-way Anova comparing percentage of grazing activity and density of topshells and limpets on emergent rock for the factor Cover: with high barnacle cover (Barnacle: > 80%) and with low cover (Rock: < 10% barnacle cover) at mid shore level at naturel grazer density for 2 consecutive 15 days periods (trial 1, trial 2) in August 2004 (n=8). Density data were (ln+1) transformed. (Cochran's test non significant in all case). ns: non significant; ∗: $P<0.05$

		Grazing						Density					
		Limpet			Topshell			Limpet			Topshell		
	DF	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Cover (Co)	1	134.84	1.28	ns	444.68	4.45	∗	3.27	1.59	ns	0.04	0.03	ns
Trial (Tr)	1	0.69	0.01	ns	13.40	0.13	ns	0.01	0.01	ns	3.67	3.43	ns
Co×Tr	1	48.24	0.46	ns	42.12	0.42	ns	0.17	0.08	ns	0.01	0.01	ns
Residual	28	105.51			99.89			2.05			1.07		

intensity was significantly lower in high barnacle cover plots (fig. 4.18, table 4.15).

In addition, although no significant differences were observed in grazer density between rock with high barnacle cover (Barnacle: $> 80\%$) and rock with low cover (table 4.15), grazer individual numbers, especially limpets, were recorded to be higher in plots with high barnacle cover (fig. 4.18).

Species recruitment Significant differences in species distribution depending on the shore level (High, Mid, Low) and the grazer treatments (natural (+G) or reduced (-G) grazer density) were highlighted by the interaction between shore level and grazer treatments (Le×Gr) in August 2003 and 2004 (table 4.16). These results were presented earlier (see Exp 1. General Pattern of Succession on emergent rock).

Barnacle cover, dominated by *Chthamalus* spp., was significantly reduced by the clearance in August 2002 in the scraped plots compared to the mature plots (ANOVA, Aug03: F=60.88, $P<0.001$, Aug04: F=14.24, $P<0.001$) (fig. 4.19 and SIMPER, appendix, table E.10).

In plots at reduced grazer density (-G), *Fucus vesiculosus* and *Fucus spiralis* (average abundance over the 3 shore levels or at the mid and low shore) were positively affected by the presence of barnacles (mature plots) (fig. 4.19 and SIMPER, appendix, table E.10). However,

Table 4.16: PERMANOVA and Pair-wise *a posteriori* comparisons based on Bray-Curtis dissimilarity comparing assemblages of species in mature and scraped plots (Treatment (Tr): mature, scraped) on emergent rock between shore levels (Le: High, Mid, Low) and herbivore treatments (Gr: natural (+G) and reduced (-G) grazer density) in August 2003 and 2004 (1 and 2 years after the start of experiment). Data were fourth-root transformed. ns: non significant; ∗∗∗: $P<0.001$; ∗∗: $P<0.01$; ∗: $P<0.05$.

		Aug 03			Aug 04		
Source	df	MS	*F*	*P*	MS	*F*	*P*
Le	2	1670.54	3.85	∗∗	3821.04	6.44	∗∗∗
Gr	1	9709.34	22.36	∗∗∗	11182.85	18.85	∗∗∗
Tr	1	19191.09	44.19	∗∗∗	1725.30	2.91	∗
Le×Gr	2	1211.08	2.79	∗	3033.33	5.11	∗∗∗
Le×Tr	2	969.89	2.23	∗	234.80	0.40	ns
Gr×Tr	1	-718.56	-1.65	ns	779.87	1.31	ns
Le×Gr×Tr	2	354.51	0.82	ns	182.22	0.31	ns
Residual	36	434.25			593.26		

Pair-wise *a posteriori* comparisons: test among levels of the factor Treatment (Tr)

Aug 03							
Tr (Le)					Le (Tr)		
Groups	Scraped *t*	*P*	Mature *t*	*P*	Levels	*t*	*P*
(High, Low)	1.83	∗	1.71	∗	High	4.87	∗∗∗
(High, Mid)	1.15	ns	1.16	ns	Mid	3.47	∗∗∗
(Low, Mid)	1.21	ns	1.20	ns	Low	2.11	∗

Fucus spiralis was observed in higher abundance in cleared plots on the high shore (fig. 4.19). In general, *Fucus serratus* abundance was not influenced by the presence or absence of barnacles in plots at reduced herbivore density (-G) (SIMPER, appendix, table E.10), but its percentage cover in mature plots appeared to be higher at the mid shore and lower at the low shore (fig. 4.19). Ephemeral species such as *Ulva intestinalis* and *Porphyra* spp. (in August 2003) developed mostly in plots at reduced grazer density (-G) and were enhanced by the absence of barnacles (fig. 4.19 and SIMPER, appendix, table E.10). At the end of the experiment, *Ralfsia verrucosa* was also observed in higher percentage cover in plots at reduced grazer density (-G) where barnacles were cleared (fig. 4.19 and SIMPER, appendix, table E.10). *Verrucaria* spp. had also higher abundances in plots cleared in August 2002 regardless of the presence or absence of herbivores (fig. 4.19 and SIMPER, appendix, table E.10). Finally, in plots at natural grazer density *Semibalanus balanoides* recruited in higher proportion in scraped plots (fig. 4.19 and SIMPER, appendix, table E.10).

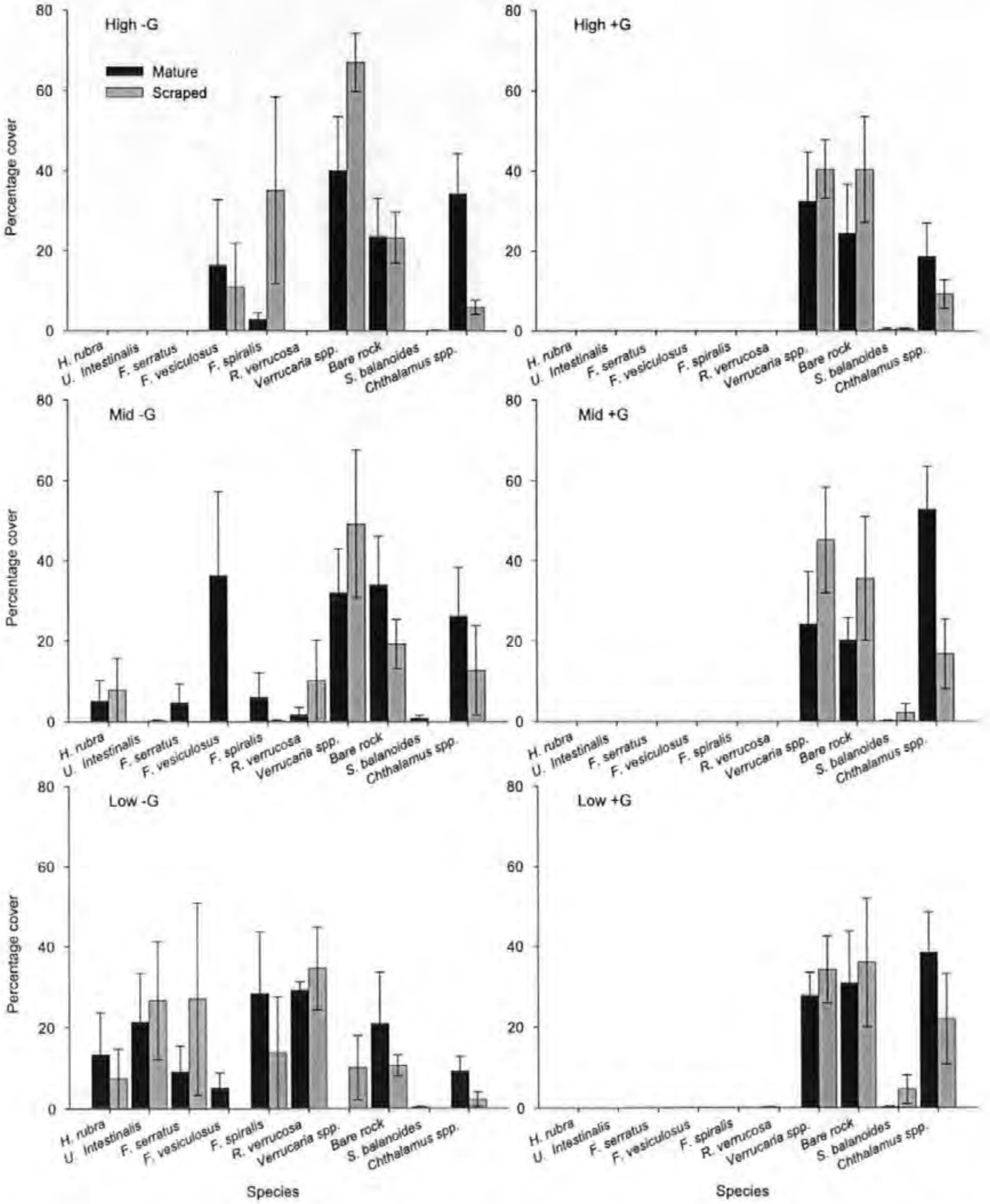

Figure 4.19: Exp3. Role of barnacles. Percentage cover in August 2004 of *Hildenbrandia rubra*, *Ulva intestinalis*, *Fucus vesiculosus*, *F. serratus*, *F. spiralis*, *Ralfsia verrucosa*, *Verrucaria* spp., bare rock, *Semibalanus balanoides*, *Chthamalus* spp. in mature and scraped plots in August 2002 at each of three shore levels: High, Mid and Low shore on emergent rock at reduced grazer density (-G) and natural grazer density (+G). Data are mean of percentage cover (±SE) of 2 replicate 20×20cm quadrats averaged for each of the 4 replicate plots (n=4).

4.4 Discussion

In this discussion a brief summary of the results is given; then factors influencing successional trajectories are considered. Firstly, the influence of the physical gradient and the timing of disturbance are discussed. The factors influencing succession in rockpools and emergent rock have then been considered in turn. Finally, outcomes of various experiments have been synthesized in relation to the applicability of models of succession. Positive, negative and neutral interactions found in the present investigation have been addressed in the context of Bertness and Callaway's model (1994) in the General Discussion (chapter 5).

Different successional pathways resulted from colonisation patterns and species interactions were observed, which were modulated by physical stress, life history characteristics of each species and consumer pressure. Species distribution was influenced by differences in abiotic factors, such as physical stress among shore heights and between rockpools and emergent rock. Colonisation started at different times of the year resulted in different initial successional sequences, although convergence occurred after 21 months. Consumer pressure shaped successional sequences according to species-specific herbivore resistance; although still present in all sequences, palatable species dominated succession in plots with reduced grazer density, in contrast to non-palatable species at natural grazer densities.

Influences of physical gradients

There was a clear difference between rockpools and emergent rock habitats as a result of different stress intensities influencing assemblages. For instance, species more tolerant of desiccation such as *Ulva intestinalis* and *Porphyra* spp. were found in higher abundance on emergent rock. In addition, no barnacles were observed in the rockpools. This has been explained by Palmer (pers. com. in Dethier, 1984) by greater predation from carnivores in rockpools due to constant immersion. However, this did not seem the case at Wembury, perhaps because of the very different pool of predators in the North East Atlantic compared to the North Pacific. Other factors, such as a lack of settling cues or available space due to crustose species (e.g. *Ralfsia*), low dissolved oxygen level, accumulation of toxine or predation by *Nucella lapillus* may be operating to exclude barnacles (Singletary and Shadlou, 1983). At Wembury, some species such as *Fucus serratus* and *Phymatolithon* spp. were observed at higher shore heights in rockpools than their limits on emergent rock. Such extension of species distribution in rockpools has also been documented on Northeast American shores (Johnson and Skutch, 1928; Femino and Mathieson, 1980; Chapman and Johnson, 1990). Some species, such as *Sargassum muticum*, *Phymatolithon* spp. and *Corallina* spp. were found only or in higher abundance in rockpools of Wembury Point as in previous studies: for example, *Sargassum muticum* has been reported to be unable to withstand desiccation (Norton, 1977) although it has been reported on low shore emergent rock at other latitudes (e.g. in north of Spain, Fernandez, 1999), and *Phymatolithon* spp. and *Corallina* spp., which were usually restricted to pools and damp areas on the northwest coast of North America (Padilla, 1984). Rockpools have been defined as a refuge from desiccation (Underwood and Jernakoff, 1984) and from wave action by Chapman (1990b) who found *Fucus distichus* strictly restricted in pools on an exposed shore of the Northwest Atlantic in North America. The opposite was observed with other fucoids, which were only present on emergent rock owing to a combination of high consumer pressure and algal competition excluding them from rockpools (Lubchenco, 1982). In addition, a higher species diversity occurs in rockpools compared to emergent rock at Wembury and in the South West England in general (pers. obs.).

Different patterns of succession were observed at different shore heights in both rockpools and on emergent substrata. As shown in chapter 2, there was an increase of physiological stress with longer isolation from the sea. Therefore, this physical stress affected the species involved in the course of succession and set their upper distribution limits (Dethier, 1984). All the successional experiments run at Wembury showed significant differences in assemblages between the high and low shores, with the mid shore being a transition zone for both rockpools and emergent rock. Those differences appeared earlier on emergent rock (more stressful environment) than in rockpools. In rockpools, species that recruited at higher levels on the shore were more tolerant of harsh conditions (e.g., *Phymatolithon* spp., *Fucus serratus*, *Fucus spiralis*). In the low shore rockpools, less tolerant species were dominant (e.g., *Sargassum muticum*, *Corallina* spp. and *Lithophyllum incrustans*). On the mid shore, rockpool assemblages were composed of a mix of high and low shore species with a canopy formed by fucoids and *Sargassum muticum* and with substrata colonised by a combination of Phymatolithon spp. and *Corallina* spp.. According to Dethier (1984) low shore pools are more subject to wave action, which could, when combined with the proximity of sand, explain the greater proportion of sand accumulated there. Moreover, sand was trapped in the pools at reduced grazer density by the high density of erect algae growing there, but did not affect the course of succession as suggested by Airoldi (1998). On emergent rock, similar patterns appeared during successional stages. High shore colonisation was dominated by *Verrucaria* spp., *Chthamalus* spp., *Fucus vesiculosus* and *Fucus spiralis* and on the low shore by *Ralfsia verrucosa*, *Hildenbrandia rubra*, *Phymatolithon* spp., *Ulva intestinalis*, *Fucus serratus* and *Semibalanus balanoides*. Evidence of species distribution affected by physiological stress and harsher physical conditions have been reported in other studies (Dethier, 1984; Underwood and Jernakoff, 1984).

Timing of disturbance

There was no overall long-term effect of initiation time on the outcome of the succession in both rockpool and emergent rock when considering both timing since the beginning of the succession and seasons. Successions started in August 2002 and in February 2003 converged toward the same end point assemblages after 21 months, exhibiting what can be defined as canalised succession (Berlow, 1997). However, distinct species assemblages were present during early colonisation. Similar patterns were reported during early succession as a result of seasonal differences among species reproduction, recruitment and growth, which may influence the colonisation end-point (Hawkins, 1981; Hawkins and Hartnoll, 1983b; Breitburg, 1985; Benedetti-Cecchi and Cinelli, 1996; Benedetti-Cecchi, 2000b). When succession was studied over some years, similar outcomes were observed in some experiments (Benedetti-Cecchi and Cinelli, 1996; Benedetti-Cecchi, 2000a), but also divergent trajectories occurred owing to a priority effect from the dominant species (Benedetti-Cecchi, 2000b). Weak priority effects were recorded at Wembury in both rockpool and emergent rock with fucoid species, but they did not affect the final assemblages. *Fucus spiralis* and *Fucus serratus* were more abundant towards the end of the experiment when clearances were made in August 2002; in contrast *Fucus vesiculosus* was more abundant in plots cleared in February 2003. Each *Fucus* species was favoured when clearance occurred during their reproductive periods. It is worth noting that the invasive species *Sargassum muticum* was not affected by the initiation time and became rapidly dominant in all mid and low shore rockpool assemblages.

Succession in rockpools

During early succession in rockpools at reduced grazer density, ephemeral species, *Ulva intestinalis*, *Scytosiphon lomentaria*, *Ceramium* spp. and the invasive species *Sargassum muticum*, were among the first and most abundant colonisers. *Sargassum muticum* recruited in the first weeks after the experiment was initiated and persisted. Succession was started during the fertile period of *Sargassum muticum* and this species dominated from early stages of colonization. Benedetti-Cecchi (2000b) found similar results with *Cystoseira* in cleared plots in intertidal pools of the Northwest Mediterranean during its main period of recruitment. He concluded that *Cystoseira* had a priority effect in the early stages of succession only when succession was started during its main reproductive period. However, *Sargassum muticum* also recruited and dominated in plots cleared in February 2003 outside its reproductive period (Arenas and Fernandez, 1998; Fernandez, 1999) although ephemeral species recruited first. Therefore, there were no priority effects from *Sargassum muticum*. There was neutral interactions between ephemeral species and juveniles of *Sargassum muticum* as expected considering the work of Viejo (1997) between these opportunistic and free space colonisers. Significantly higher recruitment of *Sargassum muticum* was recorded at reduced grazer density in space liberated by clearing compared to mature assemblages. This observation shows the ability of the highly aggressive invasive character of the opportunistic perennial *Sargassum muticum* to colonise free space - probably in response to its ability to proliferate vegetatively as well as reproduce sexually via new propagules (Norton, 1976; Ambrose and Nelson, 1982; Paula and Eston, 1987; Viejo, 1997).

In general, where grazers were manipulated in rockpools at Wembury, ephemeral species had no detectable effect on perennial species and later colonisers recruited and established abundantly. Conversely, previous work on succession in rockpools, attributed a deleterious effect of early arriving species on later colonists (Dethier, 1984; Chapman, 1990b). For example, Lubchenco (1982) observed that ephemeral species precluded the development of *Fucus* by monopolizing the substrata (60-70% cover). In the present study, ephemeral species did not colonise the plots in dense thick mats and may have left enough free space for canopy species to recruit. In addition, during late succession in rockpools and low shore open rock areas at reduced herbivore pressure, ephemeral species which were usually observed as epiphytes on canopy (pers. obs., Hawkins and Harkin, 1985) did not have any detectable effect on the canopy as found by Lubchenco (1982). This contrasts with Parker *et al.* (1993) who attributed a reduction of cover owing to the presence of epiphytes.

The most abundant late successional species in rockpools at low consumer pressure were the encrusting *Ralfsia verrucaria* and the canopy forming *Sargassum muticum*, *Fucus serratus* and *Fucus spiralis*. In the present investigation, interactions between late perennial colonisers were not studied, but in New England (USA), Lubchenco (1982) suggested that *Ralfsia* spp. may have a beneficial effect on recruitment and establishment of fucoids. Moreover, manipulation of perennial species showed that canopy cover had a deleterious effect on ephemeral species in Wembury rockpools as found in previous works (Lubchenco, 1982; Hawkins and Harkin, 1985; Chapman, 1990a; Benedetti-Cecchi, 2000b) perhaps due to the capacity of the canopy to sweep the substrata and reduce light and space when already well established (Hawkins, 1981; Reed and Foster, 1984; Kennelly, 1987; Jenkins *et al.*, 1999b; Benedetti-Cecchi, 2000a).

In rockpools at normal grazer density, grazer resistant species developed and dominated succession. The first species to recruit was *Phymatolithon* spp., showing a considerable germination of propagules at the beginning of the experiment; therefore, its rapid growth could not only be attributed to either the development of remaining fragments or lateral growth. Indeed, Irvine and Chamberlain (1991) defined *Phymatolithon* spp. as a successful pioneer species. In later stages of succession *Lithophyllum incrustans* and *Corallina* spp. both appeared along with the canopy species *Sargassum muticum* and *Himanthalia elongata*. Most encrusting and articulated calcareous species (e.g. *Phymatolithon* spp., *Lithophyllum incrustans*, *Corallina* spp.) were found with lower abundance in rockpools at reduced consumer consumption. It is likely that high density of ephemeral algae and canopy forming species in those reduced grazer treatments inhibited them by pre-empting space. However, competition for light is unlikely as crustose and articulated calcareous algae can live under low light conditions (Johansen, 1981; Dethier, 1994). Herbivores removed ephemeral species and prevented their deleterious effect on grazer resistant species, as observed in previous studies (Sousa, 1979b; Lubchenco, 1982; Benedetti-Cecchi, 2000a). In addition, encrusting and articulated calcareous species were commonly recognised as well adapted to resist consumer pressure (Littler and Littler, 1980; Lubchenco and Cubit, 1980; Dethier, 1981; Steneck and Watling, 1982; Steneck, 1982; Lubchenco *et al.*, 1984; Padilla, 1984; Steneck and Dethier, 1994). The canopy species *Sargassum muticum* and *Himanthalia elongata* also escaped grazing in Wembury rockpools left at natural herbivore density. *Sargassum muticum* was still affected by herbivory, having lower abundances at natural grazer densities than when consumer pressure was reduced. A positive relationship with abundances of *Corallina* spp. suggested *Sargassum muticum* was protected against grazing when recruiting amongst it (i.e. associational defence). In addition, *Sargassum muticum* became the dominant and almost unique canopy species in rockpools at natural herbivore density in the present study either by filling an "unoccupied niche" (Fletcher and Fletcher, 1975) or by outcompeting other probable canopy species such as *Fucus serratus*. Other forms of defence were proposed in earlier studies such as refuge size (Dayton, 1975; Lubchenco, 1983) or chemical defences (Duggins and Dethier, 1985), possibly explaining the resistance of *Himanthalia elongata*. Furthermore, the morphological shape of germling, juvenile and adult *Himanthalia elongata* (i.e. button like holdfast) may also act as protection against grazers. Canopy species, in particular *Sargassum muticum*, did not have any effects on encrusting calcareous species as also shown in rockpools by Viejo (1997). This contrasts to Hawkins and Harkin (1985) who showed on emergent rock that calcareous species were susceptible to desiccation when canopy such as *Fucus serratus* was removed (see also Jenkins *et al.*, 1999b). However, the effect of *Sargassum muticum* could not be separated from that of *Corallina* spp. as they were both manipulated as perennial species. However, the slight increase from *Phymatolithon* spp. which was observed after manipulation of both canopy and the erect part of *Corallina* spp. could be ascribed to the high competitive ability of encrusting coralline algae which can overgrow even articulated coralline species (see Padilla, 1984).

During late succession in rockpools at natural grazer density, the perennial species *Sargassum muticum* and *Corallina* spp. produced a beneficial effect on ephemeral species which occurred mostly as epiphytes on these perennial species (pers. obs.). Epiphytes, which have been reported as common on *Sargassum muticum* (Arenas *et al.*, 1995), were protected from herbivores by establishing among *Corallina* spp. and *Sargassum muticum*.

A conceptual model of species interaction during succession was inferred from these observations (fig. 4.20). Algae were divided in two groups with respect to their palatability for grazers. Consumers negatively affected the palatable ephemeral and canopy species, which had a negative effect by preempting less palatable species such as encrusting and calcareous articulated species. Herbivores, therefore, had an indirect positive effect on non-palatable species by removing palatable ones. Moreover, non-palatable algae had a direct negative effect on consumers by acting as a barrier against them and providing associational defences (Bertness and Callaway, 1994) with palatable species. Therefore, grazers had an indirect positive effect

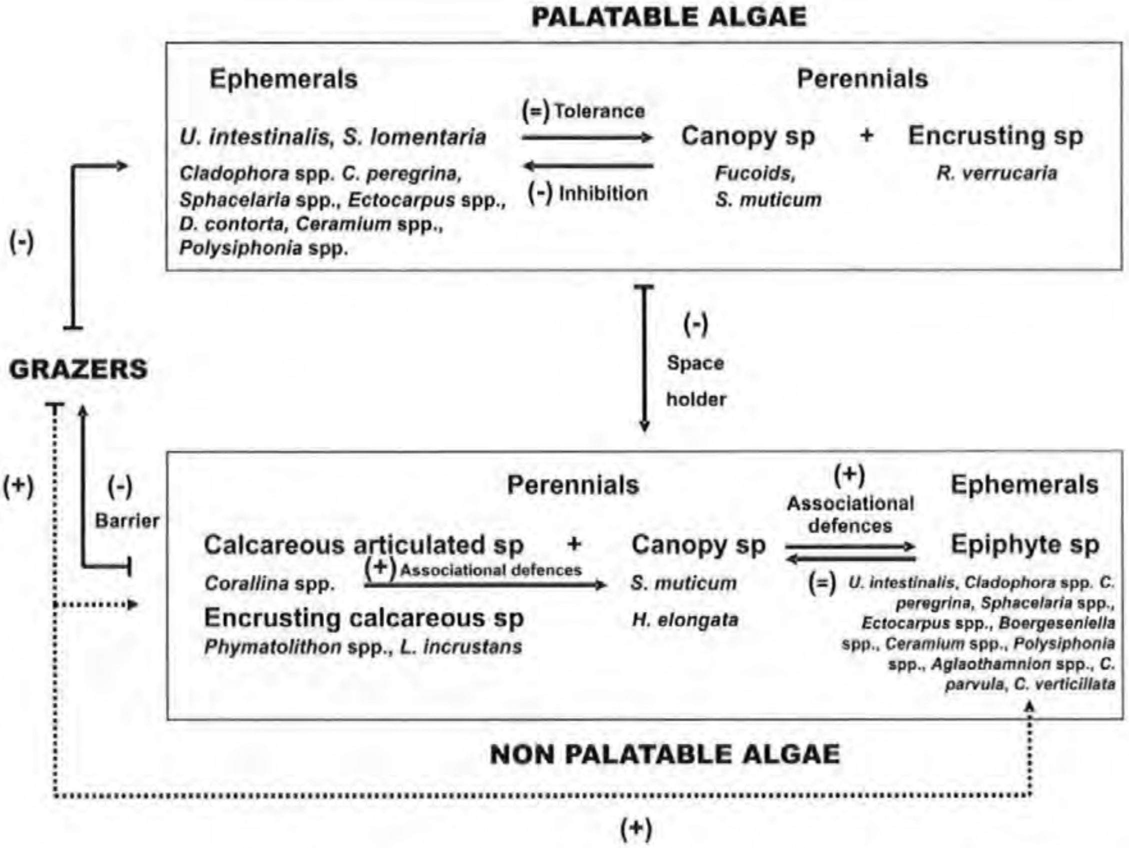

Figure 4.20: Conceptual model of interspecific interactions during succession in rockpools. Positive interactions are represented by (+), negative interactions by (-) and no detectable interactions (neutral) by (=). Plain lines represent direct interactions and dashed line indirect ones.

on ephemeral palatable algae that appeared in late succession under strong consumer pressure; whereas in contrast non-palatable *Corallina* spp. had a direct beneficial effect acting as a refuge for palatable algae.

Succession on emergent rock

The inhibition model has been reported to occur more often in succession on rocky shores (Connell and Slatyer, 1977; Sousa, 1979b; Denley and Underwood, 1979; Hawkins, 1981; Hawkins and Hartnoll, 1983b; Breitburg, 1985; Dungan, 1986; van Tamelen, 1987; Farrell, 1991; Sousa and Connell, 1992) and usually as a consequence of ephemeral algae inhibiting the establishment of later colonizers (Sousa, 1979b, 1984b; Lubchenco, 1983). On the emergent rock at Wembury, algae directly inhibited the establishment of barnacles by preempting space and overgrowing them, reducing barnacle growth and increasing their mortality (pers. obs.) as found in several previous studies (Denley and Underwood, 1979; Hawkins, 1983; Underwood *et al.*, 1983; Dungan, 1986; van Tamelen, 1987; Farrell, 1991). In addition, limpets directly inhibited algal growth, and therefore, limpets had an indirect positive effect on barnacle settlement as reported in earlier works (Sousa, 1979b; Branch, 1981; Hawkins and Hartnoll, 1983b; Hawkins, 1983; van Tamelen, 1987; Benedetti-Cecchi, 2000a). Succession in algal species at reduced grazer density was observed, with ephemeral species, *Ulva intestinalis* and *Porphyra* spp. occurring as early successional species which weakly inhibited the later colonising *Fucus* spp. Indeed, the presence of ephemeral species did not preclude *Fucus* spp. from establishment but did reduce their abundance. Hawkins (1981) reported similar results in scraped limpet exclusion areas on the Isle of Man. Other studies have shown that ephemeral algae at reduced consumer pressure had deleterious effects, thereby preventing the establishment of later colonisers (Menge, 1976; Lubchenco, 1983; Kim, 1997). At Wembury, once established on the emergent rock at low consumer pressure, fucoids generally had a negative effect on ephemeral species by out-competing for light and space as observed in previous studies (Hawkins, 1981; Sousa *et al.*, 1981; Dayton *et al.*, 1984; Reed and Foster, 1984; Kennelly, 1987; Jenkins *et al.*, 1999b; Benedetti-Cecchi, 2000a). The three species of *Fucus* present during the later stage of succession prevented *Porphyra* spp. from recruiting, but only *Fucus spiralis* and *Fucus vesiculosus* had obvious negative effects on *Ulva intestinalis* blooms, while *Fucus serratus* exhibited a weak inhibition or tolerance effect on *Ulva intestinalis*.

