# POPULATION ECOLOGY OF A TURF FORMING RED ALGA, *OSMUNDEA PINNATIFIDA* FROM THE ISLE OF MAN, BRITISH ISLES

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# Population Ecology of a turf-forming red alga, *Osmundea pinnatifida* from the Isle of Man, British Isles

Thesis submitted in accordance with the requirements of
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by

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**To Mum and Dad**

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# CHAPTER 1

# GENERAL INTRODUCTION

Many studies have categorised seaweed into different groups according to their individual photosynthesic performance based on surface area: biomass, e.g. the 'functional-form model' (Littler, 1980; Littler and Littler, 1980; Littler and Arnold, 1982). However, on the shore most plants do not grow as isolated individuals, but as clumps, mat, blankets or turfs. For example, in *Fucus* stands only 20% of the plants'surface is exposed to air at low tide (Schonbeck and Norton, 1979). In tightly-packed turfs almost the entire plant is obscured by its neighbours so that only the tips are exposed. So, it is not the morphology of the plants that matters, but perhaps that of the whole stand.

Although we know that plants living within turfs are partially protected from desiccation and herbivory, their productivity is less than that of isolated individuals because of self-shading and intraspecific competition (Hay, 1981a; Taylor and Hay, 1984; Hackney *et al.*, 1989). But little is known about the relative performance of different sized turfs or those in different habitats. For example, at first when size is small growth rate is very high, but later it is constrained by intraspecific-competition or increasing allocation of resources to sexual reproduction (Hughes, 1989). Thus patch size may influence the growth and performance of the population.

### Role of turfs on the shore

Seaweeds provide both habitat and food for many marine organisms. The habitat preference of many invertebrates is closely tied to their selection of diets and they are also attracted to algae that provide the best protection and living sites (Hayward, 1988; Pavia *et al.*, 1999). Algal turfs, however, not only provide shelter or food, they also accumulate sediment (Nuemann *et al.*, 1970; Stewart, 1983; D'Antonio, 1986; Whorff *et al.*, 1995). On some rocky shores the only sediment that is found is that trapped by congested turfs. Generally, sediment is known to adversely influence species diversity on rocky shores and to act as a disturbance factor for marine organisms (Seapy and Little, 1982; Little and Smith, 1988). Also, it has adverse effects on gametophytes of kelps by coating the space available for settlement, smothering the plants, scouring or cutting off the light and nutrients (Devenny and Volse, 1978; Norton, 1978). Sediment within turfs, however, is less likely to move, and forms a packed relatively stable layer, thus providing an additional microhabitat for sediment-loving organisms, and potentially increasing species diversity on the shore.

The role of sediment in intertidal turfs of *Rhodomela larix* (Turner) C. Agardh was investigated by D'Antonio (1986). These turfs served as refuges from large herbivores. The trapped sediment eliminated epiphytes and small herbivores such as amphipods and gastropods which are able to colonise and consume the plants, and also protected the lower part of plants from exposure stresses during summer. The relationship between intertidal *Corallina* turfs and sediment has been studied in detail (Stewart, 1982, 1983, 1989). Stewart (1983) proposed that seasonal changes in the abundance of some perennial epiphytes on *Corallina* turfs were related to the presence and movement of sediment on the shore. Moreover, she suggested that sediment may affect the abundance of the turfs indirectly by regulating the amount of grazers (Stewart, 1989). The consequences of mobile and trapped sediment are, therefore, complex and varied. Sediment does not only increase habitat diversity on the shore it also influences the plants themselves.

Turfs may also influence marine organisms outside the turfs. They monopolise the shore, occupying large areas, thus inhibiting recruitment (Sousa, 1979; Sousa *et al.*, 1981; D'Antonio, 1986; Kennelly, 1987; Miles and Meslow, 1990; Camus, 1994; Worm and Chapman, 1998). Once established, turfs will gradually encroach on the surrounding space as a result of their vegetative growth (Sousa, 1979; Sousa *et al.*, 1981; D' Antonio 1986; Guiry and Womersley, 1993). However, little is known about the expansion of turfs.

## *Laurencia* turfs

Species of the red algal genus *Laurencia* (Rhodomelaceae, Ceramiales) are a common component of subtropical and tropical marine floras (Taylor, 1960; Cribb, 1983; Lewis, 1984). There are more than 140 species worldwide (Nam *et al.*, 1994). In Hawaii alone, 15 species of *Laurencia* have been recorded (Saito, 1969; McDermid, 1988), several of which form 'turf' and some of these turfs cover more than 50% of the inhabited intertidal zone (McDermid, 1988). In the British Isles, there are six species (Maggs and Hommersand, 1993) and *L. pinnatifida* (Hudson) Lamouroux is the most common turf-former on the shores of the Isle of Man.

Recently, Nam *et al.* (1994) proposed that the genus *Laurencia* should be split into two, *Laurencia* and *Osmundea*, because of the differences in vegetative structure and reproductive morphology. *L. pinnatifida* was moved into the genus *Osmundea*, which has spermatangial branches arising directly from apical and epidermal cells in the apical pit of branchlets; and tetrasporangia produced from random epidermal cells.

Red algae in general have a complex life history in which there is an alternation of sexual and spore producing phases. In *Osmundea pinnatifida*, these phases are represented by plants that are morphologically identical. The male and female organs are borne on different plants and after fertilization the zygote develops into a carposporophyte that is 'parasitic' upon the female plant. The zygote undergoes mitotic division within the carposporangium so that numerous spores are produced from a single zygote (Maggs and Hommersand, 1993).

The carpospores generate into another spore-producing plant, the tetrasporophyte, whose spores give rise to the sexual plant, thus completing the life history. Such a life cycle is called the '*Polysiphonia*-type' and is common in many red algae species (Lee, 1980). The plants of each phase may have different ecological requirements and limitations and may therefore appear seasonally when conditions are favorable (South and Whittick, 1987). However, the life history is not obligatory and in many red algae the phases can exist independently and many even have different geographical distributions (Dixon, 1973).

*Osmundea pinnatifida* occurs on exposed to moderately exposed shores and forms extensive turfs on bedrock and binds sand over the rock (Maggs and Hommersand, 1993). These turfs grow in two directions: upward and outward. Upward growth determines thallus height, and outward growth expands the turf by means of the stoloniferous holdfast creeping over the rock (Fig. 1.1). Also, there is a vegetative mechanism by which the upright branches bend over to colonise areas of bare substratum (Godin, 1981). Such two-directional growth is also found in other seaweeds such as 'crust' forming algae e.g. *Ralfsia*, *Hildenbrandia*, *Scytosiphon* and *Corallina*. The crustose form of *Ralfsia* is more resistant to grazing than the erect phase, which becomes more dominant during winter when there are fewer herbivores (Dethier, 1981). In *Corallina*, the basal crusts resist both disturbance and herbivory; and can recover rapidly if damaged to give rise to new erect axes (Littler and Kauker, 1984). Thus, having different phases and two growth forms endows the plants with an added degree of 'ecological flexibility'. However, little is known of the growth of *Osmundea* or whether its life forms are an adaptation to counter stressful conditions.