Where ephemeral species inhibited later successional stages, herbivores accelerated succession by removing ephemeral species (Menge, 1976; Lubchenco, 1983; Kim, 1997; Benedetti-Cecchi, 2000b). However, the results of the present investigation showed that consumers stopped succession. Indeed, the fact that no other species than barnacles (*Chthamalus* spp., *Semibalanus balanoides* and *Elminius modestus*) and lichens, such as *Verrucaria* spp. established during late successional stages in plots at natural herbivore density could be due either to strong consumer pressure (Lubchenco and Gaines, 1981; Sousa *et al.*, 1981; Lubchenco *et al.*, 1984; Menge *et al.*, 1986) or to small barnacle size (van Tamelen, 1987). High densities of *Littorina littorea* were able to prevent colonization and growth of *Fucus* and any other algae on the coast of New England, North America (Lubchenco, 1983; Bertness *et al.*, 1983). In addition, in the present study, the absence of algae in the mature community dominated by adult barnacles and exposed to a natural grazer density shown that large size barnacles did not allow algae to escape from grazing activity and become established as suggested by van Tamelen (1987) and Farrell (1991). Moreover, grazing intensity measured on the shore of Wembury was similar between bare rock and barnacle dominated areas and even at times greater limpet grazing was recorded in high barnacle cover plots. Herbivore density was also higher in barnacle dominated areas. These results were not consistent with the common idea that barnacles reduce grazing activity and consumer density by preempting for foraging, movements, space and attachment for herbivores (Hawkins, 1981; Hawkins and Hartnoll, 1982, 1983b; Underwood *et al.*, 1983; Dungan, 1986; van Tamelen, 1987; Farrell, 1991; Benedetti-Cecchi, 2000a) and that limpets have greater impact on extensive bare rock (Hawkins, 1983). This may reflect the smaller size of *Chthamalus* spp. compared to *Semibalanus balanoides* studied in previous works. However, the results of the present investigation supported the suggestion that barnacles provide protection and secondary substrata for limpets (Hawkins and Hartnoll, 1982, 1983b; Underwood *et al.*, 1983; Dungan, 1986). Therefore, barnacles did not reduce herbivore activity in the present study. Consequently, among dense barnacle areas and at low consumer pressure, barnacles mediated habitat ameliorations on the emergent rock of Wembury, rather than associational defences (Bertness and Callaway, 1994), by altering the substrata (Farrell, 1991), for example by protecting propagules from desiccation.

Indeed, when herbivores were manipulated, algae recruited and established in plots with high barnacle cover. However, barnacles had an inhibitory effect on the ephemeral *Ulva intestinalis* and *Porphyra* spp., on the encrusting *Ralfsia verrucosa* and on *Verrucaria* spp., which had higher abundances in low barnacle cover areas. Similar negative effects were found in previous studies for ephemeral algae (Hawkins, 1981; Kim, 1997; Benedetti-Cecchi, 2000a) and for *Ralfsia* (Dungan, 1986). Benedetti-Cecchi (2000a) suggested that the negative effect of barnacles was attributable to its filtering activity, which reduced the spores of ephemeral species; It was also attributed to competition for space by Dungan (1986). Habitat amelioration was also observed from barnacles with a positive effect on *Fucus spiralis* and *Fucus vesiculosus* at reduced grazer density but no detectable effect on *Fucus serratus*. Similar facilitation was found by Hawkins (1981) on the Isle of Man, where *Fucus* bypassed early stages of succession in the presence of barnacles. Barnacles have been defined as a bank and refuge for germlings of *Fucus* (Hawkins, 1981; Lubchenco, 1983) compared to bare or scraped rock with its importance depending on the intensity of consumer pressure (Lubchenco, 1982; Farrell, 1991). This could explain why other researchers (e.g. Kim, 1997) found facilitation from barnacles for *Fucus* at natural herbivore pressure which must have been lower than at Wembury or in the Isle of Man. The present work did not show any detectable effect from *Fucus* spp. on barnacles. However, previous studies found a negative effect from *Fucus* spp. (Hawkins, 1983; Petraitis and Dudgeon, 2005) which was attributed to sweeping on exposed shores (Hawkins, 1983) although, it was also found that *Fucus* spp. promoted establishment of barnacles by protecting them from desiccation (Hawkins, 1983; Jenkins *et al.*, 1999b).

A conceptual model summarising direct, indirect, positive or negative interactions between species involved in the succession on emergent rock discussed above is presented fig. 4.21.

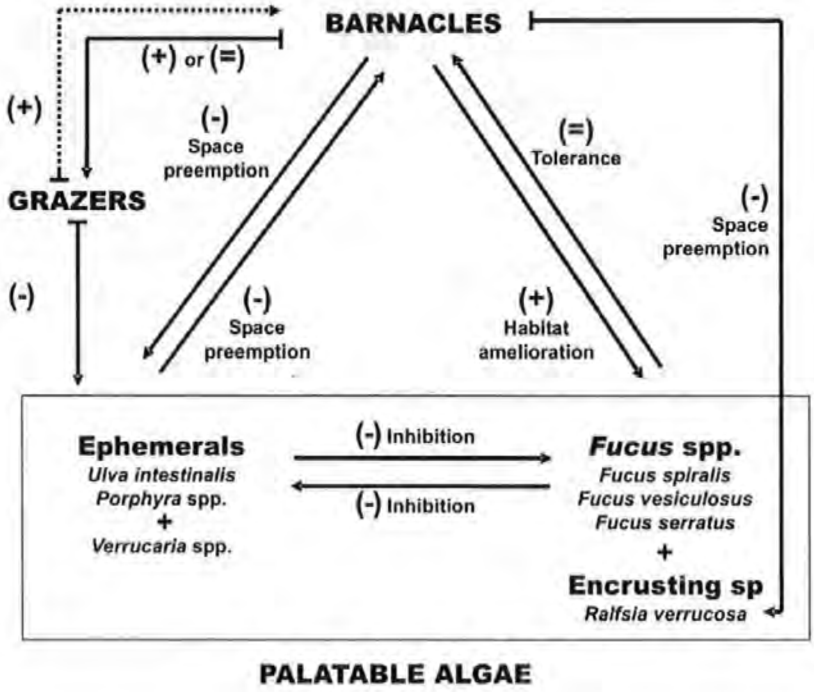

Figure 4.21: Conceptual model of interspecific interactions during succession on emergent rock. Positive interactions are represented by (+), negative interactions by (-) and no detectable interactions (neutral) by (=). Plain lines represent direct interactions and dashed line indirect ones.

Consistency with models of succession

Physical stress directed succession along different pathways, acting on species distributions among shore heights and habitats (rockpool and emergent rock). However, interspecific interaction types were similar among shore heights even if the species involved were different, but interactions changed between rockpools and emergent rock owing to large dissimilarity in physical stress (e.g. desiccation) and consumer pressure.

Herbivores had a major influence on succession (Lubchenco and Menge, 1978; Lubchenco and Gaines, 1981; Hawkins and Hartnoll, 1983a; Farrell, 1991; Sousa and Connell, 1992; Benedetti-Cecchi, 2000a) by allowing the establishment of non-palatable species

(Benedetti-Cecchi, 2000a) which without consumer pressure were out-competed by vulnerable algae with stronger interspecific interactions (Steneck, 1982). Therefore, consumer pressure led to completely different successional sequences. Farrell (1991) reported that grazers would accelerate, slow or leave succession unaffected corresponding to all three models proposed by Connell and Slatyer (1977) - namely inhibition, tolerance, facilitation. In the present study, strong grazer activity stopped or directed succession along different pathways. In addition, no grazer reduction owing to an increase in algal abundance was observed during late succession as documented in previous works (Hawkins, 1981; Underwood and Jernakoff, 1981; Dungan, 1986). On emergent rock, barnacle establishment did not reduce grazing intensity. Also in rockpools, growth of encrusting calcareous and *Corallina* spp. did not decrease availability of food resources (*Patella ulyssiponensis* feeds on encrusting corallines species (Hawkins and Hartnoll, 1983a)) or substrata for adhesion. Therefore, establishment of non-palatable species during late succession was not the consequence of a decrease in herbivore abundance as predicted by Farrell (1991). In the present study, unpalatable later successional species in rockpools were acting as a barrier against grazing and protected vulnerable species by associational defences as described in Bertness and Callaway (1994) model.

In rockpools at reduced consumer pressure, early ephemeral successional species did not monopolize the substrata but established in small clumps. Early colonists had no effect on the establishment of the later perennial canopy and encrusting colonists, corresponding to the tolerance model of Connell and Slatyer (1977). However, the later colonists once well established exerted a strong negative effect on early species, corresponding to the inhibition model of Connell and Slatyer (1977). This successional trajectory was predicted by Benedetti-Cecchi (2000a).

In rockpools at natural herbivore density, there was no clear successional sequence as calcareous grazer resistant colonists established during early succession and continued to develop through time without influencing consumer pressure. Associational defences (Bertness and Callaway, 1994) were then recorded and allowed vulnerable species to establish among the non palatable species. These events corresponded to what was expected by Benedetti-Cecchi (2000a) model.

On emergent rock, barnacles recruited in the presence of herbivores whose foraging was not affected by the rugosity of the barnacles. Consumer activity stopped succession which in case of a lower foraging would be promoted by barnacle habitat amelioration (Bertness and Callaway, 1994) and lead to *Fucus* spp. as later colonisers. When herbivore pressure was suppressed, early ephemeral algae became well established and monopolised most of the substrata and had an inhibitory effect (Connell and Slatyer, 1977) on barnacles and reduced later successional species abundances but did not preclude then from establishing. These interspecific interactions were envisaged by Benedetti-Cecchi (2000a).

In conclusion, the results of the present investigation showed the important role of physical gradients and herbivory in structuring communities by influencing species recruitment. The outcome in terms of assemblages composition was predictable according to the resistance of species to grazing along with the nature of species interactions (positive or negative) which were dictated by physical stress.

Chapter 5

General discussion

The focus of my experimental of work has been an examination of the Bertness and Callaway model (1994) during succession using the intertidal rocky shore and specifically rockpools and emergent rock as a test system. In this general discussion, I begin by introducing the Bertness and Callaway model (1994). Secondly, the system in which the Bertness and Callaway model (1994) was tested is described, with its natural environmental gradients and the experimental creation of a consumer pressure gradient in the habitats studied. Thirdly, the consequences of such gradients for the nature of species interactions structuring assemblages are considered during succession. Finally, the implications of the observed species interactions on ecological processes, outcomes and their relation to the Bertness and Callaway (1994) model are discussed.

5.1 Bertness and Callaway's model background

Positive species interactions, although considered important community structuring forces by early ecologists (e.g. Phillips, 1909; Clement, 1916; Allee *et al.*, 1949; Stephenson and Stephenson, 1949; Lewis, 1960; Newell, 1976), were largely ignored because of the focus on negative interactions, such as competition and predation for decades (e.g. Connell and Slatyer, 1977). There has been, however, a recent renewal of interest (Bertness and Callaway, 1994; Jones *et al.*, 1994; Callaway, 1995; Callaway and Walker, 1997; Bertness and Leonard, 1997; Bertness *et al.*, 1999b; Menge, 2000; Bruno and Bertness, 2001). Contemporary ecology considers positive and negative interactions to have equally important effects in assemblage organisation (Wilson and Agnew, 1992; Bertness and Callaway, 1994; Jones *et al.*, 1994; Bruno *et al.*, 2003). They usually operate together giving rise to complex combinations of competitive and facilitative effects within a single community between similar organisms (Callaway and Walker, 1997; Bruno *et al.*, 2003). Attempts have been made to include them in general conceptual models and to refine paradigms (e.g. Bruno *et al.*, 2003).

Positive interactions can be defined as a beneficial effect from one species to another or several species without being detrimental to any of them (Bronstein, 1994; Bertness and Callaway, 1994; Bertness and Leonard, 1997; Bruno and Bertness, 2001; Bruno *et al.*, 2003). This includes direct and indirect interactions that are usually interspecific but can also be intraspecific (such as positive density dependence, Bertness and Leonard (1997); Bertness *et al.* (1999a) but see Bruno *et al.* (2003). Positive interactions can also be facultative or obligatory, trophic or non-trophic (Bertness and Leonard, 1997; Bruno *et al.*, 2003). In marine habitats, positive interactions are usually commensal (Hay, 1986), although mutualisms occur, it is currently overlooked (Stachowicz and Hay, 1999). Care is needed to distinguish between positive interactions that occur between successional stages, when a later coloniser needs the presence of an early one in order to recruit, which were defined as facilitation by Connell and Slatyer (1977) and the beneficial effect of one organism on another in a mature community.

Positive interactions are mediated by several mechanisms: (1) the amelioration of stress in harsh habitats for example, extreme heat and desiccation stress in intertidal rocky shores (Bertness and Leonard, 1997; Bertness *et al.*, 1999b; Leonard, 2000); (2) associational defences with unpalatable prey offering refuge to palatable species from consumers (Pfister and Hay, 1988; Skilleter, 1994; Bertness and Callaway, 1994), which in marine habitats corresponds to the repellent plant definition of Atsatt and O'Dowd (1976) by physical obstruction or chemical means (Hay, 1986; Poore and Hill, 2005); (3) the reduction of predator density by plant neighborhood (enemies hypothesis: Root, 1973; Hacker and Bertness, 1996; Stiling *et al.*, 2003).

Positive interactions usually occur in harsh environments between species that are competitors in benign conditions (Bertness and Callaway, 1994). Hence, high biotic or abiotic stress can switch interactions from negative to positive (Callaway and Walker, 1997; Bruno *et al.*, 2003). Several species have been identified as being involved in such positive switches (Wilson and Agnew, 1992) and are defined as nurse plants (e.g. Niering and Whittaker, 1963; Callaway and Walker, 1997, for review) or ecosystem engineers (Jones *et al.*, 1994). Bruno and Bertness (2001) recommended the use of the term foundation species (*sensu* Dayton, 1972) when referring to those species. Therefore, positive, negative and neutral interactions need to be investigated together along with the influence of abiotic and biotic stresses to develop knowledge on community structuring (Menge, 2000). Studies often decoupled them by controlled laboratory or mesocosm experiments (Bertness and Callaway, 1994), although they are closely interrelated as shown in the present work.

Bertness and Callaway's model (1994) focused on direct non-trophic positive interactions based on the assumption that the intensity of environmental stress and consumer pressure gradients are generally inversely related (Bruno and Bertness, 2001). The following predictions made from this model were tested in my work with multifactorial experiments using rockpools and emergent rock: (1) associational defences will only occur in benign environments under high grazing pressure (i.e. in rockpools at natural herbivore density); (2) habitat ameliorations will only occur in harsh physical conditions and low grazing pressure (i.e. on emergent rock where herbivores are removed); and (3) at low level of physical stress and consumer pressure, competition will be the main interaction between algal species (i.e. in rockpools at reduced herbivore density and on emergent rock at natural grazer density). In order to study those interactions, an appreciation of the stress and consumer gradients in the model system is required.

5.2 Environmental stress and consumer pressure gradient in the model system

Intertidal habitats exhibit sharp environmental gradients over short distances making them ideal for the study of positive interactions (Raffaelli and Hawkins, 1996; Bertness and Leonard, 1997; Bertness *et al.*, 1999b). In addition to tidal elevation, the coexistence of rockpools and emergent rock within metres on rocky shores provided the opportunity to investigate the effect of habitat-driven differences in desiccation stress on assemblage structure during succession. Rocky shores have been the subject of numerous investigations on community structure (e.g. Connell, 1961b; Paine, 1966; Menge, 1976) but most have focussed essentially on how stress modulates negative interactions (Connell, 1961b,a; Paine, 1966, 1969; Odum, 1969; Connell and Slatyer, 1977, i.e. competition and predation) rather than the direct effect of environmental stress on assemblages (Bertness *et al.*, 1999b). Intertidal species distributions have been found to be limited by severe physico-chemical stress due to water loss and excessive temperature on the upper shore whereas their lower limit are largely set by biological factors such as competition and herbivory (Connell, 1972; Carefoot, 1977; Menge and Sutherland, 1987). However, biological factors can also set the upper limits of low shore species (Underwood and Jernakoff, 1981; Hawkins and Hartnoll, 1985; Boaventura *et al.*, 2002). More recently, positive interactions such as habitat amelioration due to high density of organisms or buffering from canopy species were also reported to influence species upper limits (Hay, 1981; Bertness and Leonard, 1997; Bertness *et al.*, 1999b; Jenkins *et al.*, 1999c; Leonard, 2000; Jenkins *et al.*, 2004).

In the present investigation, a clear pattern of species distribution was observed over the intertidal gradient in both rockpools and emergent rock (e.g. Rockpool high shore: *Phymatolithon* spp., *Fucus serratus*, *Fucus spiralis*; rockpool low shore: *Sargassum muticum*, *Corallina* spp. and *Lithophyllum incrustans*; Emergent rock high shore: *Verrucaria* spp., *Chthamalus* spp., *Fucus vesiculosus* and *Fucus spiralis*; Emergent rock low shore: *Ralfsia verrucosa*, *Ulva intestinalis*, *Fucus serratus* and *Semibalanus balanoides*). Gradients of physico-chemical parameters were found in pools, with the high shore rockpool community experiencing the most extreme environment (e.g. temperature, salinity). In addition, differences in assemblages between rockpool and emergent rock reflected the great differences in desiccation stress between these habitats (e.g. greater abundances of *Ulva intestinalis*, *Porphyra* spp., barnacles on emergent rock and *Sargassum muticum*, *Corallina* spp. in pools). The former which never experience emerged conditions and the latter regularly exposed to excessive water loss. Therefore, changes in environmental stress across shore height, rockpool and emergent rock conditions constitute a good gradient to study the role of positive, negative and neutral interactions during community establishment and to test Bertness and Callaway's model (1994).

Although, habitat ameliorations are well documented in marine habitats (see Bruno and Bertness, 2001, for review) little attention have been given to the role of associational defences (Stachowicz, 2001). Investigations have been made on associational defences against mesograzers (e.g. Wahl and Hay, 1995; Karez *et al.*, 2000; Poore and Hill, 2005), cnidaria (e.g. Kerr and Paul, 1995), urchins (e.g. Pfister and Hay, 1988; Gagnon *et al.*, 2003) and fish (e.g. Hay, 1986; Littler *et al.*, 1986), but to my knowledge no studies have examined the importance of associational defences against gastropod herbivores.

The results of my work confirmed the assumptions of Dethier (1982) and Lubchenco (1982) that consumer pressure was higher in rockpools than on emergent rock. This was mainly explained by a movement of the limpet *Patella vulgata* into pools during high tide rather than higher herbivore densities or greater specific ability of *Patella ulyssiponensis* to graze under constant immersion (chapter 3). In addition, my observations confirm the principle on which the Bertness and Callaway model (1994) is based that environmental stress and consumer pressure are inversely related as also suggested by Menge and Sutherland (1987). Mobile herbivores tend to avoid highly stressful environments, and therefore, their densities and grazing activity are reduced in those habitats (Menge, 1978; Witman and Grange, 1998; Bruno and Bertness, 2001). Although it was the case concerning foraging activity, no relationship appeared between the greater consumer pressure and the generally lower herbivore densities in rockpools in the current investigation.

In addition to the naturally greater grazing intensity in rockpools than on emergent rock, manipulation of herbivores in both habitats created a gradient of consumer pressure. Rockpools at natural grazer density had the highest consumer pressure followed by grazer manipulated pools, then emergent rock left at natural density and finally herbivore manipulated emergent rock had the lowest foraging activity (see fig. 5.1 x axis and chapter 4). At natural herbivore density, grazing intensity in rockpools was recorded up to two times higher than on emergent rock. Manipulations of herbivores were more efficient with limpets than topshells, although topshell removal still allowed algae to escape grazing before their rapid recolonisation. Therefore, limpets rather than topshells were responsible for most effects due to herbivore removal. In addition, limpets had a greater effect on algal recruitment more by feeding on bedrock than topshells that feed preferentially on algal fronds or when browsing on rock surface have a less efficient radulae (Hawkins and Hartnoll, 1983b; Hawkins *et al.*, 1989a).

In the current investigation, manipulation of herbivores in both rockpools and on emergent rock created a consumer pressure gradient which was inversely related to the physical stress gradient as in the Bertness and Callaway model (1994). Changes in the intensity of these gradients had a significant influence on the nature of species interactions observed during my experiments on outcomes during succession such as sequence of colonisation and their trajectories.

5.3 Species interactions across physical stress and consumer pressure gradients

My work showed that the nature of interactions switched between positive, neutral and negative effects during succession with respect to environmental stress (between rockpool and emergent rock) and with the consumer pressure gradient.

At low physical stress and high consumer pressure (i.e. in rockpools left at natural herbivore density), facilitative associational defences occurred, with *Corallina* spp. allowing the palatable *Sargassum muticum* to establish by acting as a barrier against grazing. Once established, both species mediated other associational defences with several palatable ephemeral species growing as epiphytes (see fig. 5.1). These interactions took place in mid and low shore rockpools which corresponded to the distribution limit of the species involved, whereas in high shore rockpools *Phymatolithon* spp. dominated the community. In benign environments with low consumer pressure (i.e. rockpools at reduced herbivore density), negative interactions dominated succession (see also Lubchenco, 1982; Chapman, 1990b; Benedetti-Cecchi, 2000b). Early ephemeral colonisers did not have a detectable effect on the establishment of later perennial colonisers probably due to the fact that ephemeral species did not recruit in dense mats. However, together with *Fucus* canopy species, *Sargassum muticum*, which facilitated ephemerals under high consumer pressure, had an inhibitory effect on ephemeral species (see fig. 5.1 and also Viejo, 1997). This inhibition occurred across all three shore heights studied, with *Fucus* spp. and *Sargassum muticum* at the high shore and *Sargassum muticum* only at mid and low shore. Negative interactions also dominated the successional process on emergent rock at natural herbivore density which implied that it can be considered as a benign environment according to the Bertness and Callaway model (1994). Although foraging intensity was moderate on emergent rock at natural grazer density, herbivores completely inhibited algal establishment, and instead barnacles together with *Verrucaria* spp. dominated the plots. There was an inhibitory effect from barnacles on *Verrucaria* spp. by space pre-emption. Successional sequences were stopped there by herbivores across the intertidal gradient (see fig. 5.1, see also Sousa *et al.*, 1981; Lubchenco, 1983). Finally, in a harsh physical environments and at low consumer pressure (i.e. emergent rock left at natural grazer density), positive and negative interactions were recorded during succession. Barnacles facilitated the establishment of *Fucus* spp. by ameliorating the habitat conditions across the three shore heights studied (see also Hawkins, 1981; Lubchenco, 1983; Farrell, 1991). However, there were no discernible interaction (neutral) in some case: *Fucus* spp. did not have a detectable effect on barnacles which tolerated the canopy forming species (see also Hawkins, 1983; Jenkins *et al.*, 1999d). In addition, a reciprocal inhibitory effect was observed between barnacles and ephemeral species and between ephemeral species and *Fucus* spp. across the intertidal gradient (see fig. 5.1).

Rockpools at natural herbivore density can be considered as a potential habitat for associational defences due to high consumer pressure and low environmental stress. In the current investigation, the prevailing *Corallina* spp. facilitated colonisation of epiphytes and *Sargassum muticum*. Few dominant unpalatable species are responsible for associational defences (Hay, 1986), and therefore, *Corallina* spp. can be defined as a foundation species in the rockpools studied (*sensu* Dayton, 1972). This key habitat-forming species protected epiphytes against grazing, which were found growing on primary substrate in pools where herbivores were removed as suggested by Taylor (1960). Therefore, in natural communities with high consumer pressure, such as rockpools, palatable species occur more often as epiphytes (Hay, 1981). In addition, *Corallina* spp. facilitated the invasion of *Sargassum muticum* that in turn, hosted epiphytes (pers. obs.). However, beneficial effects from *Corallina* spp. and *Sargassum muticum* on epiphytes cannot be disentangled as they were both manipulated simultaneously; this should be investigated further. Analysis showed that increasing abundances of *Corallina* spp. had significant positive relationship with species richness of the rockpool community (correlation: r=0.82, P<0.001). Therefore, the positive interactions mediated by this foundation species, although increasing species diversity, facilitated the establishment of a non-native species rather than reducing the likelihood of invasion as proposed by Bruno *et al.* (2003). Moreover, the invasive species *Sargassum muticum*, by being the benefactor of associational defences with epiphytes, also contributed significantly to increase species richness (correlation: r=0.68, P<0.05) in rockpools under high consumer pressure, but not in pools with lower foraging activities.

In rockpools at natural herbivore density, *Corallina* spp. and *Sargassum muticum* recruited as first colonisers and then ephemerals established later in succession as epiphytes. This contrasts with the common view that early successional species are of a simple form, fast growing and opportunistic and that later species are slow growing with more complex morphologies (Pyefinch, 1943; Lubchenco and Menge, 1978; Sousa, 1979b; Hawkins, 1981; Lubchenco, 1983; Underwood *et al.*, 1983; Underwood and Jernakoff, 1984; Dethier, 1984; van Tamelen, 1987; Kim, 1997; Benedetti-Cecchi, 2000a). However, the traditional successional sequence occurred under reduced grazing pressure, in rockpools with ephemeral species recruiting first and then the canopy forming species. Similar results were found by Hay (1986) in temperate reef algal assemblages grazed by fish. Therefore, strong consumer pressure switched the arrival order of successional species and confirmed predictions of Benedetti-Cecchi (2000a) that high foraging activity would deflect succession in that way. In addition to changes in the sequence of colonisation, strong grazing intensity caused species interactions to switch from negative under lower consumer pressure to positive associational defences as predicted by the Bertness and Callaway model (1994). In rockpools where herbivores were manipulated, later colonists such as the canopy forming species *Sargassum muticum* and *Fucus* spp. inhibited early ephemeral colonists by shading them (see also Lubchenco, 1982; Hawkins and Harkin, 1985; Chapman, 1990a; Benedetti-Cecchi, 2000b). In contrast, in unmanipulated rockpools, early recruiting species such as *Sargassum muticum* facilitated those same ephemeral species at a later successional stage by associational defences.

Rockpools are an ideal habitat to study associational defences owing to their low environmental stress and high consumer pressure. Other beneficial associations have been observed during this investigation. For example in heavily grazed pools, limpet shells acted as protected substrate for palatable algae since they are less grazed than the actual bedrock allowing algae to proliferate on them (non analysed pers. data) probably due to limpet behaviour (stomping) which prevented other herbivores grazing on their shell (pers. obs.).

Less drastic changes in the nature of interactions were observed across the physical stress gradient. On the emergent rock at high environmental stress and lowest consumer pressure, a positive interaction (barnacles on *Fucus*) , but also negative structuring forces (e.g. between barnacles and ephemerals, ephemerals and *Fucus*) were recorded (see fig. 5.1). High barnacle abundance had beneficial effects on the establishment of *Fucus* spp. This occurred not by reducing grazing pressure, but by habitat amelioration through the buffering of desiccation stress, which promoted early growth and survival of *Fucus* germlings (see also Hawkins, 1981; Lubchenco, 1983). However, no buffering effect from environmental stress from *Fucus* canopy on the understorey was observed similar to previous studies (Bertness *et al.*, 1999a,b; Jenkins *et al.*, 1999a). In addition, expected switches between positive and negative interactions across the intertidal gradient as found in previous studies (Bertness and Grosholz, 1985; Lively and Raimondi, 1987; Bertness, 1989; Stephens and Bertness, 1991; Bertness and Leonard, 1997) were not observed between the three shore heights studied. This was probably a result of biogeographic biases owing to differences in climate regimes (Bertness and Leonard, 1997). My experiments were made at Wembury, South West England, in a temperate climate with mild summer temperatures and therefore, physical stress across shore and maximum recorded heat were not extreme enough to cause a switch from negative to positive interactions as the shore height increased. Similar results but with an opposite effect were observed by Bertness *et al.* (1999b). They demonstrated habitat ameliorations in the high shore but neutral rather than negative interactions in the low shore where a strong physical stress remained instead of an expected benign environment. In that case, the buffering effect of the *Fucus* canopy on the understorey organisms at high shore and switch from positive to negative interactions as the shore height decreased could be predicted if the present experiments had run at southern latitudes as found by Leonard (2000) or at the same latitude but in the future owing to global warming. However, differences in environmental stress (i.e. desiccation) between rockpools and emergent rock were sufficient to thoroughly test the Bertness and Callaway model (1994).

5.4 Conclusions

The present investigation generally supports the Bertness and Callaway model (1994) and the predictions made from it, with positive interactions found at the most extremes of the inversely related physical and consumer pressure stress gradients and neutral or negative ones at intermediate stress levels. Mechanisms involved in those positive interactions were as predicted by the model: associational defences occurred under high consumer pressure in rockpools and habitat amelioration on the emergent rock under low consumer pressure. However, the strength and the balance between positive and negative interactions depended on the intensity of consumer pressure and abiotic stress. The model can be limited in application due to the climate regime where investigations are made. In addition, my work revealed that greater consumer pressure could switch interactions from negative to positive associational defences involving the same species and as previously demonstrated for abiotic stress (Bertness *et al.*, 1999a,b; Leonard, 2000). This is in favour of the simplified version of Bertness and Callaway model proposed by Bruno and

Bertness (2001), who considered both environmental stress and consumer pressure acting in the same manner on the balance between positive and negative interactions. However, mechanisms by which positive interactions are mediated need to be stated (i.e. associational defences or habitat ameliorations). I also demonstrated that higher consumer pressure could also reverse the order of species colonisation during succession with respect to their palatability: resistant species establishing first and followed by palatable ephemeral species under strong consumer pressure with the opposite occurring under reduced grazing intensity.

Finally, my work has helped to refine predictions of positive interactions in intertidal habitats, which could play an important role in community response to climate change (Bertness and Leonard, 1997) but also on biodiversity and ecosystem functioning and stability (Patten and Odum, 1981).

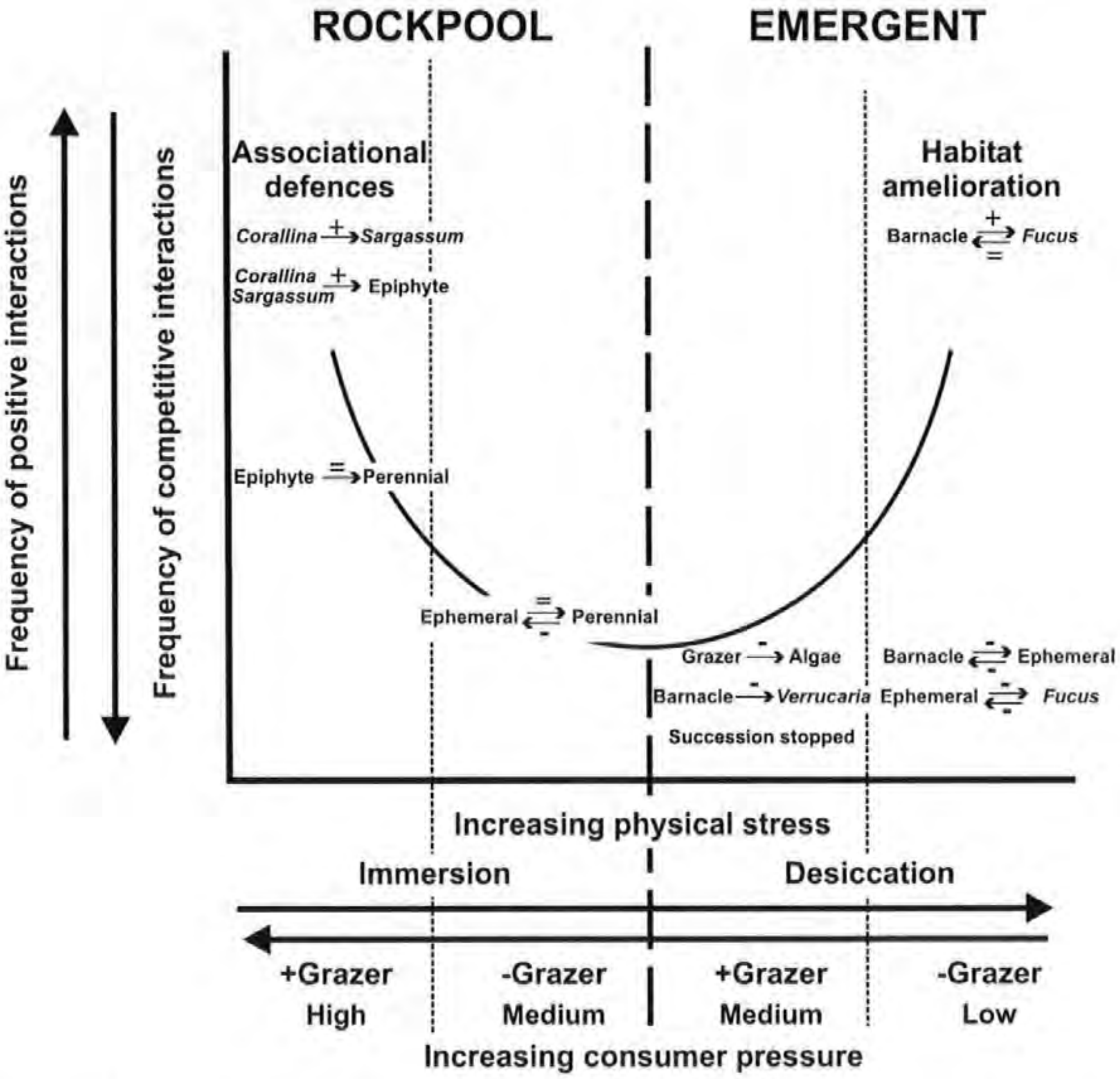

Figure 5.1: The Bertness and Callaway model (1994) as a template for species interactions (positive: +, negative: - and neutral: =) across environmental (physical stress: immersion in rockpools and desiccation on emergent rock) and consumer pressure (created by grazer manipulations: +Grazer and -Grazer) gradients observed during the investigation.

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Appendix A

Functional group species breakdown

Table A.1: Macroalgal and faunal species repartition into functional group used for the biotic sampling in chapter 2.

Articulated calcareous
Corallina elongata
Corallina officinalis

Crustose
Hildenbrandia rubra
Lithophyllum incrustans
Mesophyllum liquenoides
Phymatolithon lenormandii
Phymatolithon purpureum
Ralfsia spp.

Filamentous
Aglaothamnion spp.
Chaetomorpha linum
Cladophora spp.
Ectocarpus spp.
Polysiphonia spp.
Rhodothamniella floridula
Sphacelaria spp.

Folioses
Colpomenia peregrina
Dictyota dichotoma
Dumontia contorta
Leathesia difformis
Scytosiphon lomentaria
Ulva spp.

Corticated macrophyte
Boergeseniella spp.
Calliblepharis jubata
Ceramium spp.
Champia parvula
Chondrus crispus
Cladostephus spongiosus
Codium spp.
Gastroclonium ovatum
Gelidium spp.
Halopteris spp.
Mastocarpus stellatus
Osmundea spp.

Leathery macrophyte
Bifurcaria bifurcata
Cystoseira spp.
Fucus spp.
Himenthalia elongata
Laminaria spp.
Sargassum muticum

Animals
Patella vulgata
Patella ulyssiponensis
Littorina littorea
Gibbula umbilicalis
Osilinus lineatus

Appendix B

Dissimilarity breakdown

Dissimilarity breakdown analysis permits to identify the species responsible for differences between groups highlighted by multivariate analyses such as ANOSIM or PERMANOVA. The SIMPER analysis (similarity percentage) is one of the way to achieve it (Clarke and Warwick, 2001). SIMPER first compute the average dissimilarity $\bar{\delta}$ between all pairs of inter-group samples and break it down into separate contribution from each species to the average dissimilarity $\bar{\delta}$. For Bray-Curtis dissimilarity δ_{jk} between two samples *j* and *k*, the contribution from *i*th species, $\delta_{jk}(i)$, can be defined as:

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

with *p* being the total number of species. Then, $\delta_{jk}(i)$ is averaged over all pairs (*j*,*k*), with *j* in the first and *k* in the second group, to give the average contribution $\bar{\delta}_i$ from the *i*th species to the overall dissimilarity $\bar{\delta}$ between groups *j* and *k*. There are many pairs of samples (*j*,*k*) making up the average $\bar{\delta}_i$, and a usefull measure of how consistently a species contributes to $\bar{\delta}_i$ across all such pairs is the standard deviation SD(δ_i) of the $\delta_{jk}(i)$ values. If $\bar{\delta}_i$ is large and SD(δ_i) small (i.e large ratio $\bar{\delta}_i$/SD(δ_i)) then the *i*th species not only contributes much to the dissimilarity between the two groups but also does so consistently in inter-comparaisons of all samples in the two groups, thus it is a good discriminating species (Clarke and Warwick, 2001).

The results are presented in the tables hereafter, after the species name, the two first columns give the average abundance for each species in each of the two groups compared. The third column give the average contribution $\bar{\delta}_i$ from each species to the overall average dissimilarity $\bar{\delta}$ between the two groups. The fourth column gives the ratio $\bar{\delta}_i$/SD(δ_i) of the average contribution divided by the standard deviation of those contribution across all pairs of samples making up this average. Species are ordered in decreasing percentage contribution (Cont%) to the overall between group average dissimilarity ($\bar{\delta}$). The last column cumulates the percentage contribution of each species down the rows of the table.

Table B.1: Dissimilarity breakdown for the functional groups and species contribution to the differences between summer and winter seasons. Good discriminating functional group or species are in bold. Diss: dissimilarity.

Functional groups

	Summer	Winter	Av.Diss	Diss/SD	Cont%	Cum.%
Corticated macrophyte	19.31	6.64	11.58	1.13	26.36	26.36
Crustose	22.69	31.25	10.25	1.44	23.32	49.68
Articulated calcareous	13.58	17.31	8.92	1.40	20.3	69.98
Leathery macrophyte	7.19	5.22	5.40	1.00	12.3	82.28
Filamentous	4.58	1.89	3.36	0.99	7.64	89.92
Folioses	3.14	1.11	2.49	0.85	5.67	95.59

Species

	Summer	Winter	Av.Diss	Diss/SD	Cont%	Cum.%
Encrusting sp	22.69	31.25	11.08	1.45	23.27	23.27
***Corallina* spp.**	13.58	17.31	9.59	1.41	20.14	43.41
***Ceramium* spp.**	5.89	0.53	4.51	0.77	9.48	52.89
Sargassum	4.83	4.17	4.37	1.08	9.18	62.07
Cladophora spp.	2.67	1.56	2.65	0.76	5.56	67.63
Boergeseniella	2.19	0.53	2.01	0.40	4.22	71.85
Fucus spp.	2.28	0.78	1.97	0.64	4.14	75.99
*Gelidium*spp.	1.06	1.89	1.87	0.69	3.93	79.91
Ulva spp.	1.72	0.08	1.36	0.53	2.85	82.76
Osmundea spp.	0.69	1.31	1.26	0.57	2.65	85.41
Bare rock	1.19	0.61	1.18	0.70	2.47	87.88

Table B.2: Dissimilarity breakdown for the functional groups and species contribution to the differences between shore levels (High, Mid, Low). Good discriminating functional group or species are in bold. Diss: dissimilarity.

Functional groups for High and Mid shore level

	High	Mid	Av.Diss	Diss/SD	Cont%	Cum.%
Crustose	31.88	21.5	10.95	1.46	24.38	24.38
Articulated calcareous	9.13	17.96	10.07	1.38	22.41	46.79
Corticated macrophyte	12.25	13.25	9.76	1.13	21.73	68.52
Leathery macrophyte	8.79	7.50	6.18	1.14	13.76	82.28
Filamentous	1.50	4.58	3.31	0.93	7.37	89.66
Folioses	1.50	2.63	2.26	0.82	5.04	94.69

Functional groups for High and Low shore level

	High	Low	Av.Diss	Diss/SD	Cont%	Cum.%
Corticated macrophyte	12.25	13.42	10.43	1.13	24.83	24.83
Articulated calcareous	9.13	19.25	9.71	1.54	23.11	47.93
Crustose	31.88	27.54	8.97	1.32	21.34	69.28
Leathery macrophyte	8.79	2.33	5.92	0.91	14.09	83.36
Filamentous	1.50	3.63	2.65	0.94	6.30	89.66
Folioses	1.50	2.25	2.03	0.79	4.83	94.49

Functional groups for Mid and Low shore level

	Mid	Low	Av.Diss	Diss/SD	Cont%	Cum.%
Corticated macrophyte	13.25	13.42	11.28	1.05	27.47	27.47
Crustose	21.50	27.54	9.32	1.37	22.70	50.17
Articulated calcareous	17.96	19.25	8.07	1.47	19.65	69.82
Leathery macrophyte	7.50	2.33	4.86	1.35	11.84	81.66
Filamentous	4.58	3.63	3.67	1.05	8.94	90.6

Continued on next page

Table B.2 – continued from previous page

Species for High and Mid shore level

	High	Mid	Av.Diss	Diss/SD	Cont%	Cum.%
Encrusting sp.	31.88	21.5	11.76	1.48	23.64	23.64
***Corallina* spp.**	9.13	17.96	10.76	1.39	21.64	45.27
Sargassum muticum	5.92	5.79	5.04	1.26	10.13	55.41
***Ceramium* spp.**	3.38	4.5	4.71	0.78	9.46	64.87
Cladophora spp.	1.08	3.96	3.22	0.84	6.48	71.35
Fucus spp.	2.67	1.63	2.46	0.73	4.94	76.29
Gelidium spp.	2.04	1.29	2.10	0.71	4.21	80.51
Osmundea spp.	1.46	0.96	1.51	0.59	3.04	83.55
Bare rock	1.63	0.38	1.36	0.71	2.72	86.27
Ulva intestinalis spp.	0.67	1.25	1.31	0.54	2.63	88.9
Ulva spp.	0.46	0.79	0.94	0.40	1.90	90.8

Species for High and Low shore level

	High	Low	Av.Diss	Diss/SD	Cont%	Cum.%
***Corallina* spp.**	9.13	19.25	10.43	1.55	22.72	22.72
Encrusting sp.	31.88	27.54	9.75	1.31	21.25	43.96
Sargassum muticum	5.92	1.79	4.32	0.98	9.42	53.38
***Ceramium* spp.**	3.38	1.75	3.13	0.73	6.81	60.19
Boergeseniella spp.	0.54	3.33	2.83	0.48	6.17	66.36
Fucus spp.	2.67	0.29	2.14	0.60	4.67	71.03
Gelidium spp.	2.04	1.08	1.96	0.72	4.27	75.30
Cladophora spp.	1.08	1.29	1.52	0.68	3.31	78.61
Bare rock	1.63	0.71	1.47	0.77	3.19	81.8
Sphacelaria spp.	0.17	1.67	1.32	0.72	2.86	84.67
Osmundea spp.	1.46	0.58	1.31	0.53	2.86	87.52
Ulva spp.	0.46	1.00	1.07	0.49	2.34	89.86
Ulva intestinalis spp.	0.67	0.79	1.01	0.50	2.21	92.07

Species for Mid and Low shore level

	Mid	Low	Av.Diss	Diss/SD	Cont%	Cum.%
Encrusting sp.	21.50	27.54	10.07	1.39	22.29	22.29
***Corallina* spp.**	17.96	19.25	8.72	1.49	19.30	41.60
Sargassum muticum	5.79	1.79	4.34	1.14	9.61	51.21
***Ceramium* spp.**	4.50	1.75	3.97	0.66	8.80	60.00
***Cladophora* spp.**	3.96	1.29	3.33	0.83	7.38	67.38
Boergeseniella spp.	0.21	3.33	2.70	0.46	5.98	73.36
Gelidium spp.	1.29	1.08	1.51	0.63	3.33	76.70
Ulva intestinalis spp.	1.25	0.79	1.44	0.49	3.18	79.88
Sphacelaria spp.	0.50	1.67	1.37	0.79	3.03	82.91
Fucus spp.	1.63	0.29	1.37	0.75	3.03	85.94
Ulva spp.	0.79	1.00	1.28	0.54	2.84	88.78
Osmundea spp.	0.96	0.58	0.96	0.75	2.12	90.91

Table B.3: Dissimilarity breakdown for the functional groups and species contribution to the differences between treatments (+G,-G,-G6). Good discriminating functional group or species are in bold. Diss: dissimilarity.

Functional groups for +G and -G treatments

	+G	-G	Av.Diss	Diss/SD	Cont%	Cum.%
Corticated macrophyte	10.63	15.54	10.15	1.19	25.41	25.41
Crustose	31.04	27.63	9.18	1.42	22.97	48.38
Articulated calcareous	16.08	12.75	8.96	1.40	22.43	70.81
Leathery macrophyte	2.71	7.75	5.05	1.41	12.65	83.46
Filamentous	2.83	4.21	3.41	0.99	8.54	92.00

Species for +G and -G treatments

	+G	-G	Av.Diss	Diss/SD	Cont%	Cum.%
Encrusting sp.	31.04	27.63	9.92	1.40	22.56	22.56
***Corallina* spp.**	16.08	12.75	9.62	1.41	21.87	44.43
***Ceramium* spp.**	3.00	4.21	4.40	0.73	10.00	54.43
Sargassum muticum	2.50	5.63	4.17	1.29	9.49	63.93
***Cladophora* spp.**	1.83	3.50	3.14	0.85	7.13	71.06
***Gelidium* spp.**	1.54	2.63	2.46	0.83	5.60	76.66
Osmundea spp.	1.67	0.83	1.57	0.61	3.57	80.23
Fucus spp.	0.13	1.75	1.35	0.84	3.08	83.31
Bare rock	1.04	0.83	1.22	0.65	2.77	86.07
Ulva intestinalis spp.	0.54	0.83	0.94	0.48	2.15	88.22
Boergeseniella spp.	0.63	0.67	0.93	0.49	2.11	90.34

Appendix C

Draftman plots

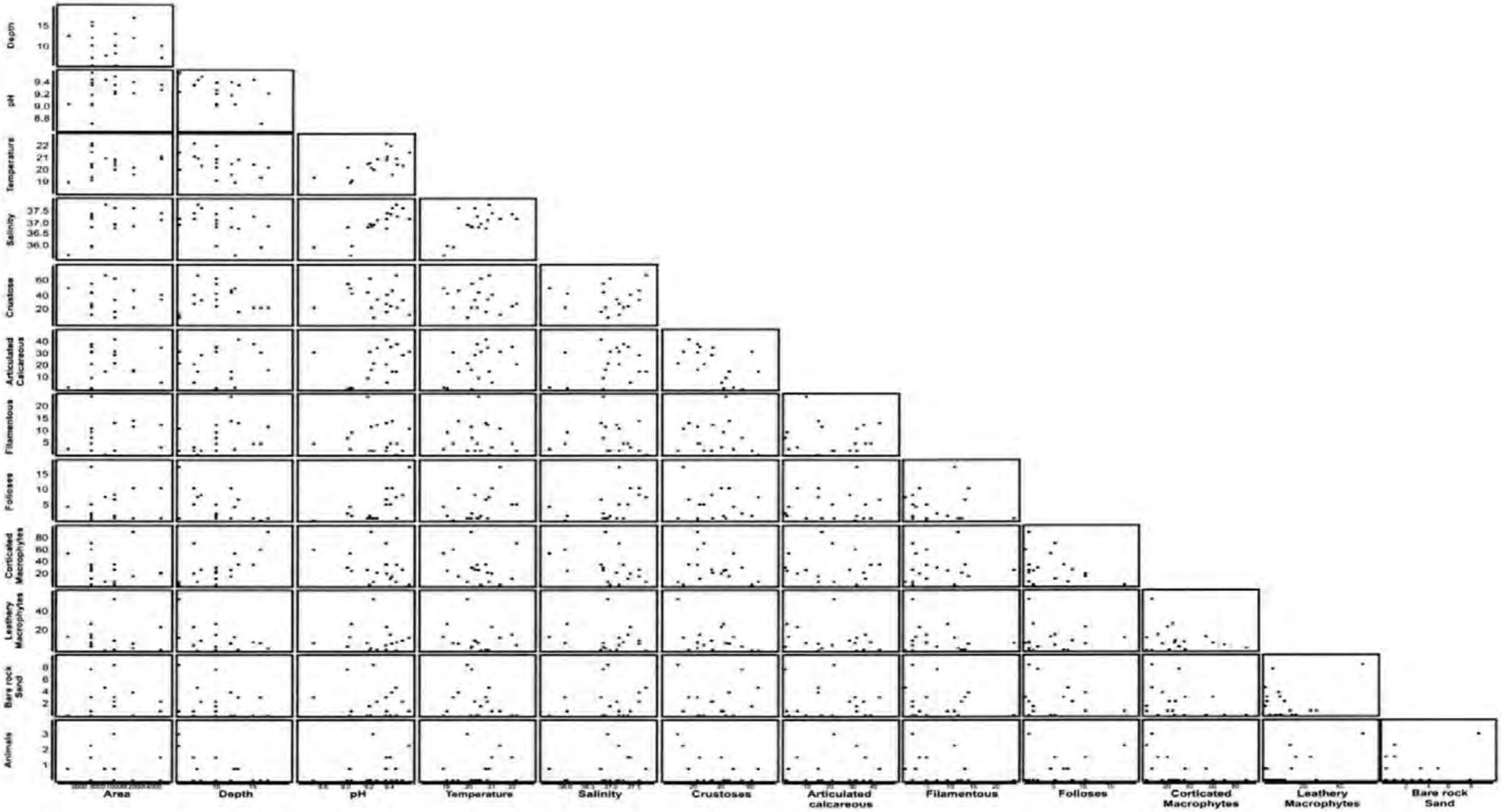

Figure C.1: Summer 2004. Draftman plots: pairwise scatter plots between all variables: Depth (max, cm), Surface area (cm^2), pH, Temperature (Degree Celsius), Salinity (ppt) and functional groups abundances: Crustose, Articulated calcareous, Filamentous, Foliose, Corticated macrophytes, Leathery macrophytes, Bare rock sand, Animals.

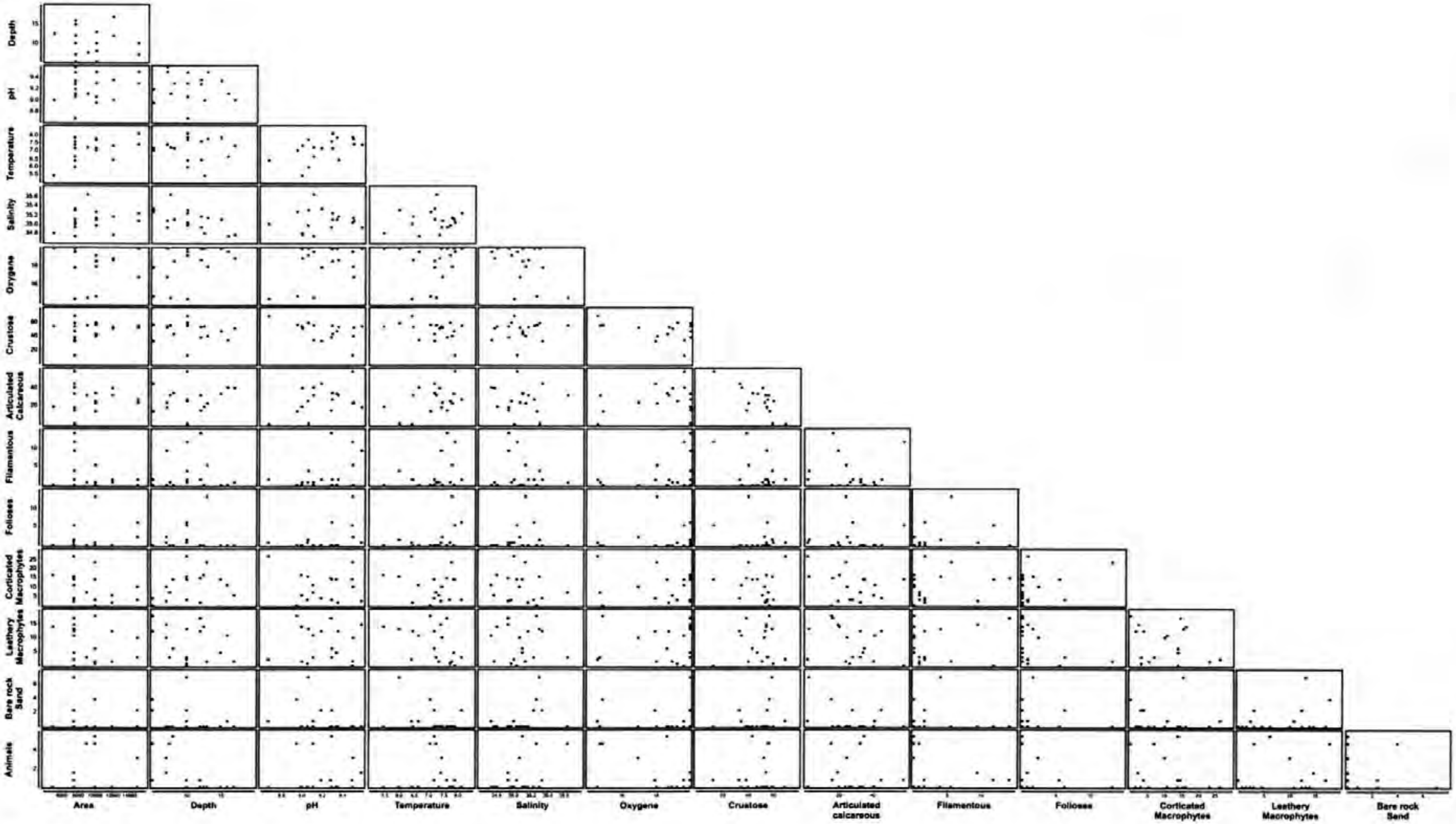

Figure C.2: Summer 2004. Draftman plots: pairwise scatter plots between all variables: Depth (max, cm), Surface area (cm^2), pH, Temperature (Degree Celsius), Salinity (ppt), Dissolved oxygen (mg.l^{-1}) and functional groups abundances: Crustose, Articulated calcareous, Filamentous, Foliose, Corticated macrophytes, Leathery macrophytes, Bare rock sand, Animals.