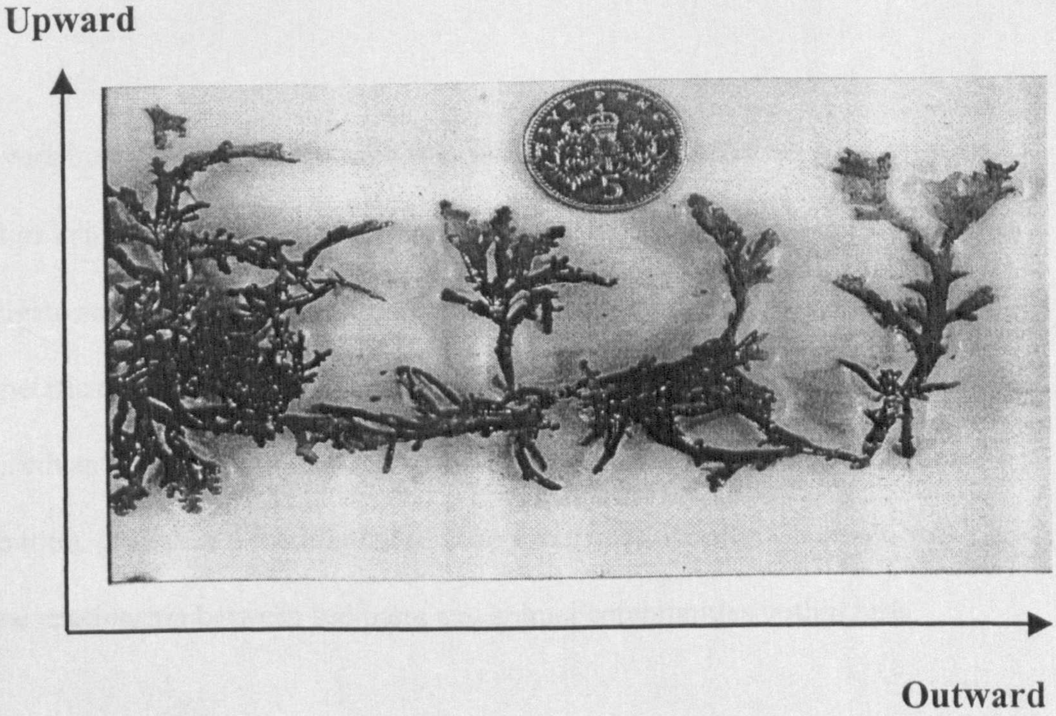


Figure 1.1. Two directions growth of the plant

*Laurencia* spp. are known to have more than 250 diverse chemical compounds, especially halogenated secondary metabolites (Erickson, 1983) which repel herbivores (Fenical, 1975; Hay and Fenical, 1988). Other species of algae also contain toxins or noxious compounds which would be expected to deter grazers. For example, *Dictyota* contains alkaloids (cited in Hawkins and Hartnoll, 1983) and phenolic compounds, diterpenoids and protein-complexing tannins are all present in various brown algae (e.g. McEnroe *et al.*, 1977; Rangan and Jensen, 1978). All these compounds have been suggested as having a defensive role against herbivory (e.g. Lubchenco, 1978; Targett, 1979; Hay, 1981b). Also fucoids, which blanket many rocky shores in temperate zones, have potent anti-grazer compounds (e.g. Norton and Manley, 1990). So perhaps being chemically defended is a necessity for perennial algae if they are to become dominant on the shore.

## Aims

The overall objective of the research is to investigate the population ecology of an algal turf using *Osmundea pinnatifida* as a model. To begin with, in chapter 2, I will investigate seasonal growth of *O. pinnatifida* as individual plants and examine intraspecific competition among turf-dwelling plants. In chapters 3 and 4 the benefits and disadvantages of being in a turf are investigated. Chapter 5 is a study of the distribution, growth and recruitment of *Osmundea* turfs. Finally, Chapter 6 will explore relationship between sediment and animal communities within turfs.

# CHAPTER 2

# Plant size variability and self-thinning within turfs

## 2.1 INTRODUCTION

Competition for resources occurs in an overcrowded stand of plants and may exert influence at the level of community, population or individual plant. At the population level, competition affects plant size and age structure (Olson and Lubchenco, 1990). For example, variation in size structure increase over time as a consequence of different growth rates of the plants. However, overgrown smaller fronds are likely to die leaving bigger fronds all of a similar size, resulting in less variation in size structure and density in the population, the so-called 'self-thinning law' (Weiner and Thomas, 1986).

Variations in size structure (size hierarchy or size inequality) have been used to describe populations as diverse as those of terrestrial plants (e.g. Weiner 1985; Weiner and Thomas 1986; Bona, 1988; Bendal *et al.*, 1989; Geber, 1989), seaweeds (e.g. Ang and De Wreede, 1992; Mart nez and Santelices, 1992; Santos, 1995; Creed *et al.*, 1996, 1998) and fish (e.g. Geffen, 1996; Imsland *et al.*, 1998). The variations in size structure of a population can be assessed graphically using histograms and by mathematical terms such as skewness, kurtosis, coefficient of variation and the Gini coefficient (Hora, 1988). The skewness coefficient (*g1*) describes the degree to which the distribution in a population departs from normality, while the coefficient of variation (*CV*) and the Gini coefficient (*G*) describe size inequality. However, the Gini coefficient is considered preferable as it is more robust than the coefficient of variance (Bendal *et al.*, 1989), and both are highly correlated (Creed *et al.*, 1996).

The 'self-thinning law' or '$-^{3}/_{2}$power law' was first proposed by Yoda *et al.* (1963) and has been applied widely both to terrestrial plants (e.g. White and Harper, 1970; White, 1980; Westoby, 1984) and seaweeds (e.g. Ang and De Wreede, 1992; Santos, 1995, Creed *et al.*,1996, 1998; Scrosati and De Wreede , 1997; Scrosati and Servíre-Zaragoza, 2000). In a dense stand of even-aged plants, the relationship between biomass and density over time follows a thinning line of slope - $^{3}/_{2}$ with an maximum intercept of 4.3, and a thinning line of slope $-^{1}/_{2}$ when mean plant weight and density are plotted on a log scale (Westoby, 1984). Most plant populations follow the self-thinning trajectory, although there may be some exceptions (e.g. Pitelka, 1984; Martínez and Santelices, 1992; de Kroon, 1993; Olesen and Sand Jensen, 1994; Santos, 1995; Scrosati and DeWreede, 1997).