Appendix D

Succession: representative species as a function of time

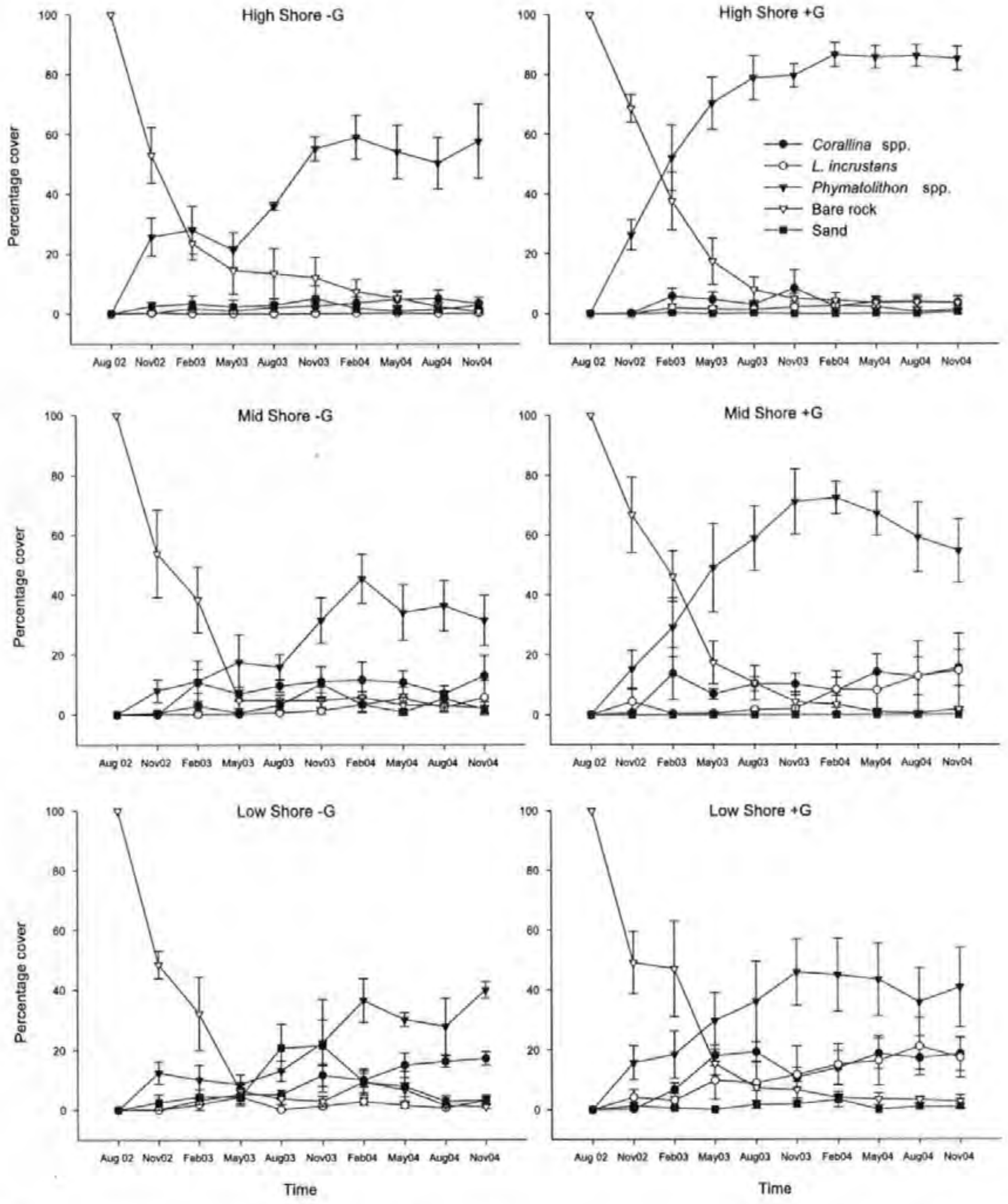

Figure D.1: Exp 1: Succession in rockpools. Percentage cover of bare rock, encrusting and coralline species: *Lithophyllum incrustans*, *Phymatolithon* spp. and *Corallina* spp. during succession started in Summer 2002 in rockpools at each of three shore levels: High, Mid and Low shore at reduced grazer density (-G) and natural grazer density (+G). Data are mean of percentage cover (±SE) of 2 replicate 20×20cm quadrats averaged for each of the 4 replicate pools (n=4).

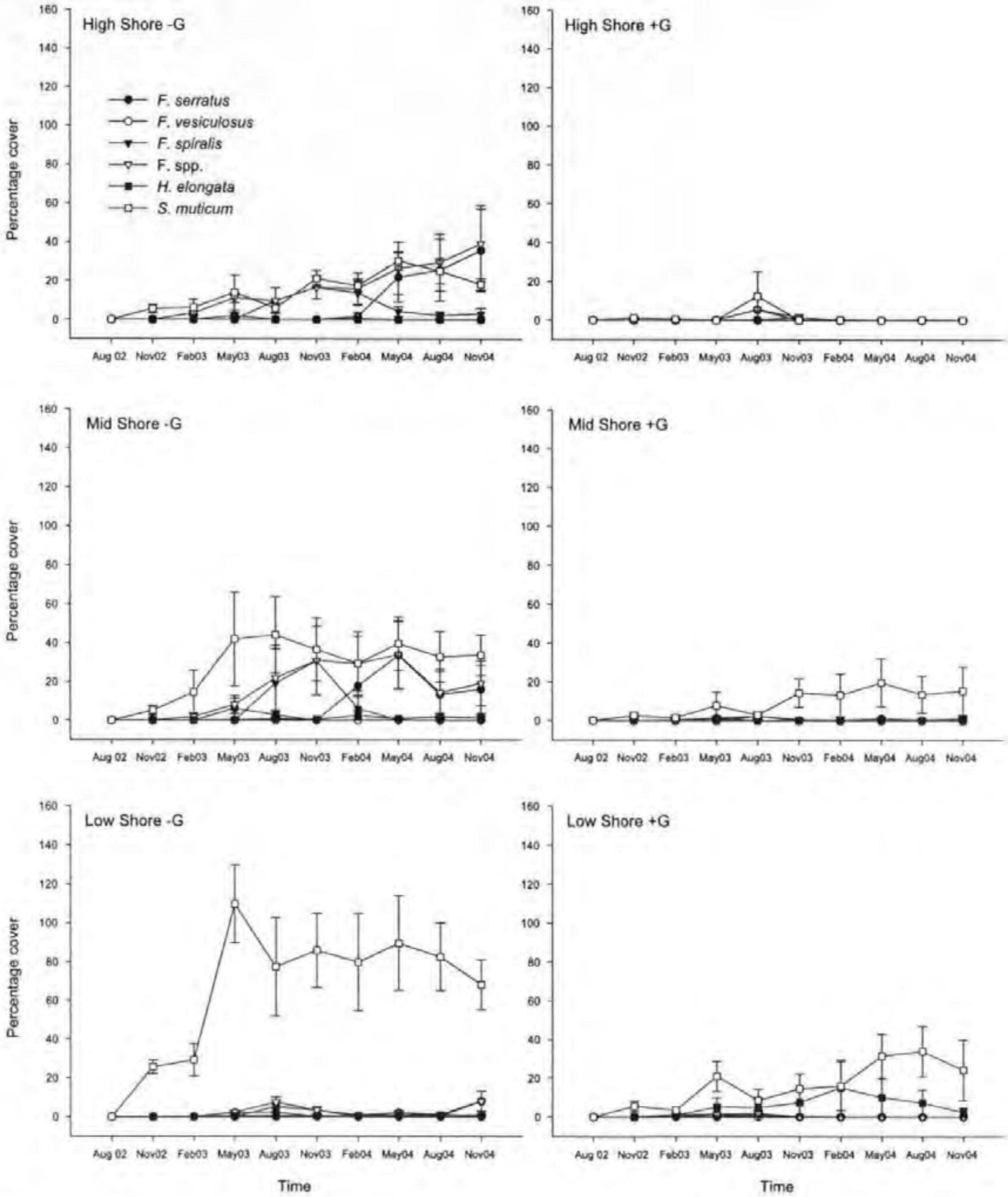

Figure D.2: Exp 1: Succession in rockpools. Percentage cover of canopy species: *Fucus serratus*, *F. vesiculosus*, *F. spiralis*, *Himanthalia elongata* and *Sargassum muticum* during succession started in Summer 2002 in rockpools at each of three shore levels: High, Mid and Low shore at reduced grazer density (-G) and natural grazer density (+G). Data are mean of percentage cover (±SE) of 2 replicate 20×20cm quadrats averaged for each of the 4 replicate pools (n=4).

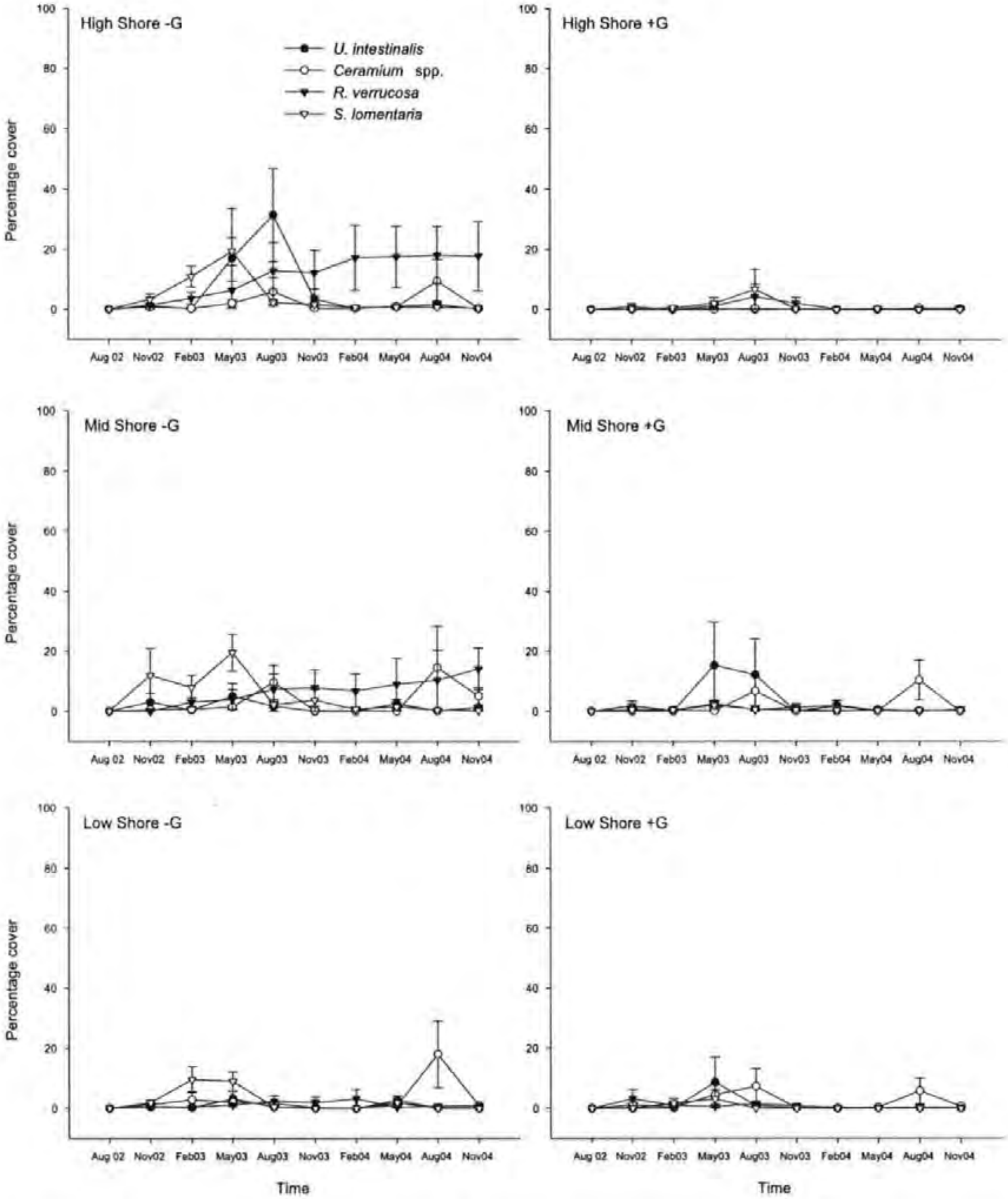

Figure D.3: Exp 1: Succession in rockpools. Percentage cover of ephemeral species: *Ulva intestinalis*, *Ceramium* spp., *Scytosiphon lomentaria* and the encrusting algae *Ralfsia verrucosa* during succession started in Summer 2002 in rockpools at each of three shore levels: High, Mid and Low shore at reduced grazer density (-G) and natural grazer density (+G). Data are mean of percentage cover (±SE) of 2 replicate 20×20cm quadrats averaged for each of the 4 replicate pools (n=4).

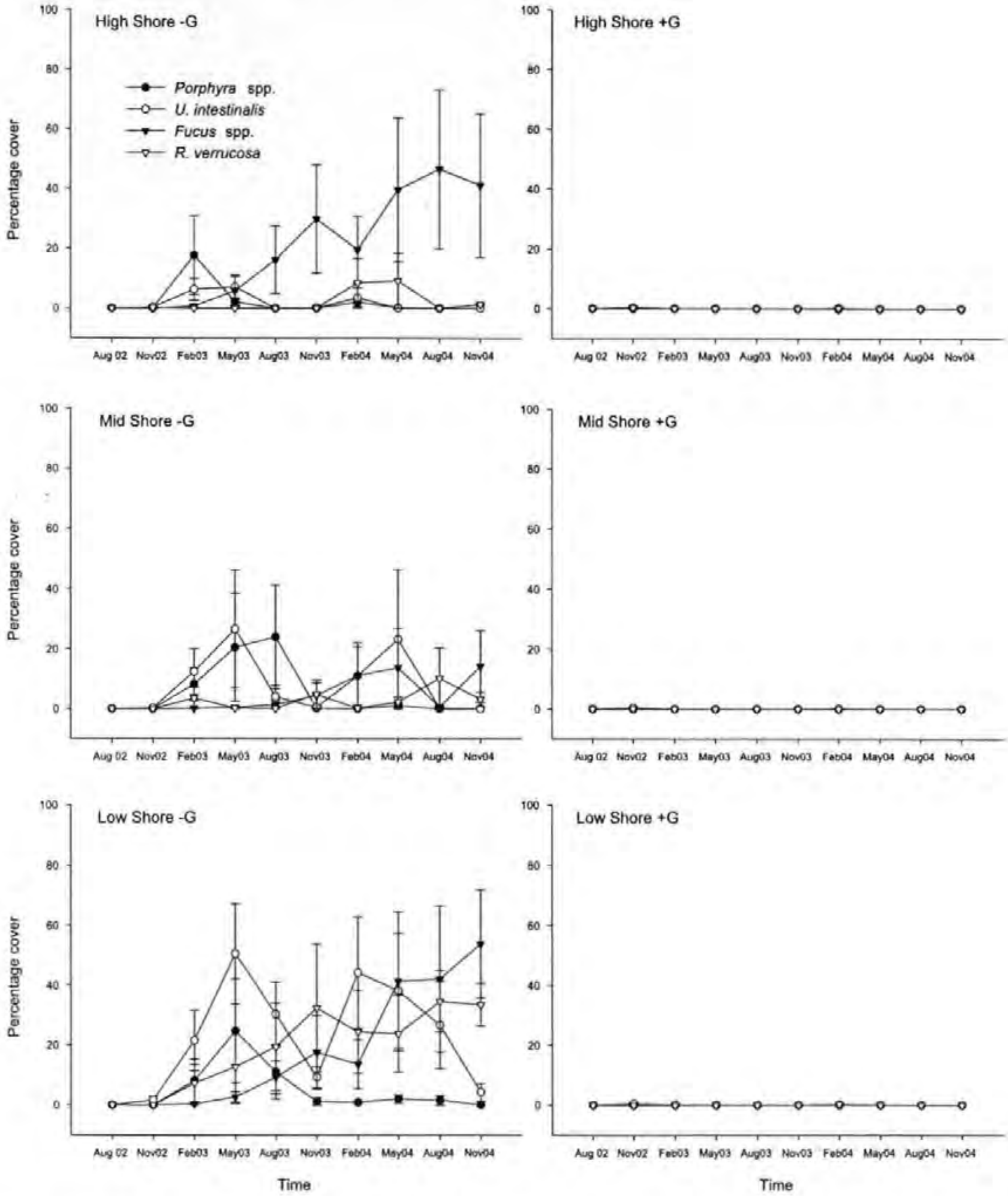

Figure D.4: Exp 1: Succession on emergent rock. Percentage cover of *Ralfsia verrucosa*, ephemerals: *Ulva intestinalis* and *Porphyra spp.* and the total cover of *Fucus spp.* during succession started in Summer 2002 on emergent rock at each of three shore levels: High, Mid and Low shore at reduced grazer density (-G) and natural grazer density (+G). Data are mean of percentage cover (±SE) of 2 replicate 20×20cm quadrats averaged for each of the 4 replicate plots (n=4).

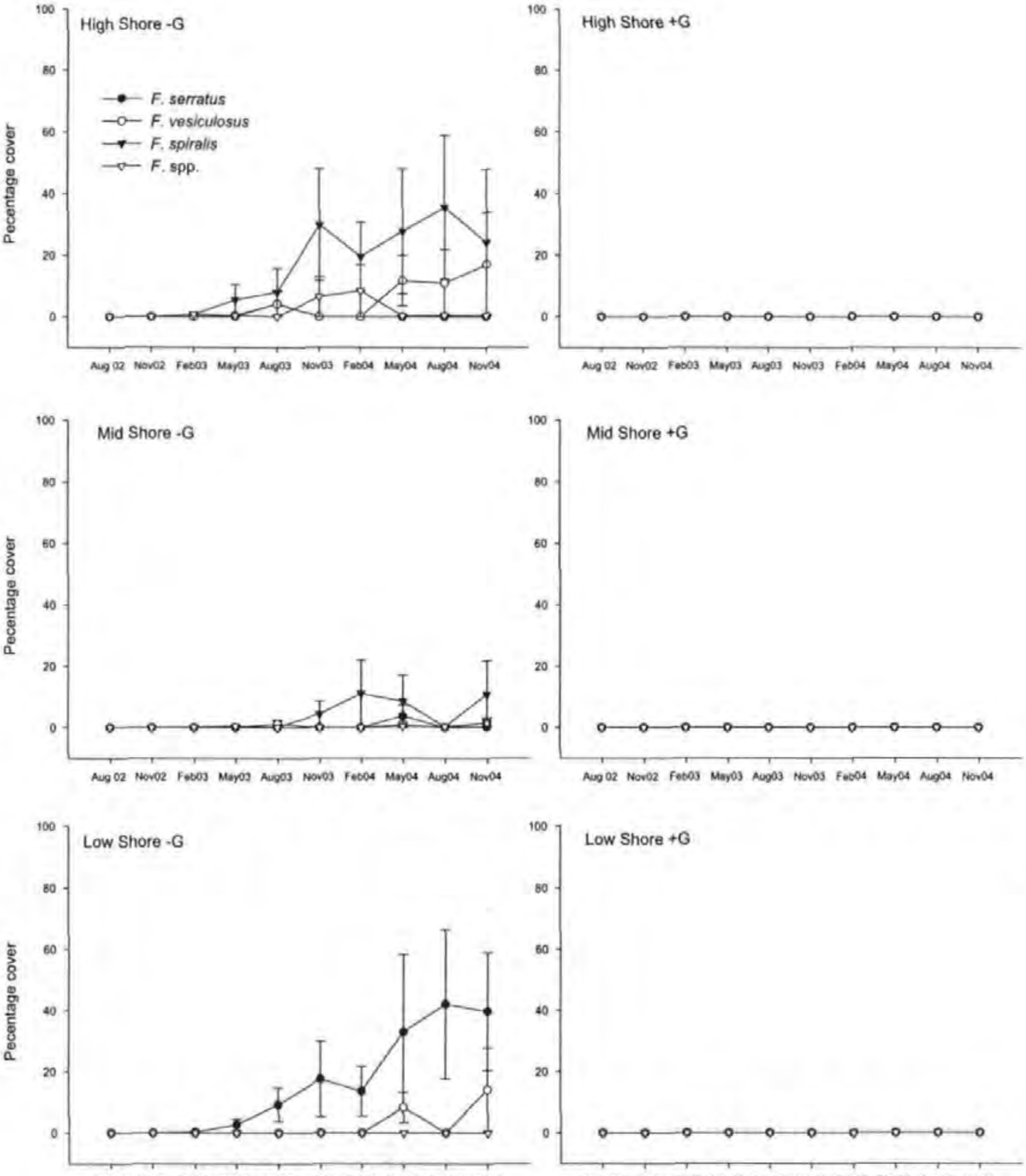

Figure D.5: Exp 1: Succession on emergent rock. Percentage cover of *Fucus serratus*, *Fucus vesiculosus*, *Fucus spiralis* species during succession started in Summer 2002 on emergent rock at each of three shore levels: High, Mid and Low shore at reduced grazer density (-G) and natural grazer density (+G). Data are mean of percentage cover (±SE) of 2 replicate 20×20cm quadrats averaged for each of the 4 replicate plots (n=4).

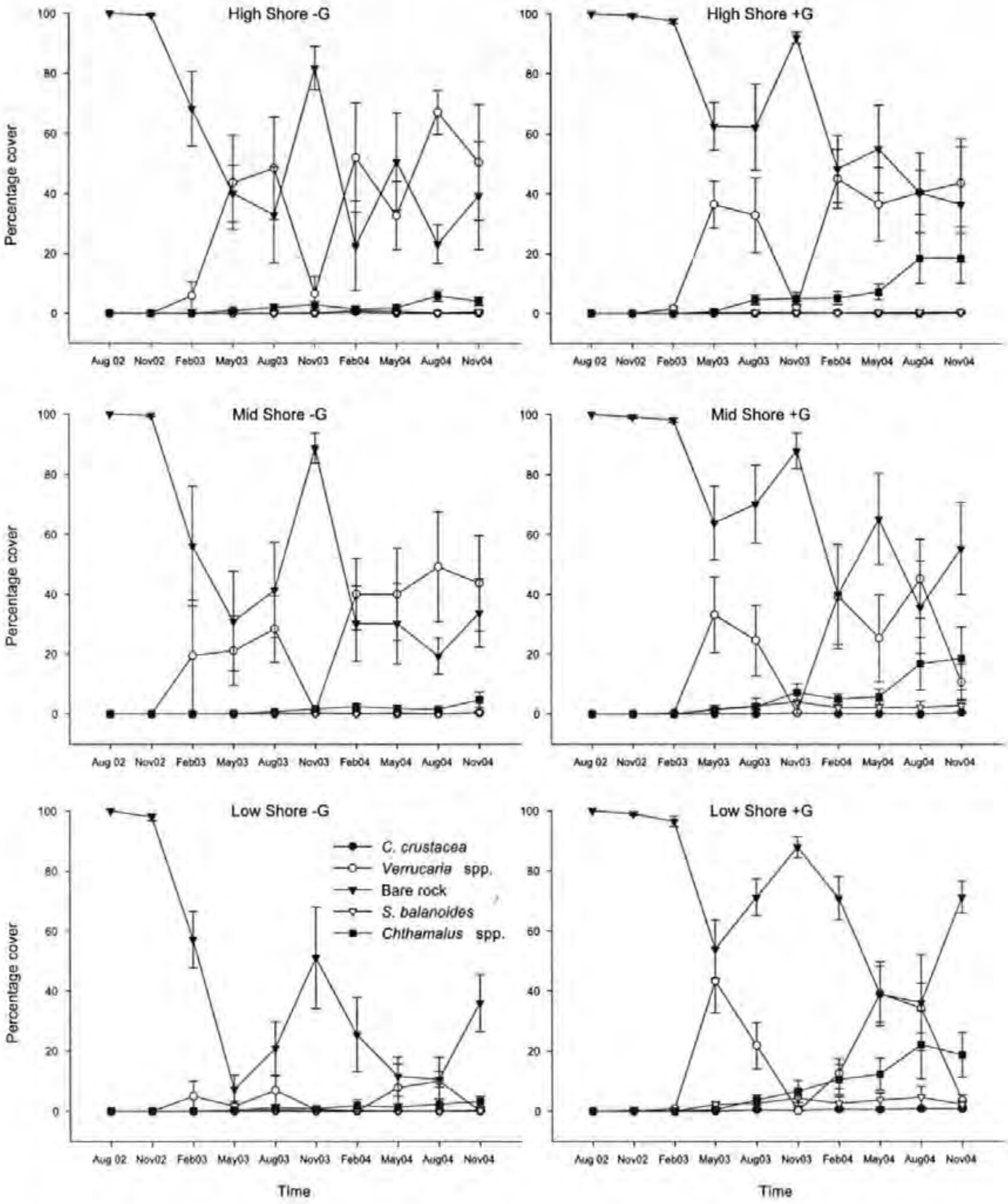

Figure D.6: Exp 1: Succession on emergent rock. Percentage cover of bare rock, barnacles: *Semibalanus balanoides* and *Chthamalus* spp., *Verrucaria spp.* and *Calothrix crustacea* during succession started in Summer 2002 on emergent rock at each of three shore levels: High, Mid and Low shore at reduced grazer density (-G) and natural grazer density (+G). Data are mean of percentage cover (±SE) of 2 replicate 20×20cm quadrats averaged for each of the 4 replicate plots (n=4).

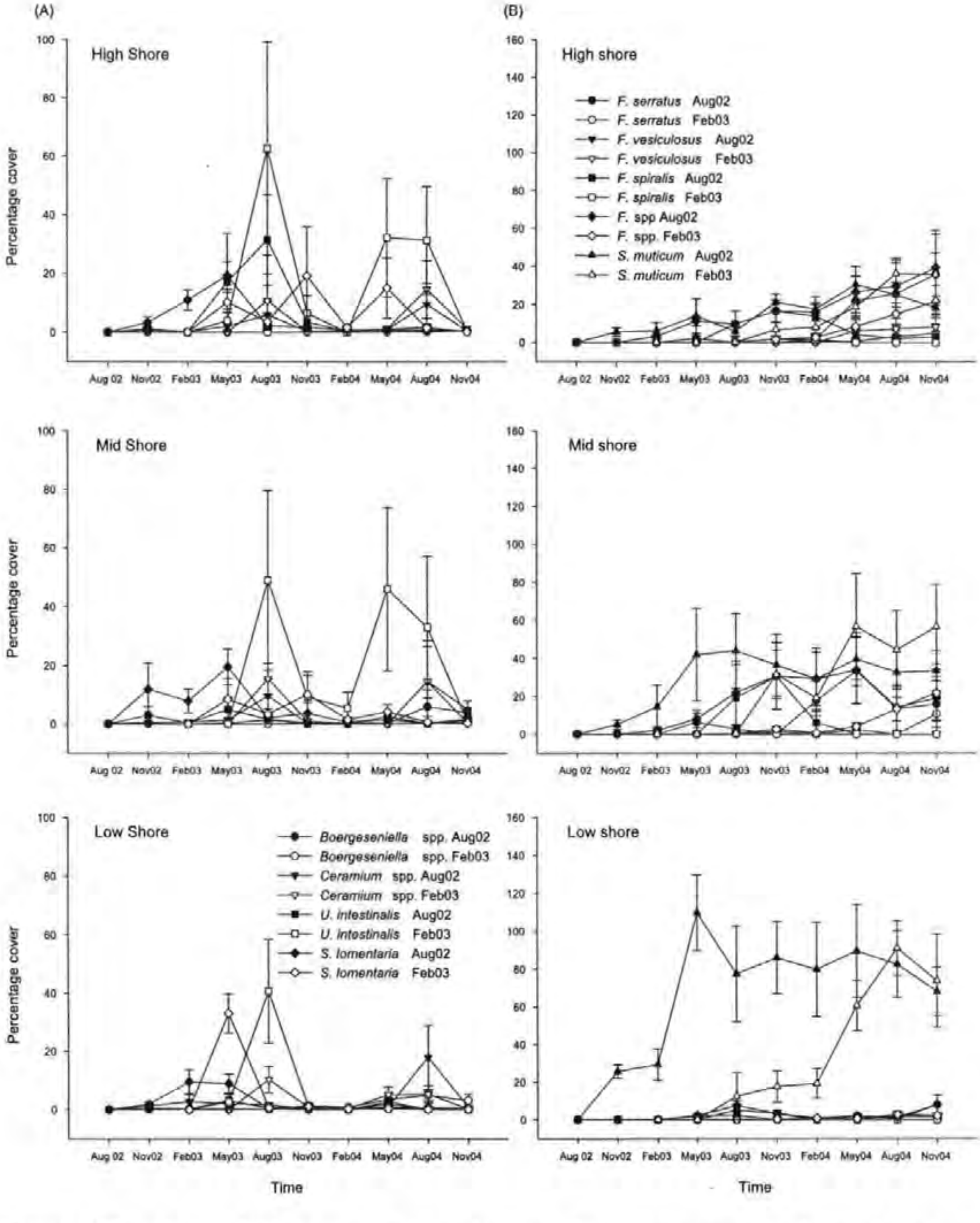

Figure D.7: Exp2. Initiation timing in rockpools. Percentage cover of ephemeral species (A): *Boergeseniella spp., Ceramium spp., Ulva intestinalis, Scytosiphon lomentaria* and canopy species (B): Fucoids and *Sargassum muticum* during succession started in August 2002 (black symbols) and February 2003 (white symbols) in rockpools at each of three shore levels: High, Mid and Low shore. All plots were at reduced grazer density. Data are mean of percentage cover (±SE) of 2 replicate 20×20cm quadrats averaged for each of the 4 replicate pools (n=4).

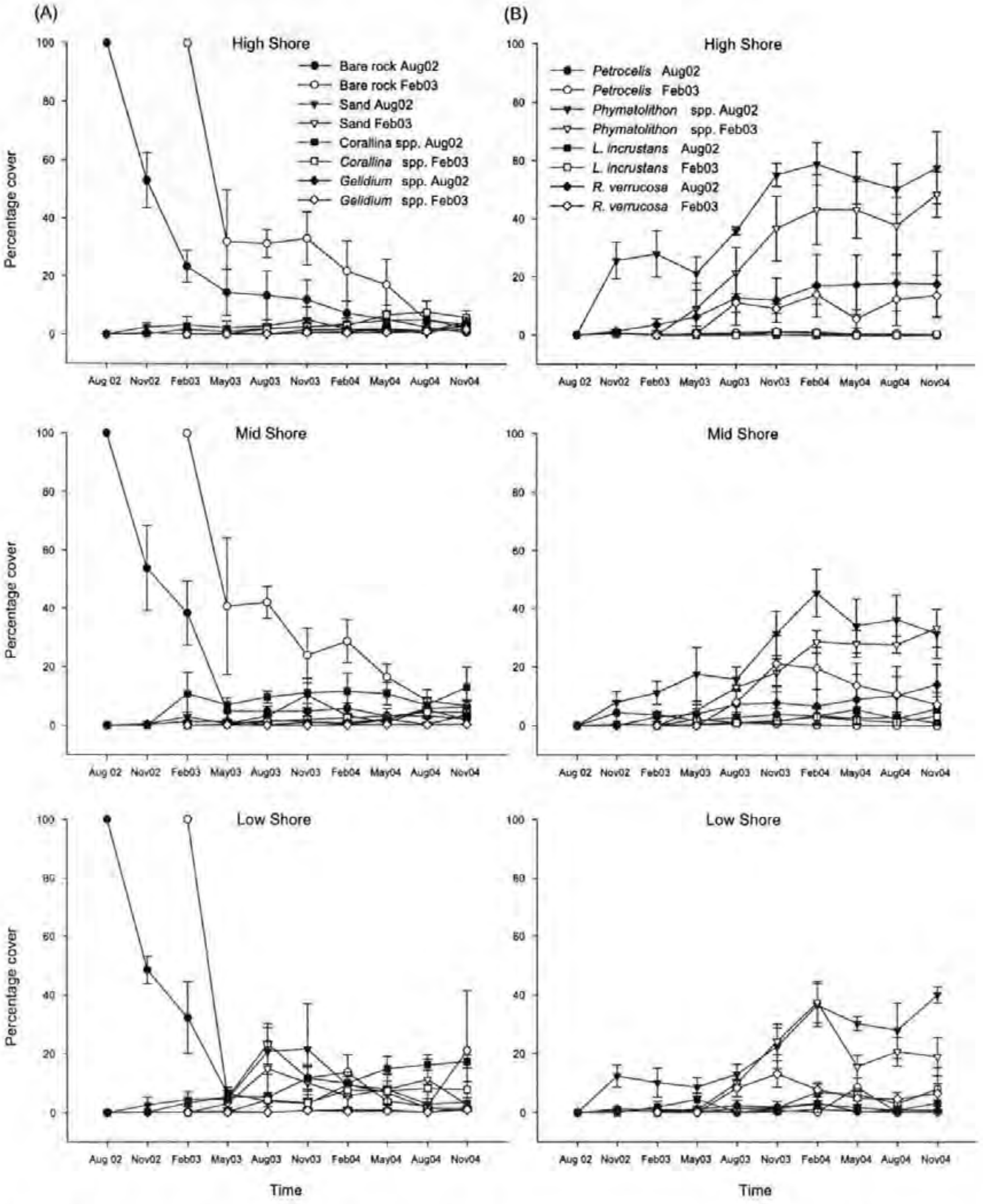

Figure D.8: Exp2. Initiation timing in rockpools. Percentage cover of bare rock, sand, *Corallina* spp. and *Gelidium* spp. (A) and incrustant species (B): *Ralfsia verrucosa*, *Petrocelis*, *Lithophyllum incrustans*, *Phymatolithon spp.* during succession started in August 2002 (black symbols) and February 2003 (white symbols) in rockpools at each of three shore levels: High, Mid and Low shore. All plots were at reduced grazer density. Data are mean of percentage cover (±SE) of 2 replicate 20×20cm quadrats averaged for each of the 4 replicate pools (n=4).

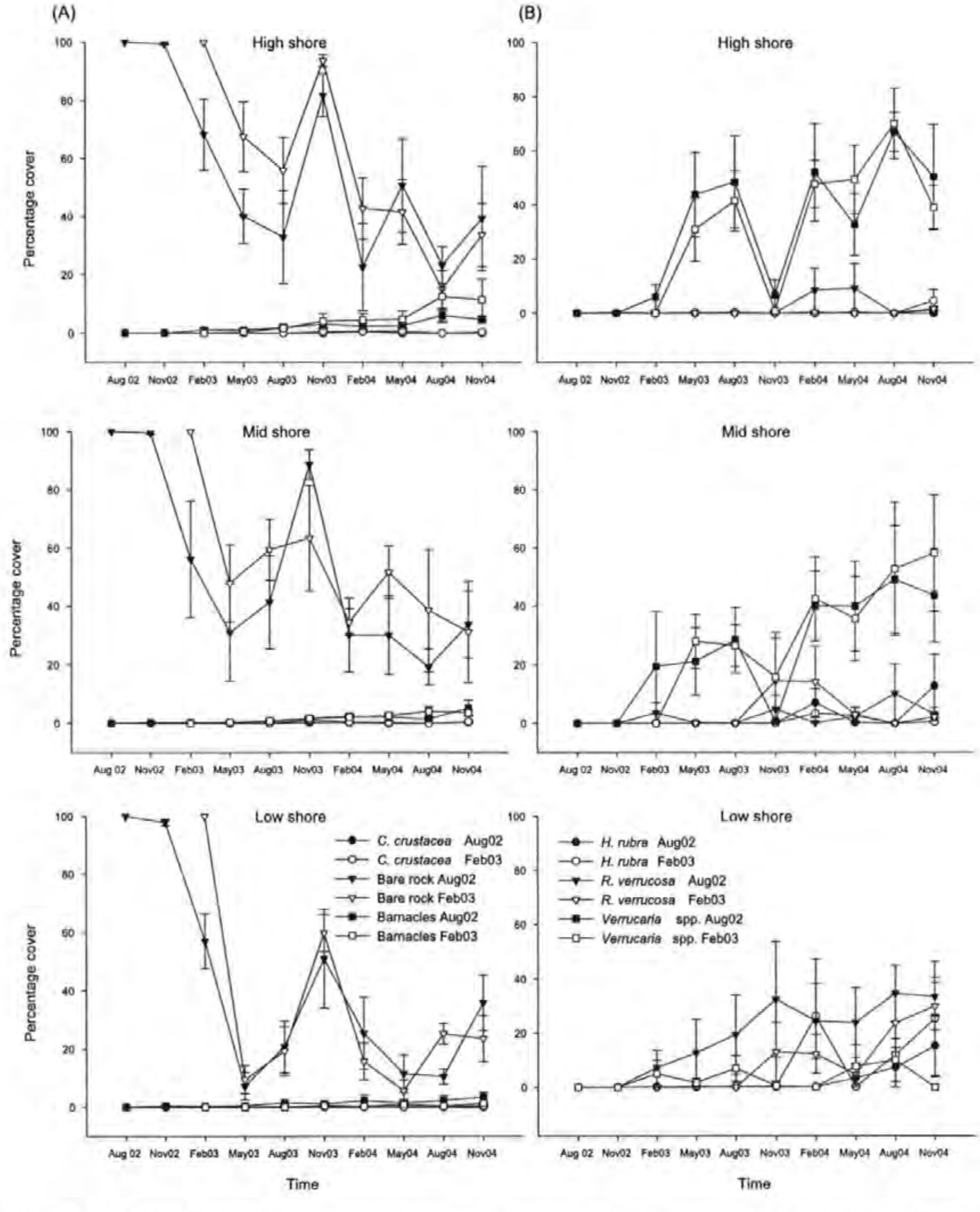

Figure D.9: Exp2. Initiation timing on emergent rock. Percentage cover of (A): bare rock, *Calothrix crustacea* and barnacles including *Semibalanus balanoides*, *Chthamalus* spp., *Elminius modestus* and encrustant species (B): *Hildenbrandia rubra*, *Ralfsia verrucosa* and the lichens *Verrucaria* spp. during succession started in August 2002 (black symbols) and February 2003 (white symbols) on emergent rock at each of three shore levels: High, Mid and Low shore. All plots were at reduced grazer density. Data are mean of percentage cover (±SE) of 2 replicate 20×20cm quadrats averaged for each of the 4 replicate plots (n=4).

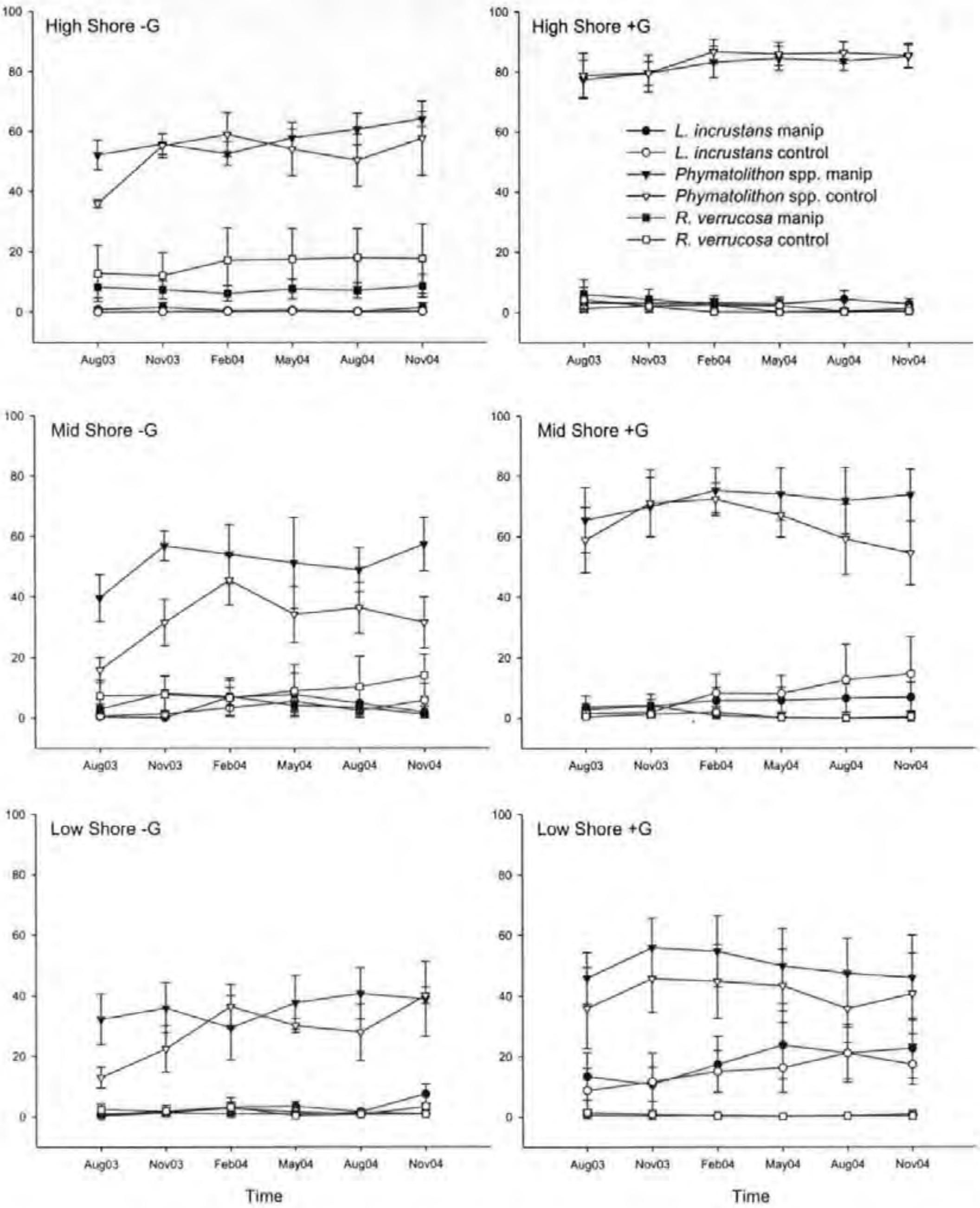

Figure D.10: Exp3. Ephemeral removal in rockpool. Percentage cover of perennial encrusting species: *Lithophyllum incrustans*, *Phymatolithon* spp., *Ralfsia verrucosa* in manipulated plot where ephemerals were removed (manip: black symbols) and in unmanipulated plots (control: white symbols) during succession started in Summer 2002 at each of three shore levels: High, Mid and Low shore in rockpools at reduced grazer density (-G) and natural grazer density (+G). Data are mean of percentage cover (±SE) of 2 replicate 20×20cm quadrats averaged for each of the 4 replicate pools (n=4).

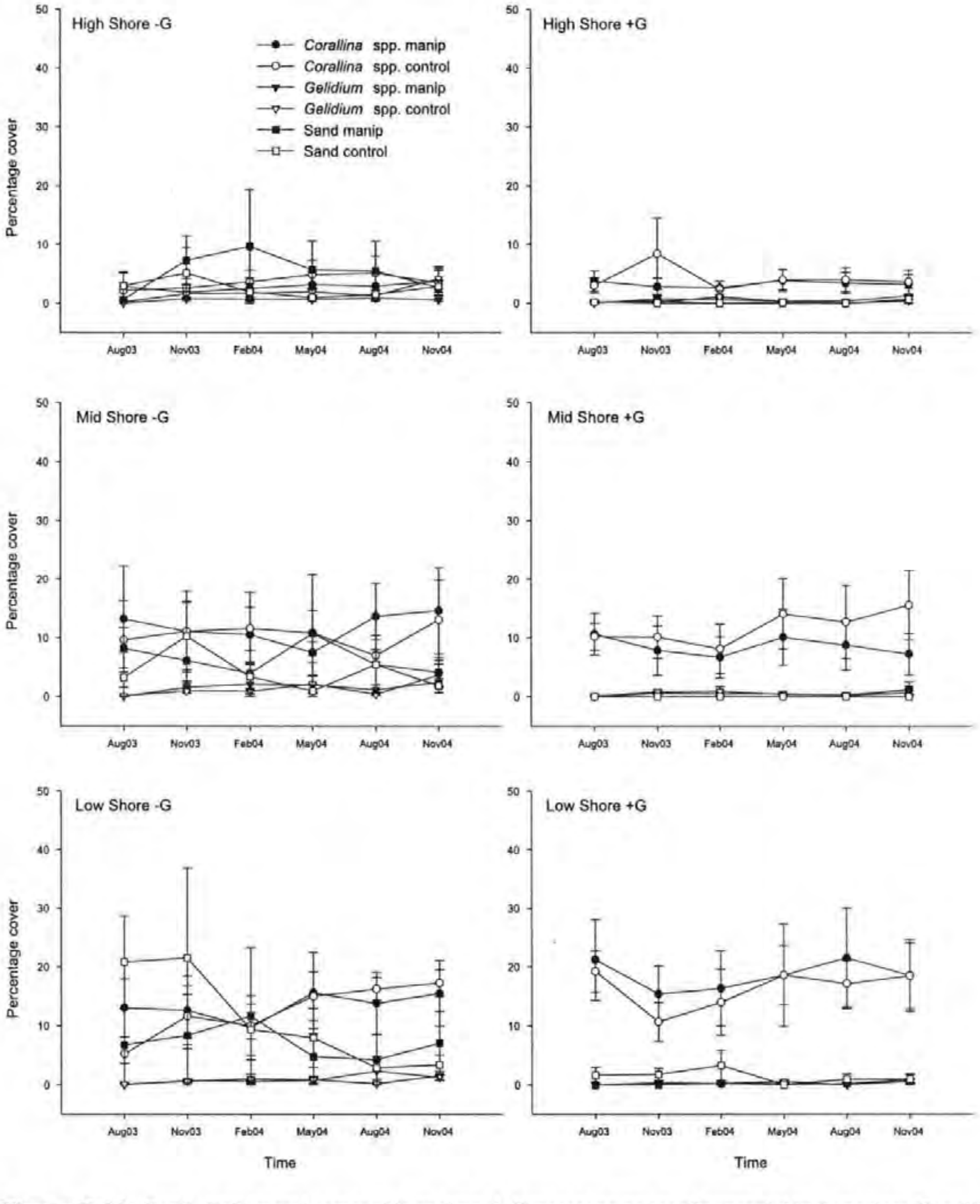

Figure D.11: Exp3. Ephemeral removal in rockpool. Percentage cover of perennial turf species: *Corallina* spp., *Gelidium* spp. and sand cover in manipulated plot where ephemerals were removed (manip: black symbols) and in unmanipulated plots (control: white symbols) during succession started in Summer 2002 at each of three shore levels: High, Mid and Low shore in rockpools at reduced grazer density (-G) and natural grazer density (+G). Data are mean of percentage cover (±SE) of 2 replicate 20×20cm quadrats averaged for each of the 4 replicate pools (n=4).

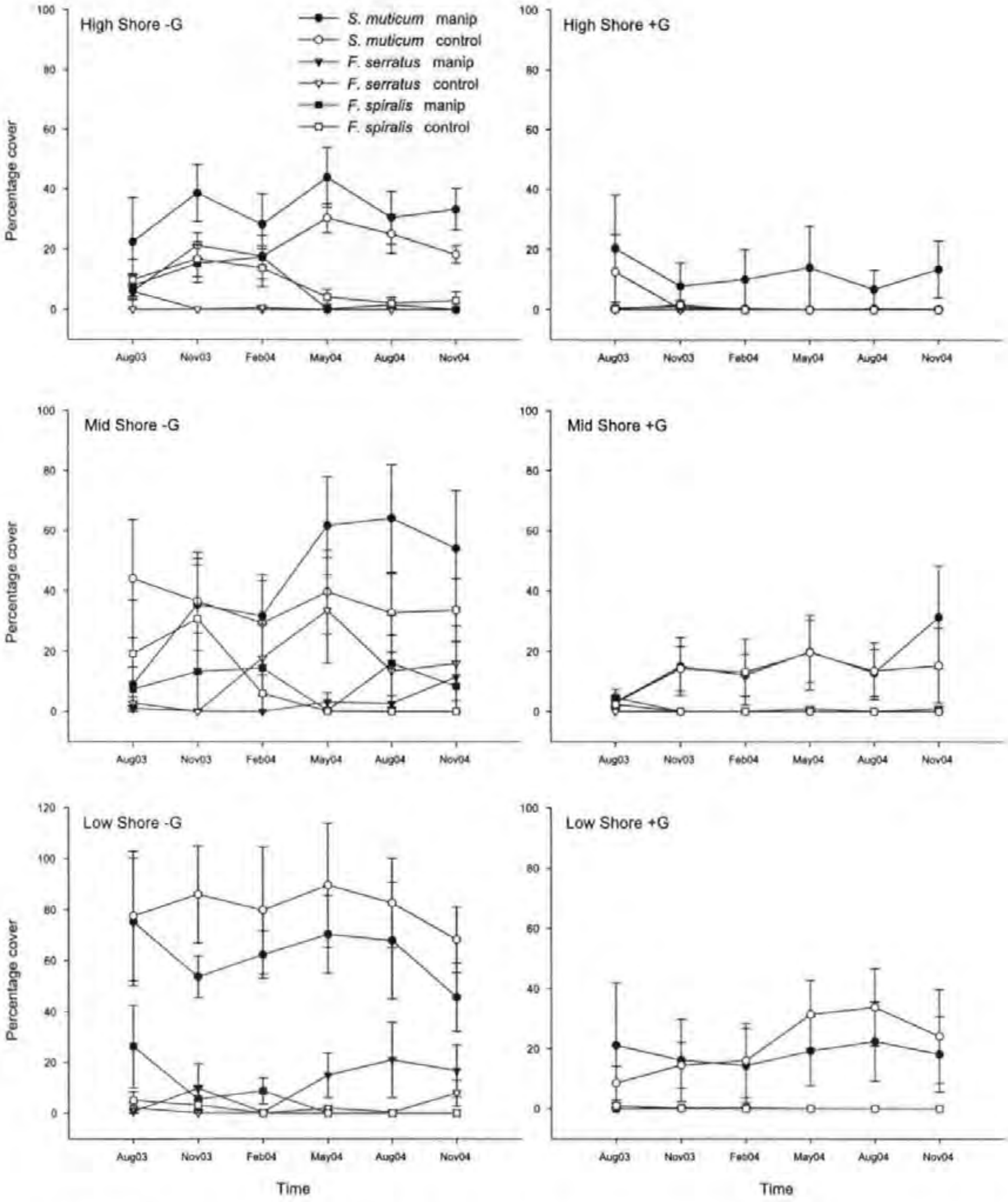

Figure D.12: Exp3. Ephemeral removal in rockpool. Percentage cover of perennial canopy species: *Sargssum muticum*, *Fucus serratus*, *Fucus spiralis* in manipulated plot where ephemerals were removed (manip: black symbols) and in unmanipulated plots (control: white symbols) during succession started in Summer 2002 at each of three shore levels: High, Mid and Low shore in rockpools at reduced grazer density (-G) and natural grazer density (+G). Data are mean of percentage cover (±SE) of 2 replicate 20×20cm quadrats averaged for each of the 4 replicate pools (n=4).

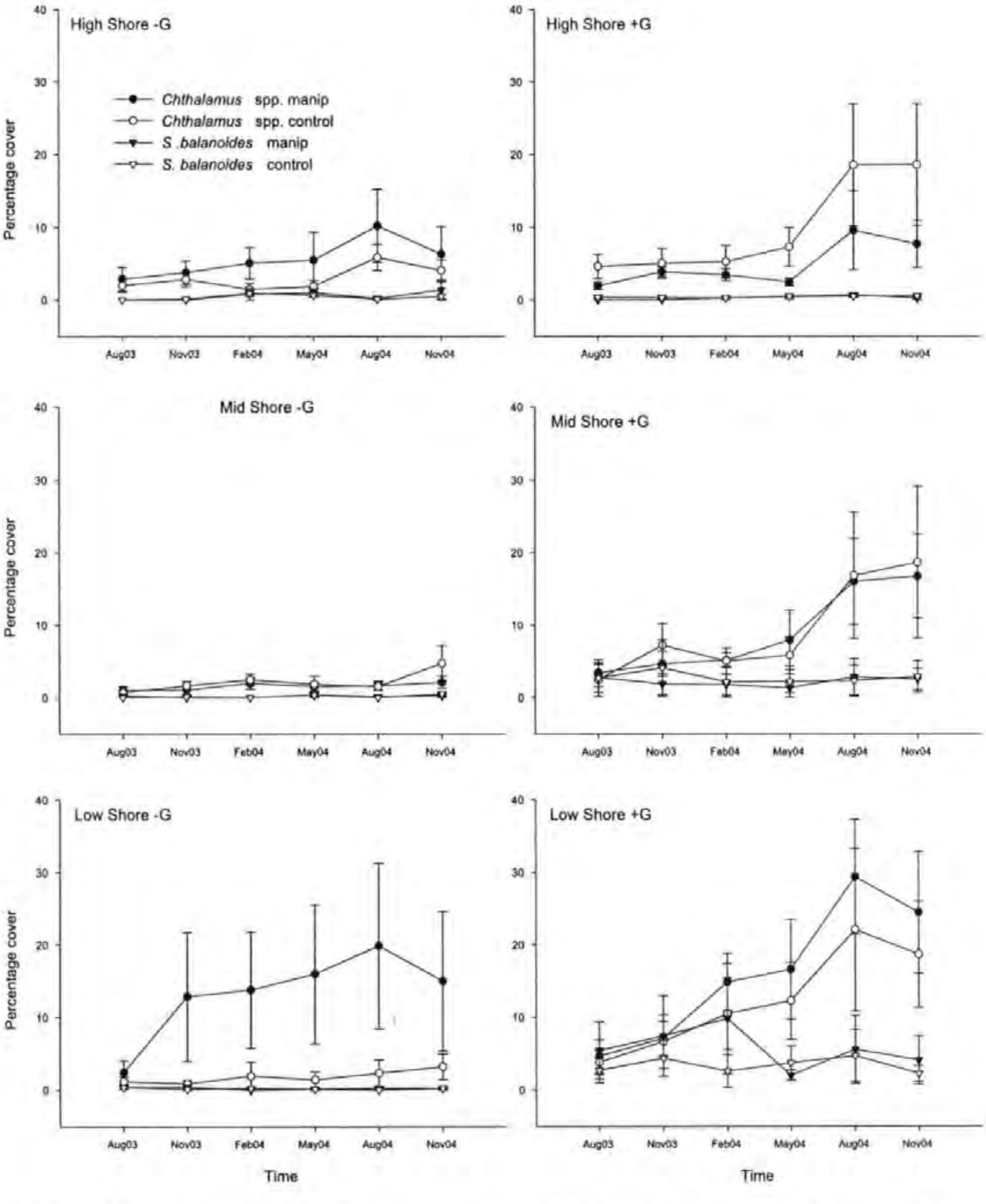

Figure D.13: Exp3. Ephemeral removal on emergent rock. Percentage cover of barnacle species: *Chthamalus* spp. and *Semibalanus balanoides* in manipulated plot where ephemerals were removed (manip: black symbols) and in unmanipulated plots (control: white symbols) during succession started in Summer 2002 at each of three shore levels: High, Mid and Low shore on emergent rock at reduced grazer density (-G) and natural grazer density (+G). Data are mean of percentage cover (±SE) of 2 replicate 20×20cm quadrats averaged for each of the 4 replicate plots (n=4).