Because *Osmundea pinnatifida* forms discrete patches, often separated by areas of rock that are devoid of seaweeds, they present an ideal situation in which to study the effects of intraspecific competition unfettered from the constraints of interspecific competition. Plants in algal turfs are known to suffer from self-shading and reduced nutrient diffusion (Hay, 1981a), but little is known about competition within such turfs. I therefore chose *Osmundea pinnatifida* as a model in which to study competition by assessing its population dynamics with respect to variations in the distribution of frond size and density within stands. This will also provide a basis for the analysis of the population ecology of this species. I hypothesized that:

(1) there are variations in frond length and frond density distribution in different regions of turfs and those change over time.

(2) turf-dwelling plants are subject to the 'self-thinning' rule.

## 2.2 MATERIALS AND METHODS

### 2.2.1 Population dynamics

Ten roughly circular patches of *Osmundea pinnatifida* turf measuring approximately 25-30 cm in diameter were monitored monthly at Port Erin (54°06′ N; 4°46′ W) on the south of the Isle of Man between 2.5-2.7 m above Lowest Astronomical Tide (LAT). This shore was chosen because it is sheltered and has few grazers (littorinid snails and limpets), thus fronds suffer little sporadic disturbance from wave action or herbivory. Patches were permanently labelled using yellow bright fluorescenct tape fixed to the rock nearby. Each patch was sampled non-destructively at 5 places: 0-2.9 cm, 3.0-5.9 cm, 6.0-8.9cm, 9.0-11.9 cm and 12-15 cm from the margin inwards to the middle. The growth and development of individual fronds were followed. Frond length, frond density and patch area were monitored from July 1998-July 1999.

Frond length was measured by inserting a long pin into the patches, five randomly selected plants were measured in each concentric zone along five radial line transects in each patch.

Frond density was measured by counting the number of upright fronds in 2.5 cm X 2.5 cm quadrats in each zone along five line transects.

Relative growth rate (RGR) of upright fronds was calculated using average frond length in each patch by following equation:

$$RGR = \frac{\mathrm{Log}_e L2 - \mathrm{Log}_e L1}{t2 - t1}$$

Where L2 and L1 are frond length (cm) at time interval for upward growth

t2 and t1 are the time interval (month)

Frond length and density were correlated with environmental conditions monitored at the same time, as well as 1, 2 and 3 months prior to sampling, to detect possible delayed effects. Air temperature, total rainfall, sunshine and wind speed data were provided by the meteorological office at Ronaldsway airport situated 15.6 km from the sample site. Seawater temperature in Port Erin Bay was measured daily by the Port Erin Marine Laboratory.

### 2.2.2 Biomass length relationship

Five *Osmundea* patches were randomly collected using a paint scraper, placed in plastic bags and transferred to the laboratory from the same shore every month during October 1998 – May 1999. On each occasion a hundred individual fronds were randomly chosen and their length and biomass were determined. Each individual frond was placed in pre-weighed foil tray, dried in an oven at 60°C and reduced to constant weight. The aim of these measurements was to convert frond length of plants in the monitored patches into plant biomass in order to calculate the relationship between log frond density and log biomass.

### 2.2.3 Quantifying size structure variability

All data analyses were computed using STATISTICA 5.5 (Stat Soft, Inc), except the Gini coefficient calculations which, following Weiner and Solbrig (1984), were done using a PASCAL program. The Skewness coefficient (*g1*) and the Coefficient of Variation (*CV*), following Sokal and Rohlf (1981) and the Gini coefficient (*G*), were computed for all patches to assess the level of inequality in both frond length and density distribution. The Skewness coefficient is a parameter quantifying deviations from a normal distribution; positive values indicate a long right tail (i. e. more small fronds and fewer large fronds) and vice versa for a negative value. In contrast, *CV* and *G* are measures of relative precision that reflect the ratio of a measure of dispersion. *G* has a minimum value of 0, when all the individuals are the same size, and a theoretical maximum of 1 when $n = \infty$ and all individuals but one are the same (theoretically 0) size. All three measurements were calculated so that the results could be compared with other workers who had used only one or other of these statistics.