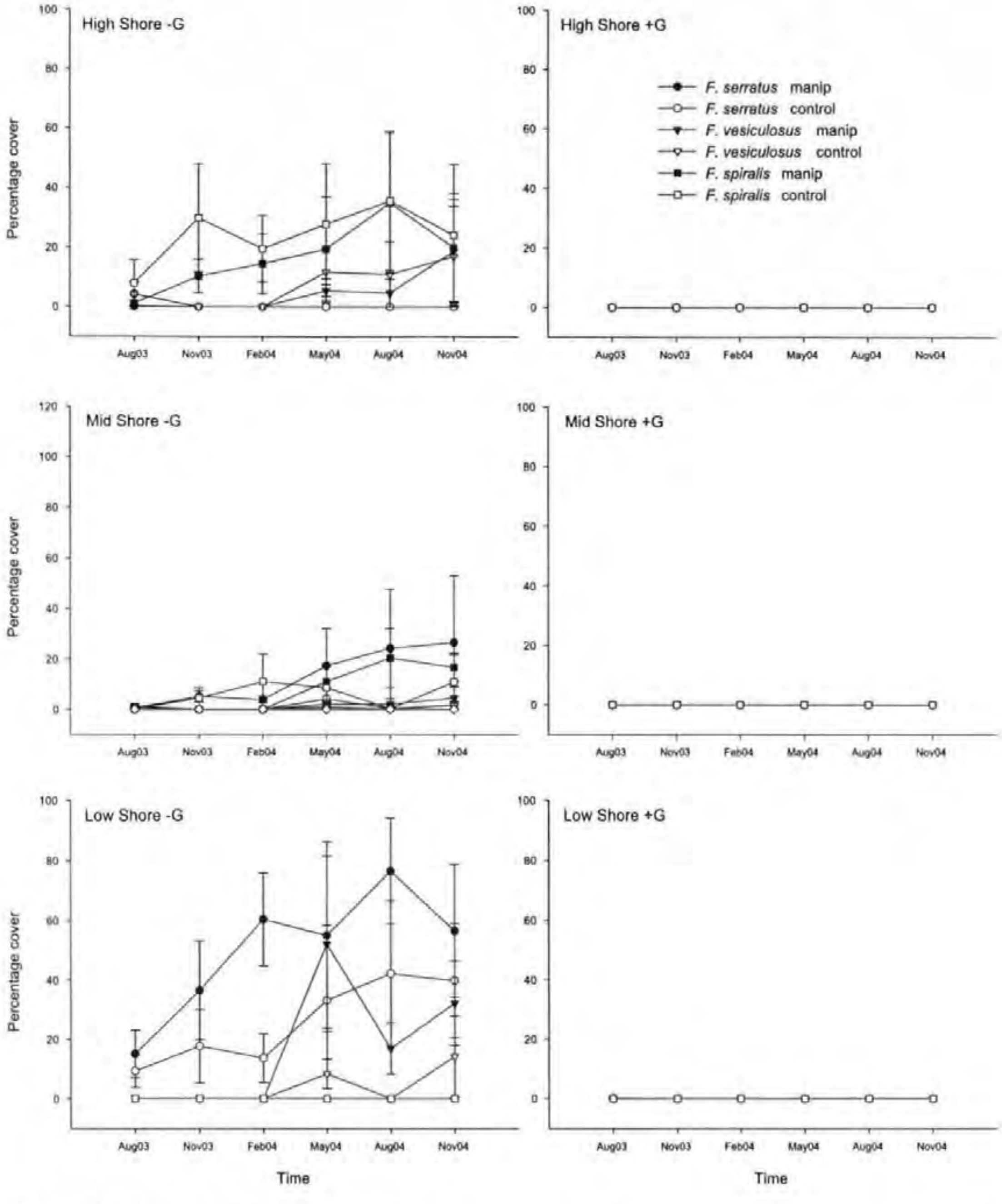

Figure D.14: Exp3. Ephemeral removal on emergent rock. Percentage cover of canopy species: *Fucus serratus, Fucus vesiculosus, Fucus spiralis* in manipulated plot where ephemerals were removed (manip: black symbols) and in unmanipulated plots (control: white symbols) during succession started in Summer 2002 at each of three shore levels: High, Mid and Low shore on emergent rock at reduced grazer density (-G) and natural grazer density (+G). Data are mean of percentage cover (±SE) of 2 replicate 20×20cm quadrats averaged for each of the 4 replicate plots (n=4).

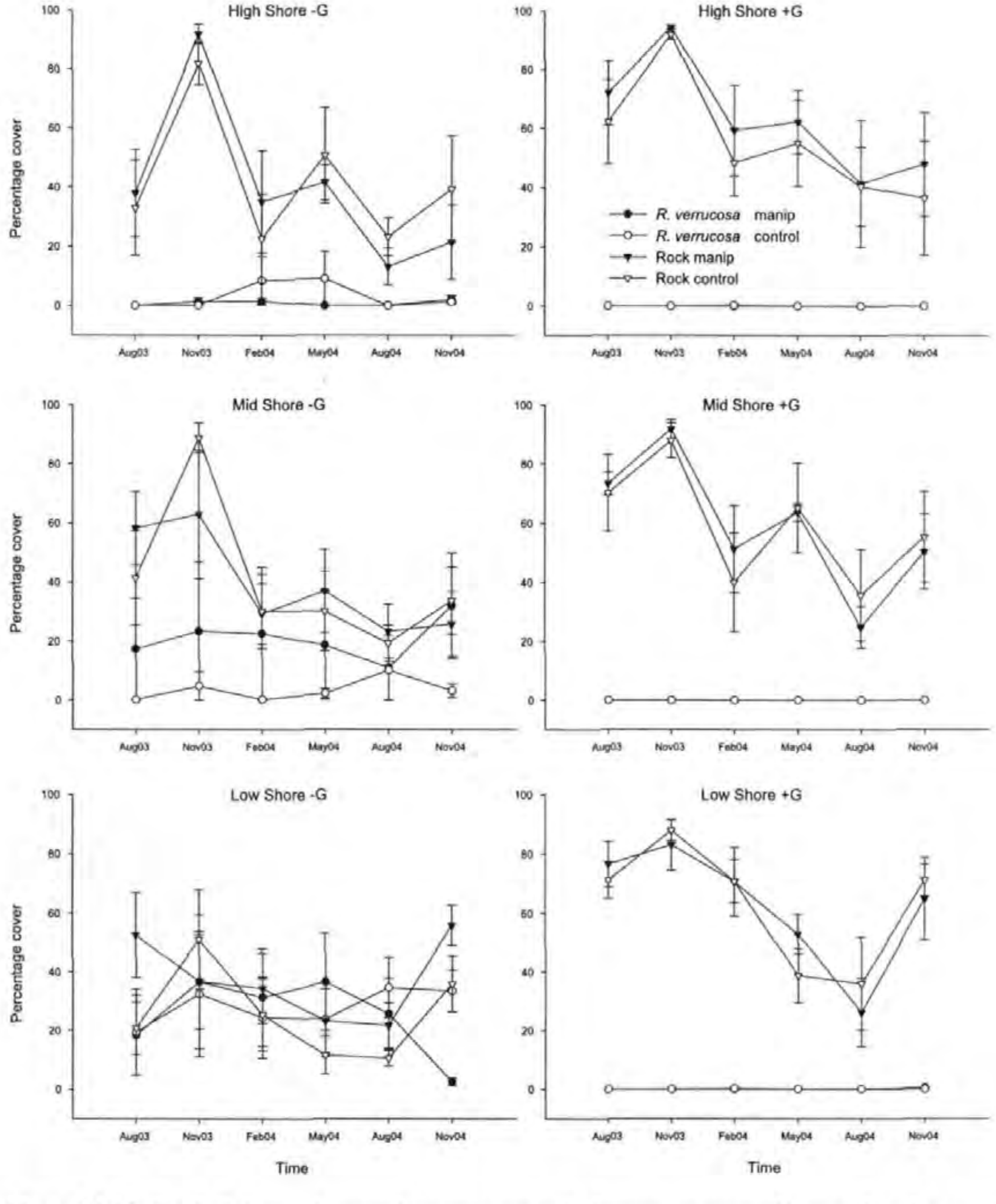

Figure D.15: Exp3. Ephemeral removal on emergent rock. Percentage cover of bare rock and encrusting species: *Ralfsia verrucosa* in manipulated plot where ephemerals were removed (manip: black symbols) and in unmanipulated plots (control: white symbols) during succession started in Summer 2002 at each of three shore levels: High, Mid and Low shore on emergent rock at reduced grazer density (-G) and natural grazer density (+G). Data are mean of percentage cover (±SE) of 2 replicate 20×20cm quadrats averaged for each of the 4 replicate plots (n=4).

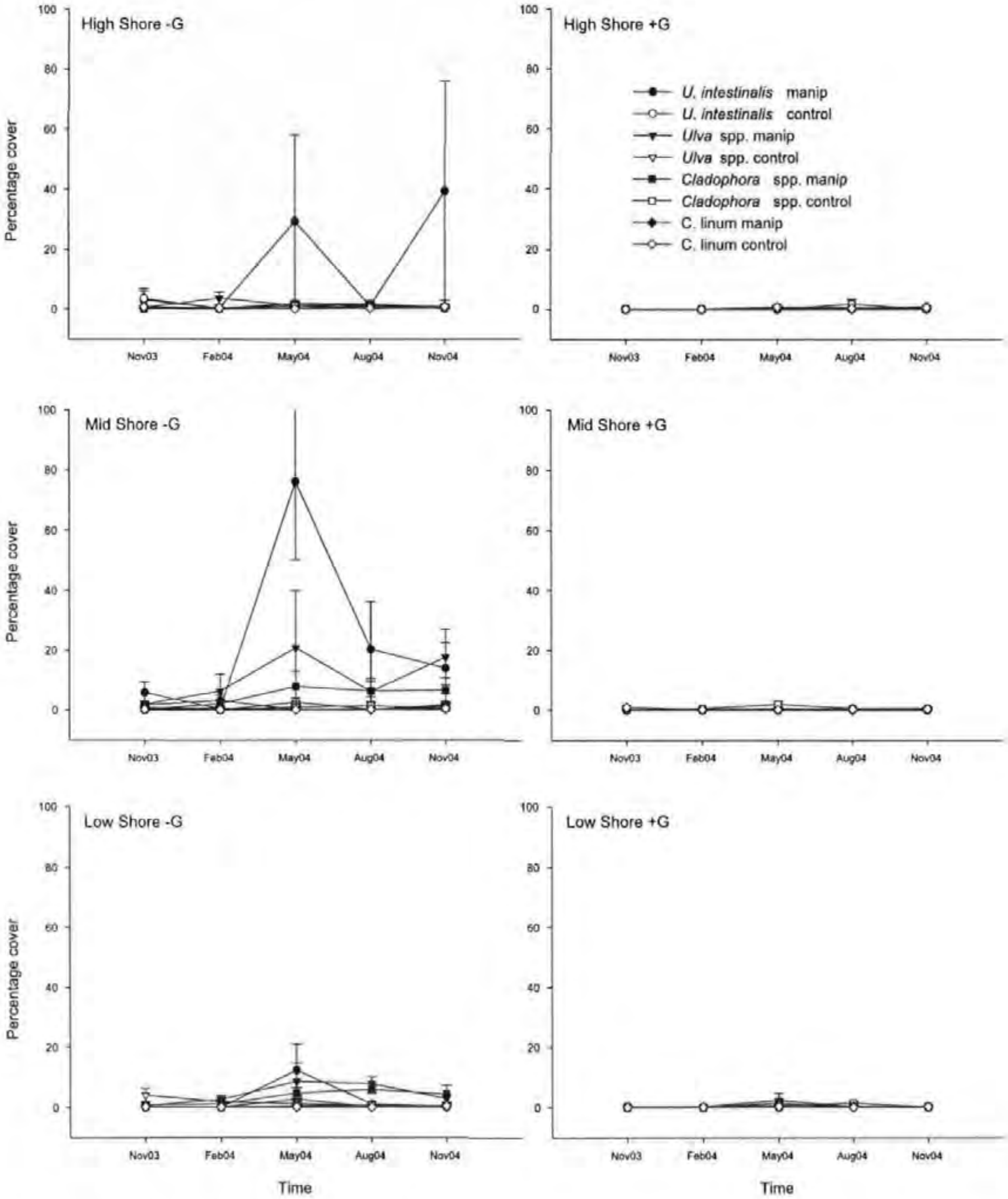

Figure D.16: Exp3. Perennial removal in rockpool. Percentage cover of green ephemeral species: *Ulva intestinalis*, *Ulva* spp., *Cladophora* spp., *Chaetomorpha linum* in manipulated plot where perennials were removed (manip: black symbols) and in unmanipulated plots (control: white symbols) during succession started in Summer 2002 at each of three shore levels: High, Mid and Low shore in rockpools at reduced grazer density (-G) and natural grazer density (+G). Data are mean of percentage cover (±SE) of 2 replicate 20×20cm quadrats averaged for each of the 4 replicate pools (n=4).

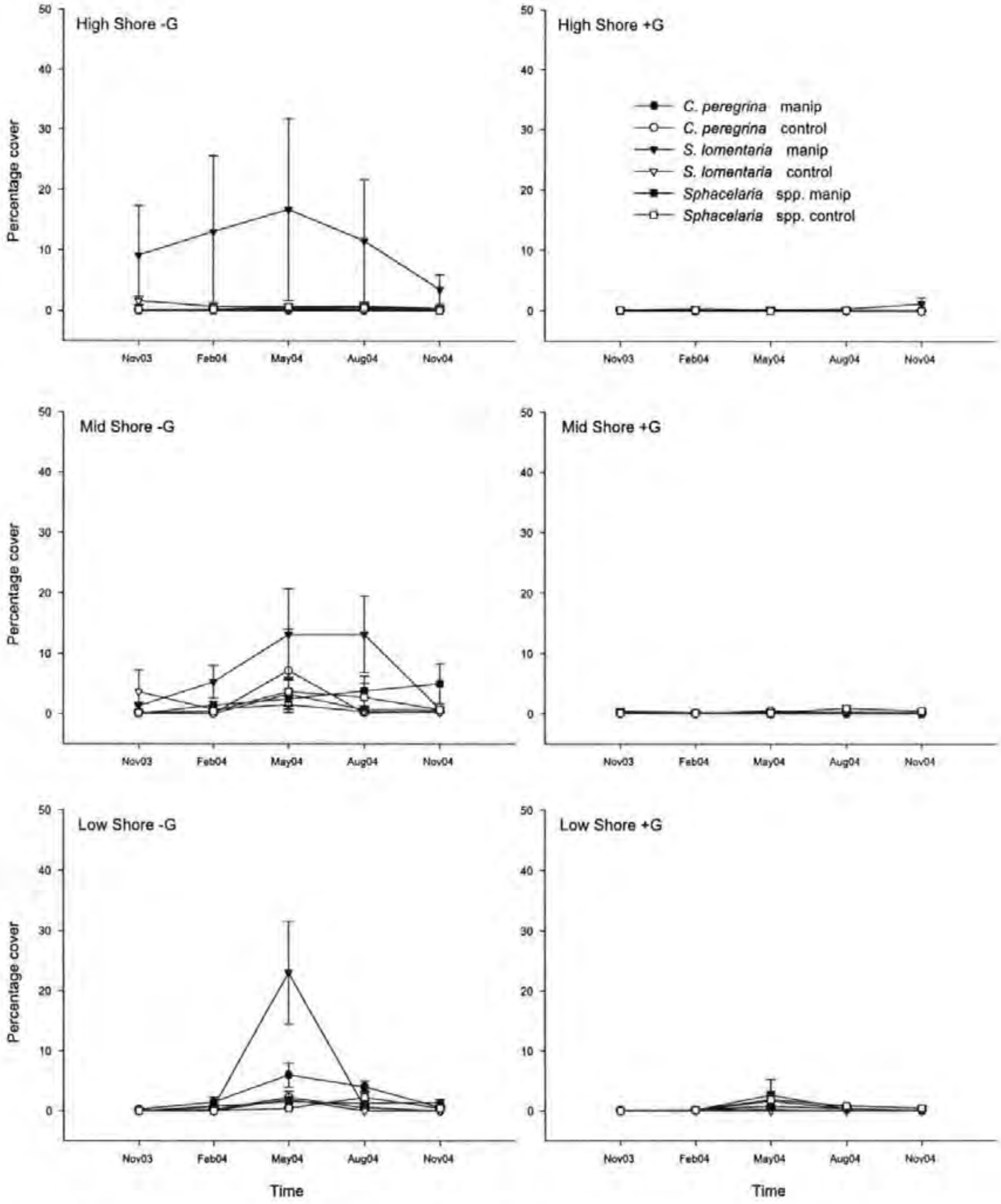

Figure D.17: Exp3. Perennial removal in rockpool. Percentage cover of red ephemeral species: *Colpomenia peregrina*, *Scytosiphon lomentaria*, *Sphacelaria* spp. in manipulated plot where perennials were removed (manip: black symbols) and in unmanipulated plots (control: white symbols) during succession started in Summer 2002 at each of three shore levels: High, Mid and Low shore in rockpools at reduced grazer density (-G) and natural grazer density (+G). Data are mean of percentage cover (±SE) of 2 replicate 20×20cm quadrats averaged for each the 4 replicate pools (n=4).

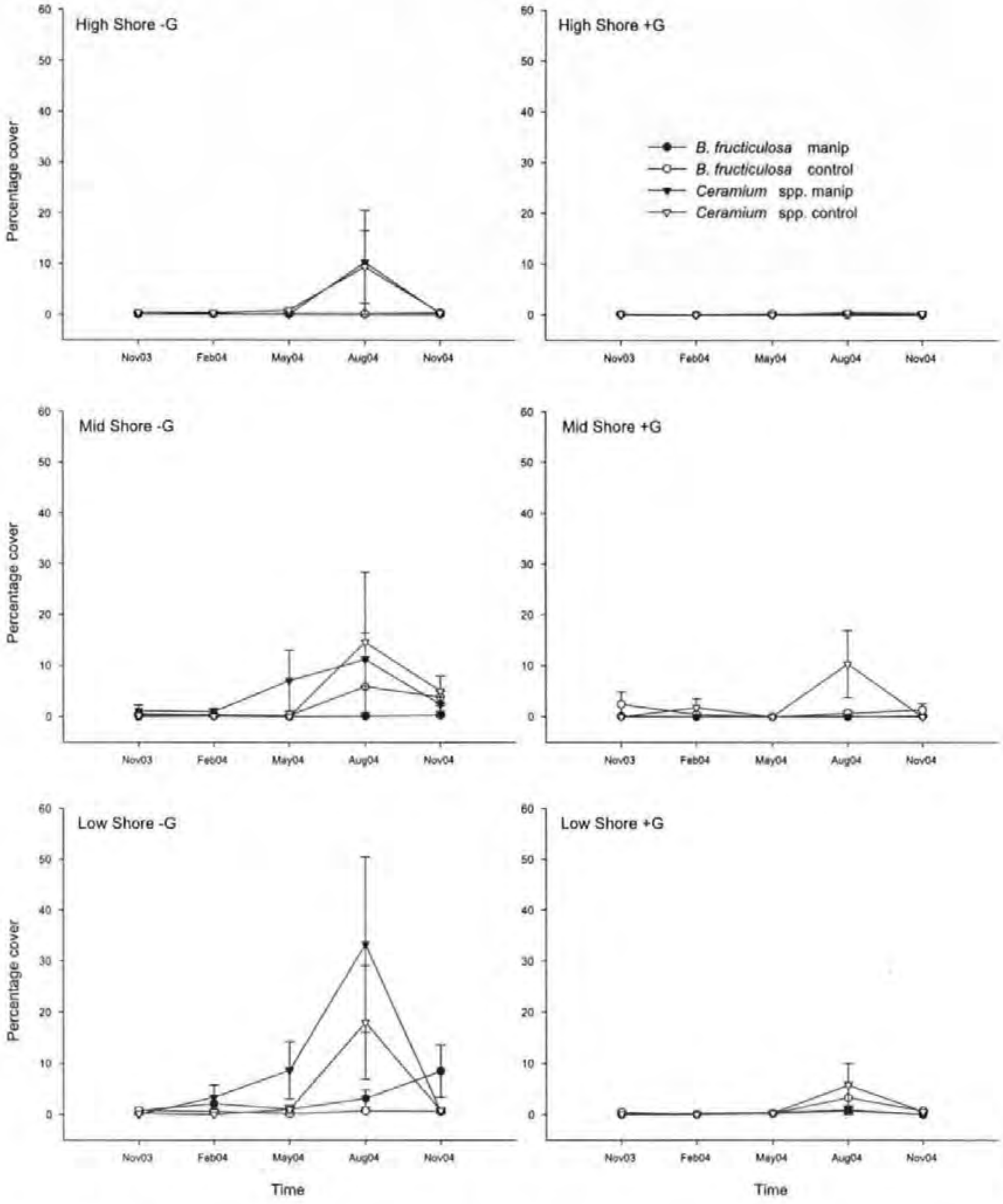

Figure D.18: Exp3. Perennial removal in rockpool. Percentage cover of red ephemeral species: *Boergeseniella fructiculosa*, *Ceramium* spp., *Petrocelis* in manipulated plot where perennials were removed (manip: black symbols) and in unmanipulated plots (control: white symbols) during succession started in Summer 2002 at each of three shore levels: High, Mid and Low shore in rockpools at reduced grazer density (-G) and natural grazer density (+G). Data are mean of percentage cover (±SE) of 2 replicate 20×20cm quadrats averaged for each of the 4 replicate pools (n=4).

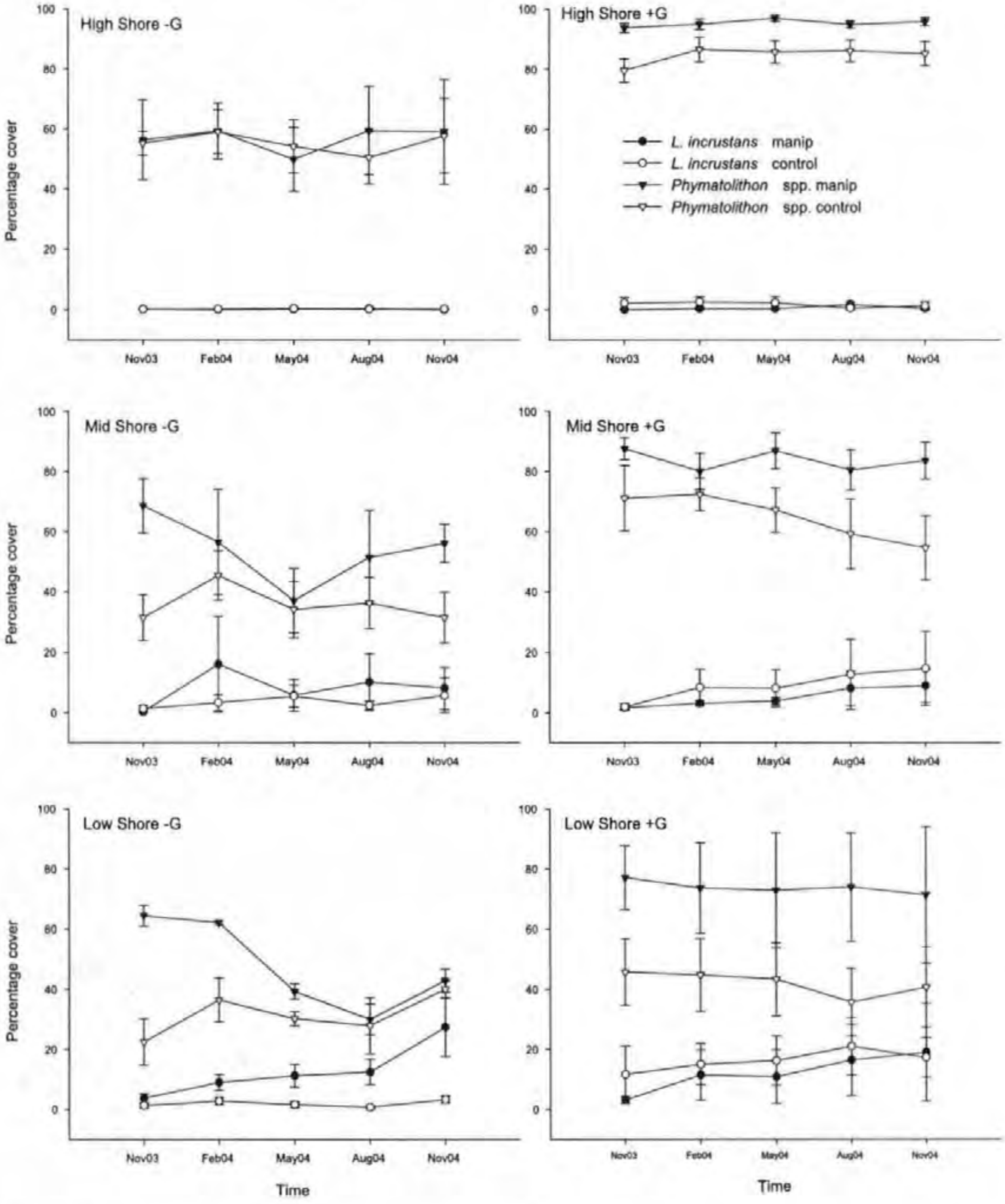

Figure D.19: Exp3. Perennial removal in rockpool. Percentage cover of encrusting species: *Phymatolithon spp.* and *Lithophyllum incrustans* in manipulated plot where perennials were removed (manip: black symbols) and in unmanipulated plots (control: white symbols) during succession started in Summer 2002 at each of three shore levels: High, Mid and Low shore in rockpools at reduced grazer density (-G) and natural grazer density (+G). Data are mean of percentage cover (±SE) of 2 replicate 20×20cm quadrats averaged for each of the 4 replicate pools (n=4).

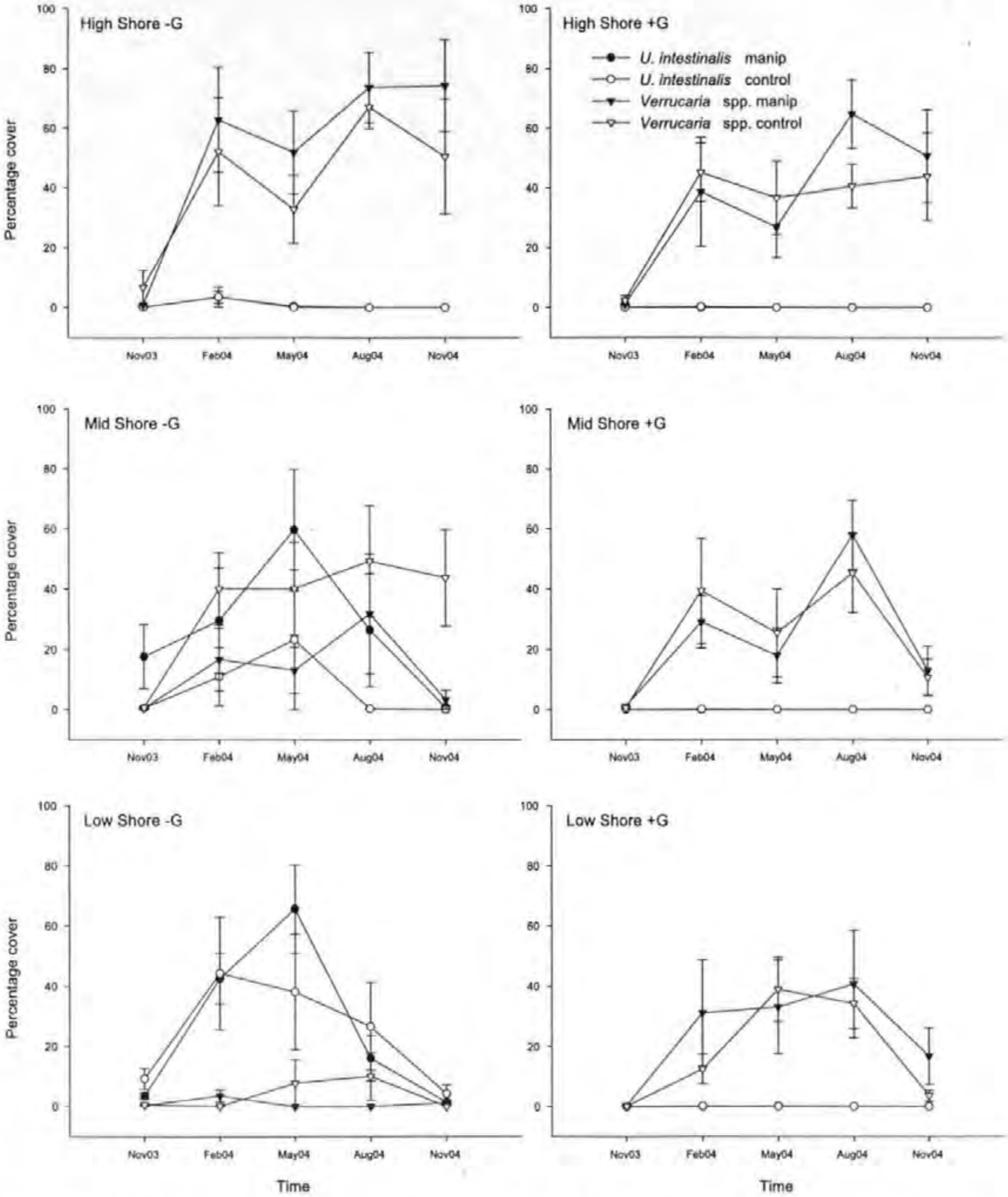

Figure D.20: Exp3. Perennial removal on emergent rock. Percentage cover of ephemeral species: *Ulva intestinalis*, *Verrucaria* spp. in manipulated plot where perennials were removed (manip: black symbols) and in unmanipulated plots (control: white symbols) during succession started in Summer 2002 at each of three shore levels: High, Mid and Low shore on emergent rock at reduced grazer density (-G) and natural grazer density (+G). Data are mean of percentage cover (±SE) of 2 replicate 20×20cm quadrats averaged for each of the 4 replicate plots (n=4).

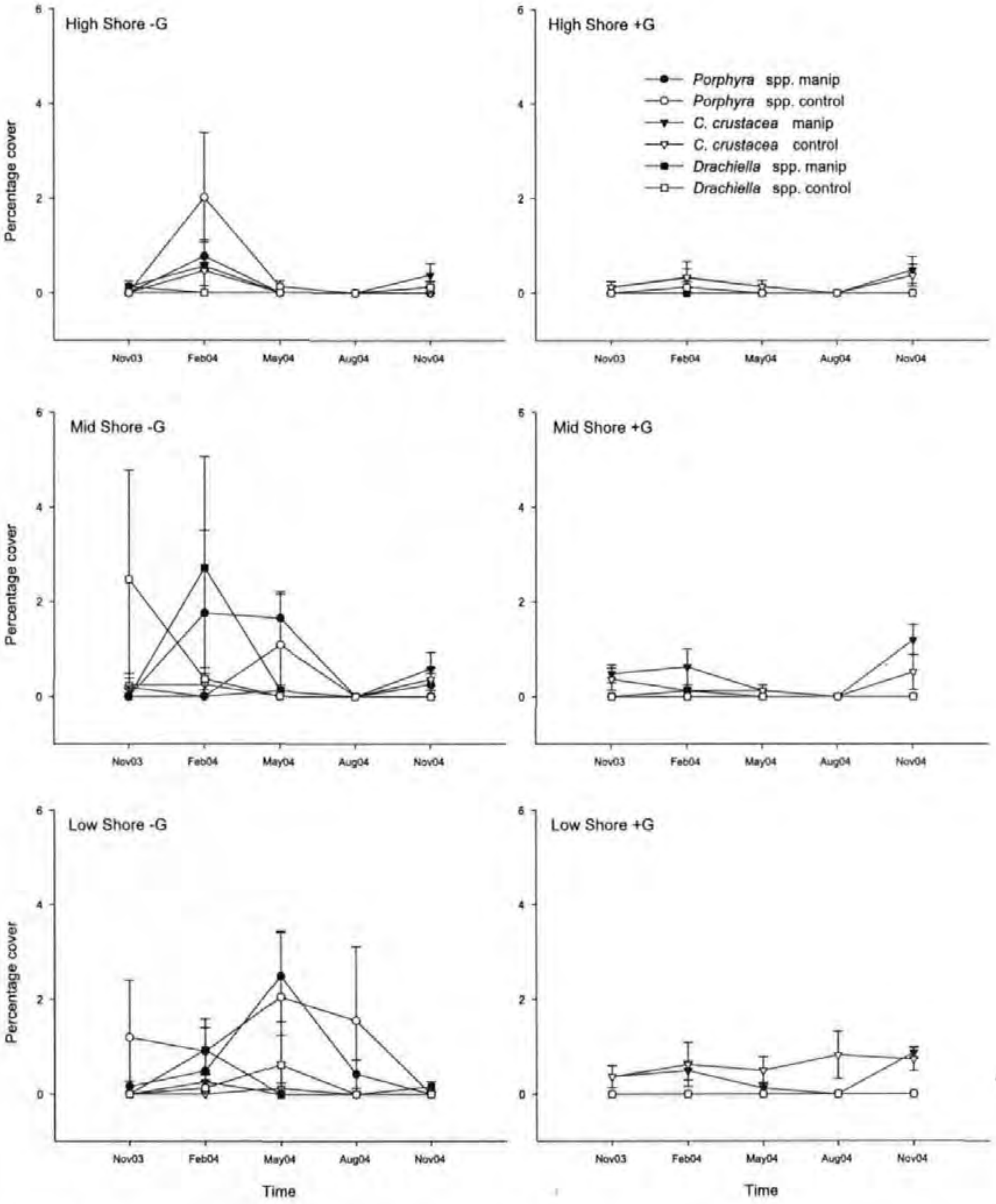

Figure D.21: Exp3. Perennial removal on emergent rock. Percentage cover of ephemeral species: *Porphyra* spp., *Calothrix crustacea*, *Drachiella* spp. in manipulated plot where perennials were removed (manip: black symbols) and in unmanipulated plots (control: white symbols) during succession started in Summer 2002 at each of three shore levels: High, Mid and Low shore on emergent rock at reduced grazer density (-G) and natural grazer density (+G). Data are mean of percentage cover (±SE) of 2 replicate 20×20cm quadrats averaged for each of the 4 replicate plots (n=4).

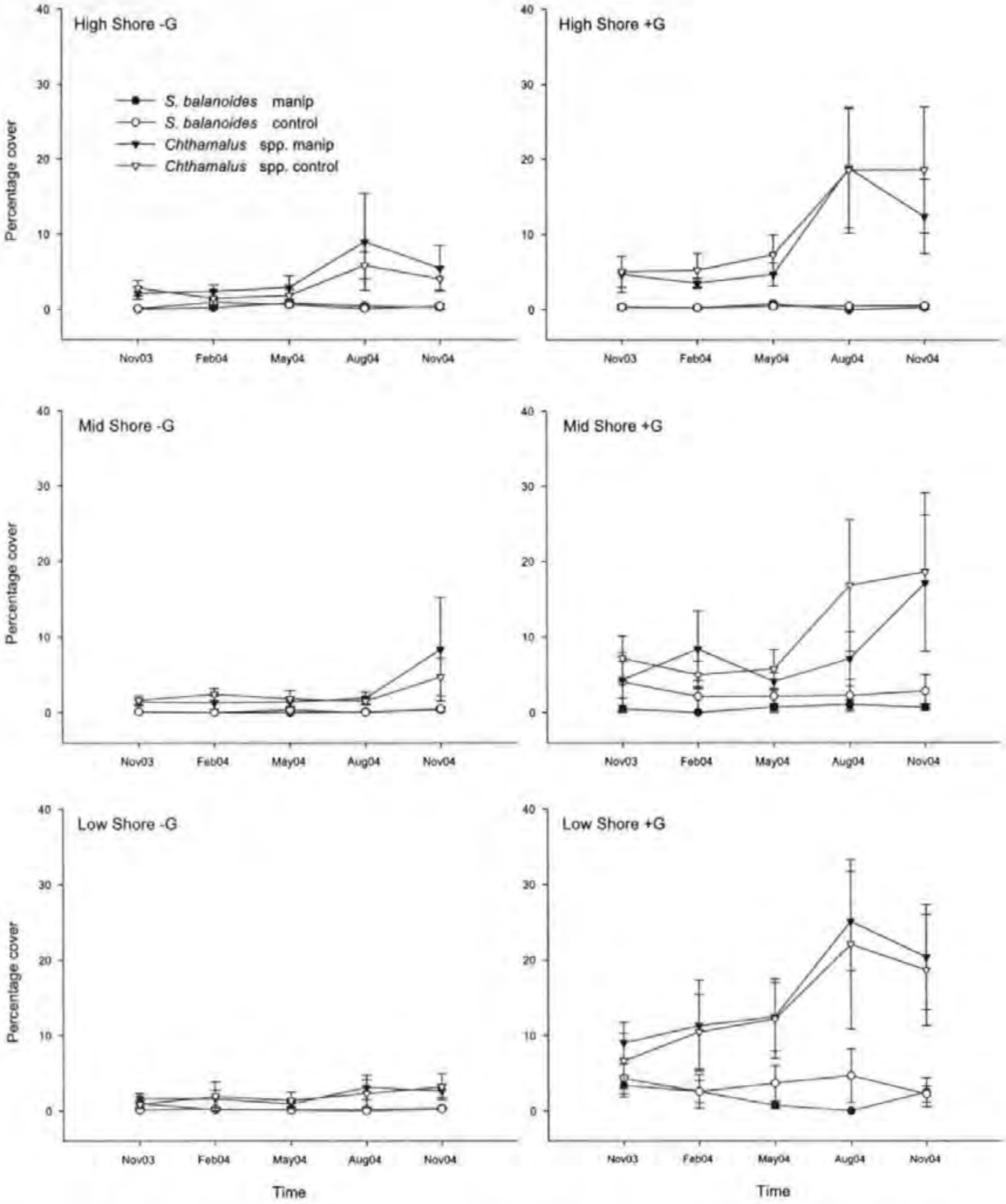

Figure D.22: Exp3. Perennial removal on emergent rock. Percentage cover of barnacle species: *Chthamalus* spp. and *Semibalanus balanoides* in manipulated plot where perennials were removed (manip: black symbols) and in unmanipulated plots (control: white symbols) during succession started in Summer 2002 at each of three shore levels: High, Mid and Low shore on emergent rock at reduced grazer density (-G) and natural grazer density (+G). Data are mean of percentage cover (±SE) of 2 replicate 20×20cm quadrats averaged for each of the 4 replicate plots (n=4).

Appendix E

Dissimilarity breakdown

See Appendix A for methods.

E.1 Succession in rockpools

Table E.1: Dissimilarity breakdown for the species contribution to the differences in rockpools between grazer treatments (natural (+G) and reduced (-G) grazer density) at the end of the experiment (November 04). Good discriminating species are in bold. Primary and secondary algal cover was sampled and represented after species name by (1c) and (2c) respectively.

-G and +G grazer treatments

Species	-G	+G	Av.Diss	Diss/SD	Cont%	Cum.%
Sargassum muticum (2c)	**5.19**	1.94	6.38	1.6	11.27	11.27
Fucus serratus (2c)	**3.02**	0.00	4.59	0.9	8.11	19.39
Ralfsia verrucosa	**2.44**	0.37	3.59	1	6.33	25.72
Lithophyllum incrustans	1.09	**2.42**	3.46	1.06	6.1	31.83
Phymatolithon spp.	6.39	**7.50**	3.43	1.35	6.06	37.89
Sargassum muticum (1c)	**2.93**	1.00	3.42	1.37	6.04	43.93
Corallina spp.	2.95	**3.16**	2.74	1.39	4.85	48.78
Gelidium spp.	**1.44**	0.44	1.98	1.32	3.5	52.27
Sand	**1.31**	0.3	1.94	1.21	3.42	55.7
Bare rock	0.81	**1.31**	1.62	1.17	2.87	58.57
Boergeseniella fruticulosa	**0.92**	0.52	1.3	1.12	2.3	60.87
Ceramium spp.	**0.82**	0.19	1.22	0.79	2.15	63.02
Osmundea hybrida	**0.58**	0.51	1.09	0.98	1.92	64.94
Acidian	**0.67**	0.48	1.07	1.02	1.89	66.83
Stone	**0.71**	0.00	1.06	0.7	1.86	68.69
Anemonia spp.	0.36	**0.54**	1.01	0.89	1.78	70.47
Fucus spp. 1a	**0.59**	0.00	0.88	0.67	1.55	72.02
Cladophora spp.	**0.59**	0.31	0.85	1.26	1.5	73.53
Osmundea pinnatifida	**0.54**	0.15	0.82	1.02	1.46	74.98
Chaetomorpha linum	**0.60**	0.44	0.79	1.19	1.4	76.38
Mesophyllum liquenoides	0.19	**0.49**	0.79	0.68	1.39	77.77
Gastroclonium ovatum 1a	0.24	**0.48**	0.77	1.06	1.36	79.14
Petrocelis	**0.49**	0.41	0.72	1.12	1.27	80.41
Fucus serratus (1c)	**0.38**	0.16	0.7	0.73	1.24	81.65
Himanthalia elogata (1c)	0.26	**0.32**	0.68	0.61	1.21	82.86
Sphacelaria spp.	**0.33**	0.31	0.65	0.9	1.15	84.01
Ulva intestinalis	**0.32**	0.13	0.59	0.67	1.04	85.05
Ulva spp.	**0.35**	0.23	0.59	0.96	1.04	86.08
Champia parvula	0.22	**0.31**	0.54	0.94	0.95	87.03
Gastroclonium ovatum 2a	0.1	**0.27**	0.48	0.53	0.85	88.81
Fucus spiralis (2c)	**0.29**	0.00	0.48	0.3	0.85	89.67
Scytosiphon lomentaria (1c)	**0.25**	0.08	0.45	0.73	0.8	90.47

Table E.2: Dissimilarity breakdown for the species contribution to the differences in rockpools between the high and low shore levels at the end of the experiment (November 04). Good discriminating species are in bold. Primary and secondary algal cover was sampled and represented after species name by (1c) and (2c) respectively.

High and Low shore level

Species	High	Low	Av.Diss	Diss/SD	Cont%	Cum.%
Sargassum muticum (2c)	1.75	**5.26**	6.63	1.4	11.65	11.65
Phymatolithon spp.	**8.33**	6.15	4.27	1.54	7.51	19.16
Corallina spp.	1.56	**4.12**	4.1	1.97	7.2	26.36
Lithophyllum incrustans	0.46	**2.74**	4.04	1.24	7.11	33.47
Fucus serratus (2c)	**2.09**	0.97	3.67	0.78	6.44	39.91
Sargassum muticum (1c)	1.26	**2.96**	3.56	1.33	6.26	46.17
Ralfsia verrucosa	**1.86**	0.56	2.76	0.94	4.85	51.02
Sand	0.93	**1.01**	1.76	1.1	3.09	54.11
Bare rock	**1.12**	0.95	1.76	1.07	3.09	57.2
Gelidium spp.	**1.09**	0.75	1.72	1.47	3.02	60.22
Acidian	0.00	**1.06**	1.67	1.25	2.94	63.16
Mesophyllum liquenoides	0.00	**0.93**	1.42	0.9	2.49	65.65
Anemonia spp.	0.37	**0.59**	1.26	0.83	2.22	67.87
Stone	0.16	**0.76**	1.2	0.73	2.11	69.98
Himanthalia elogata (1c)	0.00	**0.76**	1.14	0.71	2	71.98
Osmundea hybrida	**0.67**	0.39	1.11	1.02	1.96	73.93
Boergeseniella fruticulosa	0.20	**0.69**	0.97	1.4	1.7	75.64
Gastroclonium ovatum (1c)	0.09	**0.60**	0.9	1.13	1.58	77.22
Champia parvula	0.00	**0.50**	0.8	1.23	1.4	78.62
Chaetomorpha linum	**0.68**	0.43	0.77	1.04	1.35	79.97
Petrocelis	0.26	**0.54**	0.74	1.1	1.31	81.28
Ulva spp. 1a	0.21	**0.49**	0.73	1.17	1.29	82.57
Cladophora spp.	**0.44**	0.35	0.72	1.05	1.27	83.84
Ceramium spp.	0.28	**0.46**	0.68	1.11	1.2	85.04
Sphacelaria spp.	0.00	**0.45**	0.66	0.94	1.16	86.2
Osmundea pinnatifida	0.27	**0.31**	0.65	0.88	1.15	87.35
Fucus spiralis (2c)	**0.43**	0.00	0.61	0.37	1.07	88.42
Ceramium pallidum	0.09	**0.26**	0.46	0.8	0.81	90.19

E.2 Succession on emergent rock

Table E.3: Dissimilarity breakdown for the species contribution to the differences in rockpools between grazer treatments (natural (+G) and reduced (-G) grazer density) at the end of the experiment (November 04). Good discriminating species are in bold. Primary and secondary algal cover was sampled and represented after species name by (1c) and (2c) respectively.

-G and +G grazer treatments

Species	-G	+G	Av.Diss	Diss/SD	Cont%	Cum.%
Verrucaria spp.	**4.11**	3.36	9.44	1.27	16.85	16.85
Bare rock	5.49	**7.01**	7.03	1.25	12.55	29.41
Ralfsia verrucosa	**2.67**	0.00	5.73	1.21	10.22	39.63
Chthamalus spp. adult	1.48	**3.24**	5.11	1.52	9.11	48.75
Hildenbrandia rubra	**1.82**	1.17	4.90	0.87	8.75	57.50
Fucus vesiculosus (2c)	**1.46**	0.00	3.01	0.52	5.37	62.87
Chthamalus spp. juv.	0.75	**1.95**	2.92	1.39	5.22	68.09
Fucus spiralis (2c)	**1.31**	0.00	2.81	0.43	5.01	73.10
Fucus serratus (2c)	**1.09**	0.00	2.21	0.39	3.95	77.06
Fucus spp. (2c)	**0.97**	0.00	2.15	0.62	3.83	80.89

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Table E.3 – continued from previous page

Semibalanus adult	0.42	**1.08**	1.94	1.09	3.47	84.36
Fucus spp. (1c)	**0.63**	0.00	1.40	0.77	2.50	86.86
Calothrix crustacea	0.14	**0.55**	1.22	1.13	2.18	89.04
Fucus vesiculosus (1c)	**0.51**	0.00	1.05	0.71	1.88	90.92

Table E.4: Dissimilarity breakdown for the species contribution to the differences on emergent rock between high and low shore levels at the end of the experiment (November 04). Good discriminating species are in bold. Primary and secondary algal cover was sampled and represented after species name by (1c) and (2c) respectively.

High and Low shore level

Species	High	Low	Av.Diss	Diss/SD	Cont%	Cum.%
Verrucaria spp.	**6.32**	0.79	12.75	1.89	21.41	21.41
Bare rock	5.50	**7.12**	7.12	1.37	11.96	33.37
Ralfsia verrucosa	0.57	**2.84**	5.80	1.16	9.73	43.10
Chthamalus spp. adult	**2.40**	2.36	4.52	1.30	7.59	50.70
Hildenbrandia rubra	0.14	**2.11**	4.36	1.02	7.31	58.01
Fucus vesiculosus (2c)	**0.99**	0.91	3.25	0.53	5.46	63.47
Fucus serratus (2c)	0.00	**1.63**	3.23	0.49	5.42	68.89
Chthamalus spp. juv.	**1.34**	1.20	2.33	1.44	3.92	72.81
Fucus spp. (2c)	0.11	**1.07**	2.30	0.63	3.87	76.67
Fucus spiralis (2c)	**1.15**	0.00	2.23	0.37	3.75	80.42
Semibalanus adult	0.53	**0.85**	1.58	1.01	2.65	83.07
Ulva intestinalis 1a	0.00	**0.70**	1.41	0.55	2.37	85.44
Fucus spp. (1c)	0.09	**0.65**	1.37	0.68	2.30	87.74
Phymatolithon spp.	0.00	**0.60**	1.29	0.69	2.16	89.90
Fucus vesiculosus (1c)	0.29	**0.37**	1.11	0.77	1.87	91.77

E.3 Effect of initiation time on succession in rockpools

Table E.5: Dissimilarity breakdown for the species contribution to the differences between the time of initiation of the succession (Aug02 and Feb03) in rockpools for the 3^{rd}, 9^{th}, 15^{th}, 21^{st} moths of succession at reduced (-G) grazer density at the three shore level (High, Mid, Low). Good discriminating species are in bold. Primary and secondary algal cover was sampled and represented after species name by (1c) and (2c) respectively.

3^{rd} month of succession

Species	Aug 02	Feb 03	Av.Diss	Diss/SD	Cont%	Cum.%
Ulva spp.	0.56	**5.29**	12.13	1.38	17.61	17.61
Bare rock	**7.04**	3.52	11.16	1.50	16.19	33.79
Sargassum muticum (1c)	**3.09**	0.00	7.37	1.85	10.69	44.48
Phymatolithon spp.	**3.66**	1.36	6.73	1.78	9.77	54.25
Scytosiphon lomentaria	1.85	**3.52**	6.26	1.48	9.09	63.34
Ulva intestinalis	0.64	0.60	2.34	0.77	3.39	66.74
Sand	0.77	0.48	2.25	0.83	3.26	70.00
Cladophora spp.	0.19	1.03	2.24	0.78	3.25	73.26
Petrocelis	**0.89**	0.33	2.14	0.87	3.11	76.36

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Table E.5 – continued from previous page

Species	Aug 02	Feb 03	Av.Diss	Diss/SD	Cont%	Cum.%
Leathesia difformis	0.80	0.06	1.89	0.93	2.74	79.11
Chaetomorpha linum	0.73	0.00	1.73	0.81	2.51	81.62
Monostroma spp.	0.00	0.65	1.57	0.42	2.28	83.89
Ceramium spp.	**0.66**	0.00	1.52	1.06	2.20	86.10
Lithophyllum incrustans	0.25	**0.47**	1.40	0.69	2.04	88.13
Ralfsia verrucosa	**0.49**	0.12	1.21	0.83	1.76	89.90
Ectocarpus spp.	0.43	0.00	1.05	0.34	1.53	91.42

9th month of succession

Species	Aug 02	Feb 03	Av.Diss	Diss/SD	Cont%	Cum.%
Sargassum muticum (2c)	**4.73**	1.86	5.34	1.28	8.67	8.67
Bare rock	2.42	4.46	3.31	1.43	5.37	14.04
Scytosiphon lomentaria (1c)	3.55	1.27	3.23	1.56	5.24	19.28
Ralfsia verrucosa	1.50	**3.41**	2.95	1.51	4.79	24.07
Sargassum muticum (1c)	**3.69**	2.70	2.72	1.40	4.42	28.49
Phymatolithon spp.	3.57	**4.94**	2.71	1.22	4.41	32.90
Ulva spp. (1c)	1.93	0.00	2.32	0.89	3.77	36.66
Ulva spp. (2c)	1.67	0.00	2.05	0.51	3.32	39.99
Ulva intestinalis (2c)	0.91	0.87	1.92	0.61	3.12	43.11
Scytosiphon lomentaria (2c)	0.56	1.29	1.92	0.71	3.12	46.22
Sand	0.98	1.07	1.82	1.01	2.96	49.19
Ulva rigida (2c)	0.00	1.49	1.79	0.63	2.91	52.09
Fucus serratus (1c)	**1.37**	0.09	1.69	1.03	2.75	54.84
Corallina spp.	**1.70**	**1.44**	1.55	1.56	2.52	57.35
Ulva spp. (1c)	1.16	0.06	1.44	0.73	2.34	59.70
Ulva intestinalis (1c)	0.98	0.83	1.31	0.95	2.12	61.82
Lithophyllum incrustans	**0.75**	**1.02**	1.28	1.42	2.08	63.89
Fucus spp. (1c)	**0.89**	0.22	1.23	0.71	2.00	65.89
Ulva rigida (1c)	0.40	0.83	1.17	0.89	1.90	67.79
Ceramium spp.	1.11	0.57	1.16	1.31	1.88	69.67
Ulva linza (2c)	0.65	0.29	1.02	0.41	1.66	71.33
Osmundea hybrida	0.66	0.39	0.97	0.86	1.58	72.91
Acidian	0.00	0.74	0.94	0.76	1.52	74.43
Anemonia spp.	0.21	0.71	0.90	1.08	1.46	75.89
Petrocelis	**0.70**	**0.78**	0.87	1.27	1.41	77.30
Gelidium spp. All	**0.67**	0.39	0.86	1.20	1.39	78.69
Fucus spp. (2c)	**0.53**	0.15	0.74	0.61	1.21	79.90
Dumontia conforta (1c)	0.53	0.08	0.72	0.75	1.17	81.06
Ulva linza (1c)	0.44	0.15	0.63	1.07	1.02	82.09
Boergeseniella fruticulosa	0.22	0.46	0.63	0.95	1.02	83.11
Leathesia difformis	0.47	0.10	0.63	0.89	1.02	84.13
Ulva lactuca (1c)	0.38	0.06	0.55	0.39	0.90	85.02
Palmaria palmata	**0.42**	0.11	0.53	0.88	0.86	85.88
Ulva crinita	0.06	0.40	0.49	0.50	0.80	86.68
Chondrus crispus (1c)	**0.28**	0.08	0.48	0.38	0.78	87.46
Ulva crinita (2c)	0.00	0.42	0.47	0.39	0.77	88.23
Polysiphonia spp. All	0.34	0.06	0.45	0.42	0.73	88.96
Chaetomorpha linum	0.00	0.34	0.41	0.47	0.66	89.62
Osmundea spp.	0.07	0.27	0.37	0.75	0.60	90.22

15th month of succession

Species	Aug 02	Feb 03	Av.Diss	Diss/SD	Cont%	Cum.%
Sargassum muticum (2c)	**5.24**	**5.33**	3.50	1.32	6.21	6.21
Fucus spiralis (2c)	**2.92**	0.00	3.31	1.26	5.87	12.08
Ulva intestinalis (2c)	0.28	2.65	3.20	0.72	5.68	17.76
Sand	2.55	1.41	2.73	1.08	4.85	22.61
Bare rock	1.96	3.19	2.50	1.29	4.44	27.06
Ralfsia verrucosa	1.88	**2.48**	2.41	1.35	4.28	31.33
Phymatolithon spp.	**5.74**	**5.18**	2.36	1.25	4.20	35.53
Sargassum muticum (1c)	**3.49**	**2.80**	2.14	1.36	3.81	39.34
Corallina spp.	**2.45**	**2.23**	1.80	1.46	3.19	42.53
Ulva intestinalis (1c)	0.24	1.52	1.71	1.04	3.04	45.57

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Table E.5 – continued from previous page

Species	Aug 02	Feb 03	Av.Diss	Diss/SD	Cont%	Cum.%
Scytosiphon lomentaria (2c)	0.36	1.05	1.42	0.71	2.52	48.09
Lithophyllum incrustans	0.60	1.20	1.35	1.16	2.39	50.48
Colpomenia peregrina	0.06	1.17	1.31	0.97	2.33	52.81
Fucus spiralis (1c)	**1.15**	0.00	1.31	1.26	2.32	55.13
Petrocelis	0.66	**0.89**	1.28	0.80	2.28	57.41
Scytosiphon lomentaria (1c)	0.50	1.07	1.26	1.09	2.24	59.65
Sphacelaria spp.	0.13	1.00	1.14	1.21	2.02	61.67
Ceramium spp.	0.37	0.90	1.05	0.97	1.87	63.54
Ulva rigida (2c)	0.10	0.74	0.92	0.47	1.64	65.17
Cladophora spp.	0.29	0.89	0.91	1.26	1.61	66.78
Fucus spp. (1c)	0.00	**0.77**	0.90	1.38	1.59	68.37
Gelidium spp.	**0.82**	0.45	0.85	1.26	1.52	69.89
Acidian	0.50	0.57	0.80	1.10	1.42	71.32
Anemonia spp.	0.52	0.45	0.78	0.96	1.38	72.69
Ulva rigida (1c)	0.51	0.24	0.76	0.84	1.36	74.05
Boergeseniella fruticulosa	0.41	0.44	0.76	0.85	1.34	75.39
Osmundea spp.	0.30	0.41	0.68	0.83	1.21	76.60
Dumontia conforta (1c)	0.00	0.50	0.59	0.70	1.05	77.65
Osmundea hybrida	0.42	0.26	0.59	0.88	1.05	78.70
Ulva lactuca (1c)	0.00	0.49	0.57	0.80	1.01	79.71
Ulva linza (1c)	0.00	0.46	0.54	0.55	0.96	80.67
Ulva crinita	0.28	0.37	0.52	1.00	0.93	81.60
Fucus vesiculosus (2c)	0.00	**0.40**	0.49	0.30	0.87	82.47
Ulva spp. (2c)	0.42	0.00	0.48	0.46	0.86	83.33
Fucus serratus (2c)	0.00	**0.40**	0.47	0.48	0.84	84.17
Chondrus crispus (2c)	0.10	**0.29**	0.46	0.37	0.82	84.99
Osmundea spp. (2c)	0.00	0.36	0.46	0.36	0.82	85.81
Mesophyllum liquenoides	**0.32**	0.19	0.44	0.87	0.77	86.58
Ulva spp. (2c)	0.23	0.16	0.41	0.42	0.73	87.31
Fucus serratus (1c)	0.06	**0.34**	0.41	0.84	0.72	88.04
Chaetomorpha linum	0.31	0.05	0.39	0.73	0.69	88.73
Himanthalia elogata (1c)	**0.32**	0.05	0.38	0.71	0.68	89.41
Chondrus crispus (1c)	**0.25**	0.10	0.38	0.54	0.67	90.07

21^{st} month of succession

Species	Aug 02	Feb 03	Av.Diss	Diss/SD	Cont%	Cum.%
Fucus serratus (2c)	**2.82**	**1.26**	3.48	1.06	6.78	6.78
Sargassum muticum (2c)	**6.01**	**5.89**	3.27	1.34	6.39	13.17
Ralfsia verrucaria	**1.86**	**2.68**	3.06	1.46	5.97	19.14
Bare rock	1.84	2.20	2.53	0.78	4.93	24.07
Phymatolithon spp.	**6.12**	**5.55**	2.29	1.04	4.47	28.54
Sargassum muticum (1c)	**3.19**	**3.67**	2.07	1.39	4.05	32.58
Sand	1.10	1.58	1.94	1.27	3.79	36.37
Corallina spp.	**2.91**	**2.20**	1.89	1.27	3.68	40.05
Fucus spp. (2c)	0.00	**1.49**	1.72	0.80	3.35	43.40
Lithophyllum incrustans	**1.04**	**1.20**	1.70	0.97	3.33	46.73
Colpomenia peregrina	1.05	0.20	1.21	0.72	2.36	49.09
Fucus serratus (1c)	**0.98**	0.06	1.16	1.30	2.26	51.35
Boergeseniella fruticulosa	0.19	1.01	1.07	1.18	2.08	53.43
Ulva intestinalis (1c)	0.88	0.22	1.04	1.10	2.02	55.45
Gelidium spp.	**1.10**	**0.75**	1.01	1.12	1.98	57.43
Sphacelaria spp.	0.80	0.52	0.99	1.01	1.93	59.36
Stone	0.30	0.68	0.96	0.62	1.87	61.23
Anemonia spp.	0.10	0.82	0.96	1.03	1.87	63.10
Fucus vesiculosus (2c)	0.06	**0.66**	0.86	0.47	1.67	64.77
Chaetomorpha linum	0.11	0.76	0.85	0.73	1.66	66.42
Fucus spp. (1c)	0.23	**0.68**	0.81	1.04	1.59	68.01
Cladophora spp.	0.75	0.42	0.80	1.34	1.56	69.57
Acidian	0.57	0.41	0.77	1.18	1.50	71.07
Osmundea hybrida	0.28	0.60	0.77	1.07	1.50	72.57
Ceramium spp.	0.47	0.46	0.73	1.03	1.42	73.98
Petrocelis	**0.56**	0.25	0.71	0.87	1.39	75.37
Ulva spp. (1c)	0.16	0.52	0.67	0.80	1.30	76.68

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Table E.5 – continued from previous page

Species	Aug 02	Feb 03	Av.Diss	Diss/SD	Cont%	Cum.%
Osmundea pinnatifida	0.08	**0.56**	0.64	1.08	1.25	77.93
Scytosiphon lomentaria (1c)	0.53	0.14	0.64	1.08	1.25	79.18
Fucus spiralis (2c)	**0.52**	0.00	0.62	0.50	1.21	80.39
Scytosiphon lomentaria (2c)	0.49	0.00	0.61	0.62	1.19	81.58
Mesophyllum liquenoides	0.21	0.37	0.56	0.72	1.10	82.67
Chondrus crispus (1c)	**0.23**	**0.25**	0.50	0.68	0.98	83.65
Himanthalia elogata (1c)	**0.39**	0.06	0.45	0.75	0.89	84.53
Chondrus crispus (2c)	**0.22**	**0.16**	0.45	0.50	0.87	85.40
Ulva linza (2c)	0.41	0.00	0.44	0.37	0.85	86.26
Ulva spp.	0.38	0.00	0.43	0.68	0.84	87.10
Chylocladia verticillata (2c)	0.37	0.00	0.42	0.53	0.81	87.91
Spirorbis	0.23	0.34	0.41	1.00	0.80	88.71
Gastroclonium ovatum (1c)	0.06	0.33	0.41	0.72	0.80	89.50
Actinia spp.	0.20	0.22	0.40	0.78	0.77	90.27

E.4 Effect of initiation time on succession on emergent rock

Table E.6: Dissimilarity breakdown for the species contribution to the differences between the time of initiation of the succession (Aug02 and Feb03) on emergent rock for the 3^{rd}, 9^{th}, 15^{th}, 21^{st} moths of succession at reduced (-G) grazer density at the three shore level (High, Mid, Low). Good discriminating species are in bold. Primary and secondary algal cover was sampled and represented after species name by (1c) and (2c) respectively.

3^{rd} month of succession

Species	Aug 02	Feb 03	Av.Diss	Diss/SD	Cont%	Cum.%
Bare rock	9.95	5.81	16.08	1.38	31.11	31.11
Ulva intestinalis	0.50	4.24	15.78	1.00	30.54	61.65
Verrucaria spp.	0.00	3.48	13.34	1.27	25.81	87.46
Porphyra linearis	0.00	0.55	1.91	0.44	3.69	91.15

9^{th} month of succession

Species	Aug 02	Feb 03	Av.Diss	Diss/SD	Cont%	Cum.%
Bare rock	4.30	8.36	12.97	1.45	21.18	21.18
Ulva intestinalis	4.22	1.55	10.95	1.23	17.88	39.06
Verrucaria spp.	3.53	1.37	9.85	1.25	16.08	55.14
Porphyra linearis	2.72	0.00	7.97	0.91	13.01	68.15
Ralfsia verrucosa	0.77	**1.41**	4.85	0.68	7.92	76.07
Fucus spp. (1c)	0.69	*1.16*	3.10	1.24	5.06	81.14
Chthamalus adult	0.08	**1.06**	3.01	1.30	4.91	86.04
Fucus spp. (2c)	0.00	**1.11**	2.74	0.47	4.47	90.52

15^{th} month of succession

Species	Aug 02	Feb 03	Av.Diss	Diss/SD	Cont%	Cum.%
Bare rock	8.34	5.11	10.53	1.22	16.36	16.36
Verrucaria spp.	1.07	4.42	9.91	1.35	15.41	31.77
Ulva intestinalis	1.11	2.37	7.79	0.75	12.11	43.89
Ralfsia verrucosa	**1.90**	0.86	5.46	0.74	8.49	52.37
Fucus spiralis (2c)	**2.20**	0.10	5.02	0.79	7.81	60.18
Fucus vesiculosus (2c)	0.00	**1.97**	4.03	0.56	6.26	66.44
Fucus spp. (1c)	0.42	**0.68**	2.55	0.84	3.96	70.40
Fucus spp. (2c)	0.00	**1.03**	2.51	0.74	3.90	74.30

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Table E.6 – continued from previous page

Species	Aug 02	Feb 03	Av.Diss	Diss/SD	Cont%	Cum.%
Fucus spiralis (1c)	**1.09**	0.28	2.47	1.33	3.84	78.13
Chthamalus spp. juv.	0.36	**1.14**	2.40	1.16	3.73	81.86
Chthamalus spp. adult	**0.98**	0.40	2.10	1.27	3.26	85.12
Hildenbrandia rubra	0.00	0.69	1.88	0.30	2.92	88.04
Fucus vesiculosus (1c)	0.00	**0.74**	1.50	0.55	2.34	90.38

21^{st} month of succession

Species	Aug 02	Feb 03	Av.Diss	Diss/SD	Cont%	Cum.%
Verrucaria spp.	4.08	4.25	8.07	1.20	13.11	13.11
Fucus vesiculosus (2c)	1.51	**3.73**	6.86	1.12	11.14	24.24
Bare rock	**4.80**	**4.96**	6.00	1.29	9.74	33.98
Ulva intestinalis	2.63	0.34	5.61	0.72	9.11	43.09
Ralfsia verrucosa	**2.14**	**2.53**	5.29	1.26	8.58	51.68
Hildenbrandia rubra	0.46	1.75	3.86	0.61	6.27	57.95
Fucus spiralis (2c)	**1.61**	0.57	3.46	0.70	5.62	63.57
Fucus serratus (2c)	**1.15**	0.80	2.92	0.59	4.74	68.31
Fucus vesiculosus (1c)	0.52	**1.21**	2.39	0.98	3.88	72.20
Chthamalus spp. adult	0.62	**1.49**	2.24	1.02	3.63	75.83
Fucus spp. (1c)	**1.02**	**0.68**	1.94	1.01	3.15	78.97
Fucus spiralis (1c)	**0.65**	0.61	1.87	0.85	3.04	82.02
Chthamalus spp. juv.	**0.76**	**0.79**	1.43	1.24	2.32	84.34
Fucus spp. (2c)	0.00	**0.75**	1.41	0.43	2.29	86.63
Calothrix crustacea	0.06	0.53	1.11	1.10	1.80	88.43
Semibalanus adult	**0.41**	**0.30**	0.91	1.06	1.48	89.91
Porphyra linearis	0.43	0.00	0.91	0.56	1.48	91.39

E.5 Role of ephemeral species on later stage of succession in rockpools

Table E.7: Dissimilarity breakdown for the perennial species contribution to the differences between the manipulation treatments: removal of ephemeral species (manip) and unmanipulated plots (control) in rockpools at natural (+G) and reduced (-G) grazer density at the three shore level (High, Mid, Low). Good discriminating species are in bold. Primary and secondary algal cover was sampled and represented after species name by (1c) and (2c) respectively.

August 2004

Species	Manip	Control	Av.Diss	Diss/SD	Cont%	Cum.%
Sargassum muticum	4.78	4.48	8.14	1.27	17.68	17.68
Lithophyllum incrustans	1.73	1.47	4.40	1.00	9.56	27.23
Phymatolithon spp.	7.54	6.74	4.39	1.21	9.53	36.76
Corallina spp.	2.78	2.88	3.85	1.31	8.36	45.12
Fucus serratus	1.20	1.02	3.46	0.66	7.52	52.64
Ralfsia verrucosa	0.94	1.14	3.00	0.83	6.51	59.16
Bare rock	0.80	1.25	2.37	1.23	5.15	64.31
Sand	0.68	0.71	2.21	0.74	4.79	69.10
Fucus spp.	0.43	0.52	1.30	0.93	2.82	71.91
Stone	0.40	0.38	1.22	0.66	2.65	74.56
Gelidium spp.	0.42	0.36	1.16	0.83	2.52	77.08
Fucus spiralis (2c)	0.48	0.16	1.13	0.36	2.46	79.54
Osmundea hybrida	0.31	0.31	1.03	0.74	2.24	81.79
Anemonia spp.	0.22	0.40	1.03	0.77	2.24	84.03

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Table E.7 – continued from previous page

Species	Manip	Control	Av.Diss	Diss/SD	Cont%	Cum.%
Acidian	0.39	0.38	1.02	1.01	2.22	86.25
Mesophyllum liquenoides	0.21	0.32	0.91	0.61	1.98	88.23
Gastroclonium ovatum	0.21	0.27	0.83	0.78	1.81	90.05

November 2004

Species	Manip	Control	Av.Diss	Diss/SD	Cont%	Cum.%
Sargassum muticum	4.90	4.13	6.83	1.27	15.14	15.14
Fucus serratus	1.52	1.61	4.25	0.82	9.42	24.56
Lithophyllum incrustans	1.92	1.75	4.08	1.09	9.05	33.62
Phymatolithon spp.	7.62	6.95	3.88	1.24	8.61	42.23
Corallina spp.	2.79	3.06	3.55	1.38	7.87	50.10
Ralfsia verrucosa	1.06	1.40	2.82	0.93	6.25	56.35
Sand	1.01	0.80	2.17	1.02	4.80	61.16
Bare rock	0.85	1.06	2.05	1.17	4.55	65.70
Gelidium spp.	0.71	1.12	1.78	1.16	3.95	69.65
Acidian	0.65	0.58	1.32	1.06	2.94	72.59
Osmundea hybrida	0.54	0.54	1.30	1.03	2.89	75.49
Gastroclonium ovatum	0.42	0.45	1.20	0.89	2.66	78.15
Anemonia	0.36	0.45	1.09	0.83	2.42	80.57
Mesophyllum liquenoides	0.39	0.34	1.08	0.65	2.39	82.96
Stone	0.35	0.36	1.01	0.66	2.24	85.19
Fucus spp.	0.27	0.36	0.95	0.63	2.10	87.30
Petrocelis	0.36	0.45	0.92	1.15	2.04	89.34
Osmundea pinnatifida	0.12	0.35	0.68	0.81	1.51	90.85

E.6 Role of ephemeral species on later stage of succession on emergent rock

Table E.8: Dissimilarity breakdown for the perennial species contribution to the differences between the manipulation treatments: removal of ephemeral species (manip) and unmanipulated plots (control) on emergent rock at natural (+G) and reduced (-G) grazer density at the three shore level (High, Mid, Low). Good discriminating species are in bold. Primary and secondary algal cover was sampled and represented after species name by (1c) and (2c) respectively.

November 2003

Species	Manip	Control	Av.Diss	Diss/SD	Cont%	Cum.%
Ralfsia verrucosa	1.24	0.95	6.31	0.57	19.45	19.45
Bare rock	8.43	8.89	5.84	0.71	17.99	37.45
Fucus spp.	**1.70**	0.21	5.67	0.80	17.46	54.91
Chthamalus spp.	1.93	1.67	4.68	1.26	14.41	69.33
Fucus spiralis	0.00	**1.35**	4.21	0.58	12.99	82.32
Semibalanus balanoides	0.62	0.66	3.26	0.82	10.05	92.37

February 2004

Species	Manip	Control	Av.Diss	Diss/SD	Cont%	Cum.%
Bare rock	6.46	5.67	12.00	1.21	24.11	24.11
Ralfsia verrucosa	1.35	1.04	6.61	0.67	13.28	37.39
Chthamalus spp.	**2.25**	1.66	6.25	1.37	12.55	49.94
Fucus spp.	**1.67**	0.24	5.81	0.77	11.68	61.62
Hildenbrandia rubra	0.98	0.90	5.58	0.77	11.21	72.83

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Table E.8 – continued from previous page

Species	Manip	Control	Av.Diss	Diss/SD	Cont%	Cum.%
Fucus spiralis	0.57	**1.19**	5.15	0.65	10.34	83.17
Semibalanus balanoides	0.66	0.53	3.53	0.77	7.09	90.26

May 2004

Species	Manip	Control	Av.Diss	Diss/SD	Cont%	Cum.%
Bare rock	6.53	5.92	10.27	1.02	21.75	21.75
Fucus spiralis	**1.32**	0.94	6.13	0.63	12.97	34.72
Ralfsia verrucosa	1.29	1.07	5.69	0.69	12.04	46.76
Chthamalus spp.	**2.07**	1.86	5.58	1.21	11.82	58.58
Fucus vesiculosus	**1.25**	0.83	5.18	0.73	10.96	69.53
Fucus spp.	0.77	0.51	3.51	0.59	7.42	76.96
Hildenbrandia rubra	0.68	0.69	3.43	0.81	7.27	84.23
Semibalanus balanoides	0.59	0.69	2.92	1.04	6.17	90.40

November 2004

Species	Manip	Control	Av.Diss	Diss/SD	Cont%	Cum.%
Bare rock	6.08	6.25	10.96	0.95	21.54	21.54
Chthamalus spp.	**2.91**	2.75	7.16	1.30	14.07	35.61
Hildenbrandia rubra	1.16	1.49	5.42	0.87	10.65	46.26
Ralfsia verrucaria	1.24	1.34	5.39	0.90	10.59	56.84
Fucus spiralis	**1.34**	0.74	5.35	0.62	10.51	67.35
Fucus vesiculosus	**1.47**	0.82	4.91	0.66	9.65	77.00
Fucus serratus	**1.37**	0.58	4.08	0.50	8.02	85.02
Semibalanus balanoides	0.70	0.76	2.90	1.00	5.70	90.72

E.7 Role of perennial species on later stage of succession in rockpools

Table E.9: Dissimilarity breakdown for the perennial species contribution to the differences between the manipulation treatments: removal of ephemeral species (manip) and unmanipulated plots (control) in rockpools at natural (+G) and reduced (-G) grazer density at the three shore level (High, Mid, Low). Good discriminating species are in bold. Primary and secondary algal cover was sampled and represented after species name by (1c) and (2c) respectively.

May 2004 -G

Species	Control	Manip	Av.Diss	Diss/SD	Cont%	Cum.%
Ulva intestinalis	0.83	**1.71**	4.73	1.22	9.18	9.18
Scytosiphon lomentaria	0.66	**1.75**	4.13	1.32	8.03	17.21
Bare rock	1.15	1.13	3.18	1.07	6.18	23.39
Lithophyllum incrustans	0.75	0.97	3.01	1.15	5.85	29.24
Sand	0.71	0.71	2.92	1.08	5.68	34.92
Ulva spp.	0.28	**0.98**	2.81	1.06	5.45	40.37
Colpomenia peregrina	0.73	0.88	2.71	1.19	5.25	45.62
Ceramium spp.	0.44	**0.85**	2.51	1.16	4.87	50.49
Cladophora spp.	0.75	**1.18**	2.38	1.25	4.62	55.11
Sphacelaria spp.	0.65	0.69	2.32	1.12	4.50	59.62
Dumontia conforta	0.15	**0.72**	2.22	1.01	4.30	63.92
Ulva linza	0.32	**0.63**	2.05	1.15	3.99	67.91
Ectocarpus spp.	0.36	0.44	1.65	0.95	3.20	78.29
Chylocladia verticillata	0.33	0.25	1.35	0.69	2.61	80.90
Phymatolithon spp.	2.45	2.49	1.20	1.13	2.33	83.24
Stone	0.22	0.22	1.07	0.66	2.08	87.40

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Table E.9 – continued from previous page

Boergeseniella fruticulosa	0.22	0.19	1.00	0.70	1.95	89.35

August 2004 -G

Species	Control	Manip	Av.Diss	Diss/SD	Cont%	Cum.%
Ceramium spp.	1.45	1.50	3.92	1.30	7.15	7.15
Scytosiphon lomentaria	0.33	**1.21**	3.68	1.18	6.73	13.89
Lithophyllum incrustans	0.51	**1.05**	3.16	1.21	5.78	19.67
Ulva spp.	0.33	**0.98**	3.02	1.23	5.51	25.18
Bare rock	0.87	1.03	3.01	1.05	5.51	30.69
Sand	**0.83**	0.20	2.95	1.14	5.39	36.08
Ulva intestinalis	0.35	**0.80**	2.84	0.95	5.20	41.27
Sphacelaria spp.	0.71	0.66	2.50	1.19	4.57	45.85
Cladophora spp.	0.79	**1.36**	2.16	1.06	3.94	49.79
Colpomenia peregrina	0.32	**0.64**	2.11	1.08	3.85	53.64
Boergeseniella fruticulosa	0.49	0.41	2.08	0.97	3.80	57.44
Stone	**0.51**	0.19	1.90	0.87	3.48	60.92
Polysiphonia spp.	0.15	**0.50**	1.72	0.97	3.15	67.49
Ulva crinita	0.15	**0.45**	1.70	0.70	3.11	70.61
Phymatolithon spp.	2.41	2.53	1.59	1.35	2.91	73.51
Chaetomorpha linum	0.22	0.33	1.59	0.83	2.90	76.41
Ectocarpus spp.	0.07	**0.44**	1.54	0.83	2.81	79.22
Leathesia difformis	0.17	0.16	0.91	0.61	1.67	89.04
Ulva linza	0.10	0.10	0.68	0.42	1.24	90.27

November 2004 -G

Species	Control	Manip	Av.Diss	Diss/SD	Cont%	Cum.%
Ulva intestinalis	0.28	**1.12**	3.92	0.97	7.39	7.39
Lithophyllum incrustans	0.75	**1.10**	3.86	1.20	7.28	14.67
Ulva spp.	0.38	**1.04**	3.24	1.23	6.11	20.79
Sand	**0.93**	0.38	3.10	1.26	5.85	26.63
Bare rock	0.67	0.88	2.90	1.16	5.46	32.10
Boergeseniella fruticulosa	**0.76**	0.58	2.75	1.28	5.19	37.28
Cladophora spp.	0.63	**0.83**	2.64	1.36	4.98	42.27
Sphacelaria spp.	0.33	**0.85**	2.62	1.17	4.95	47.22
Ceramium spp.	0.70	0.63	2.49	1.13	4.70	51.92
Scytosiphon lomentaria	0.29	**0.64**	2.36	1.00	4.46	56.38
Acidian	**0.60**	0.47	2.21	1.14	4.17	60.55
Stone	**0.53**	0.35	2.13	0.94	4.02	64.57
Chaetomorpha linum	0.67	0.68	1.89	1.11	3.56	68.13
Colpomenia peregrina	0.27	**0.46**	1.61	1.01	3.04	77.97
Ulva crinita	0.24	0.23	1.41	0.70	2.67	80.64
Phymatolithon spp.	2.51	2.65	1.33	1.19	2.51	83.15
Champia parvula	0.23	0.25	1.29	0.76	2.43	85.58

May 2004 +G

Species	Control	Manip	Av.Diss	Diss/SD	Cont%	Cum.%
Lithophyllum incrustans	1.21	1.09	5.50	1.23	12.06	12.06
Bare rock	0.94	0.92	4.26	1.12	9.34	21.40
Colpomenia peregrina	**0.58**	0.15	3.30	1.19	7.23	28.63
Cladophora spp.	**0.54**	0.32	3.23	1.01	7.07	35.70
Ulva intestinalis	**0.37**	0.19	2.53	0.88	5.53	41.23
Ectocarpus spp.	0.30	0.25	2.28	0.82	4.99	46.22
Sphacelaria spp.	**0.36**	0.11	2.03	0.75	4.44	55.33
Phymatolithon spp.	2.79	3.00	1.91	1.19	4.18	59.51
Scytosiphon lomentaria	0.23	0.22	1.84	0.74	4.04	67.72
Chaetomorpha linum	0.26	0.14	1.74	0.68	3.81	75.40
Ulva xsp	0.16	0.15	1.24	0.52	2.72	80.96
Chylocladia verticillata	0.14	0.11	1.14	0.52	2.51	83.47
Boergeseniella fruticulosa	**0.16**	0.08	0.97	0.52	2.12	85.60
Dumontia conforta	**0.16**	0.00	0.83	0.44	1.82	87.41

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Table E.9 – continued from previous page

August 2004 +G

Species	Control	Manip	Av.Diss	Diss/SD	Cont%	Cum.%
Lithophyllum incrustans	1.17	1.36	5.17	1.35	11.57	11.57
Ceramium spp.	**1.10**	0.40	4.43	1.32	9.92	21.49
Bare rock	1.02	0.93	3.43	1.12	7.68	29.17
Cladophora spp.	0.78	0.60	2.75	1.05	6.15	35.32
Sphacelaria spp.	**0.64**	0.36	2.69	1.13	6.02	41.35
Chaetomorpha linum	0.24	**0.53**	2.60	1.07	5.83	47.17
Boergeseniella fruticulosa	**0.42**	0.11	2.00	0.74	4.47	56.77
Phymatolithon spp.	2.71	2.99	1.86	1.20	4.17	65.30
Colpomenia peregrina	**0.29**	0.15	1.63	0.79	3.64	68.94
Scytosiphon lomentaria	0.09	**0.22**	1.32	0.63	2.96	71.91
Champia parvula	**0.25**	0.00	1.14	0.56	2.55	77.07
Aglaothamnion spp.	**0.27**	0.00	1.12	0.55	2.50	79.57
Chylocladia verticillata	**0.17**	0.08	0.97	0.53	2.16	84.07
Polysiphonia spp.	**0.22**	0.00	0.97	0.55	2.16	86.23
Sand	**0.12**	0.09	0.81	0.42	1.81	88.04
Ulva intestinalis	**0.14**	0.00	0.75	0.44	1.69	89.73
Ulva crinita	0.08	0.07	0.66	0.42	1.48	91.21

November 2004 +G

Species	Control	Manip	Av.Diss	Diss/SD	Cont%	Cum.%
Lithophyllum incrustans	1.23	1.29	5.67	1.45	11.98	11.98
Bare rock	1.01	0.68	4.13	1.12	8.73	20.71
Chaetomorpha linum	0.46	0.55	2.98	1.05	6.29	27.00
Boergeseniella fruticulosa	**0.50**	0.08	2.58	0.96	5.45	38.34
Phymatolithon spp.	2.71	2.94	2.47	1.04	5.21	48.87
Ulva spp.	0.28	0.35	2.10	0.92	4.43	58.35
Cladophora spp.	0.32	0.21	1.98	0.84	4.17	62.52
Sphacelaria spp.	**0.32**	0.14	1.77	0.80	3.74	66.26
Sand	0.22	0.16	1.76	0.62	3.72	69.97
Ceramium spp.	**0.32**	0.00	1.69	0.68	3.57	77.13
Champia parvula	**0.36**	0.00	1.68	0.83	3.55	80.68
Scytosiphon lomentaria	0.08	**0.26**	1.56	0.62	3.29	83.98
Ulva intestinalis	0.15	0.15	1.42	0.61	3.00	86.97
Polysiphonia spp.	**0.15**	0.00	0.89	0.44	1.88	90.88

E.8 Role of barnacles during succession

Table E.10: Dissimilarity breakdown for the species contribution to the differences between the manipulation treatments: removal of barnacles (scraped) and mature plots (mature) on emergent rock at natural (+G) and reduced (-G) grazer density at the three shore level (High, Mid, Low). Good discriminating species are in bold. Primary and secondary algal cover was sampled and represented after species name by (1c) and (2c) respectively.

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Species	Scraped	Mature	Av.Diss	Diss/SD	Cont%	Cum.%
Chthamalus spp.	2.83	**5.37**	8.87	1.47	18.75	18.75
Verrucaria spp.	**5.79**	4.27	8.32	1.41	17.58	36.33
Bare rock	4.76	4.63	6.46	1.32	13.64	49.97
Ralfsia verrucosa	**1.21**	1.05	4.14	0.71	8.74	58.71
Fucus spiralis	1.07	1.18	4.11	0.67	8.68	67.39

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Table E.10 – continued from previous page

Species	Scraped	Mature	Av.Diss	Diss/SD	Cont%	Cum.%
Fucus vesiculosus	0.28	**1.30**	3.04	0.50	6.41	73.80
Ulva intestinalis	**0.78**	0.58	2.84	0.50	6.01	79.81
Hildenbrandia rubra	0.46	0.59	2.01	0.47	4.24	84.05
Fucus serratus	0.55	0.52	1.95	0.43	4.11	88.16
Semibalanus balanoides	**0.58**	0.25	1.72	0.72	3.62	91.78