### 2.2.4 Data analyses

Analyses of Variance (ANOVA) were employed to test variations in frond length, frond density, relative growth rate and all coefficients. Tests of homogeneity of variance (Bartlett's test at $P$=0.05), analyses of variance and multiple comparisons, (Tukey HSD) were performed using STATISTICA 5.5. Where gross heterogeneity of variance was found, data were transformed to meet the assumptions of the parametric statistics (Underwood, 1981).

Friedman ANOVA was employed when the data did not meet assumptions of ANOVA after a series of transformations, and multiple comparisons were tested when there were significant differences between treatments, following Zar (1984).

Best-fit line models were applied to test the relation between biomass and frond length of destructive samples using MINITAB Statistical Software (Minitab Inc., PA, USA) to convert frond length in the monitored patches to biomass. Pearson's product moment correlation was employed to investigate the strength of linear association between log biomass and log density to test whether it followed the self-thinning rule $^{-3}/_{2}$ gradient, and then slopes were fitted by means of a principal components analysis as indicated by Weller (1987).

Multiple regression was employed to test the effects of abiotic factors on the population.

## 2.3 RESULTS

### 2.3.1 Variations and growth in fronds length and frond density

There were no significant differences in relative growth rate of plants in different regions within the patch ($F_{4,2940}$= 0.038, $P$ =0.99), although it was slightly less in plants at the edge compared to those within turfs. Thus, the data were pooled to represent an average relative growth rate for the whole patch throughout the year (Fig. 2.1a), which was significantly different in different months ($F_{11,2940}$ = 1836.47, $P$ <0.0001).

There was a seasonal increase in frond length and frond density and both displayed the same pattern (Fig. 2.1b, 2.1c). New fronds started to arise at the beginning of July after most fronds had been lost in June. Frond density rapidly increased during the autumn and then frond length increased in early winter and reached its maximum in late spring.

Frond length was also less in marginal plants (Fig. 2.1b; $F_{3,3005}$ = 207.35, $P$<0.0001), but there was no difference among plants away from the margin.

Frond density increased sharply during July - December and tended to reach its maximum later in the winter. There was a significantly difference in different months ($F_{12,3185}$ = 2705.59, $P$ < 0.0001), but no difference in different regions within turfs (Fig. 2.1c; $F_{4,3185}$ = 1.55, $P$ =0.18) although the plants were slightly less dense at the turf margin.

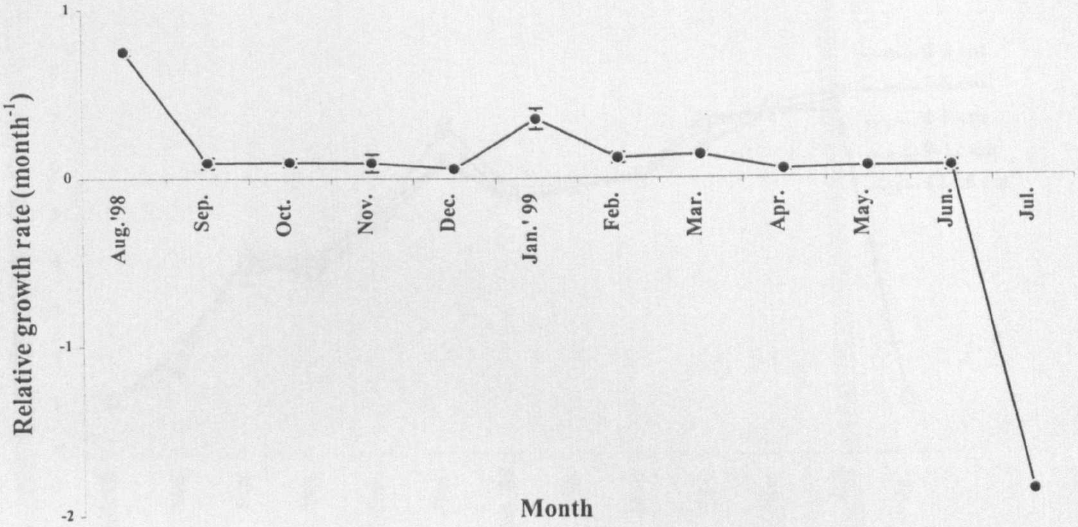


Figure 2.1a. The relative growth rate of *Osmundea pinnatifida* relative growth rate.

Bars = ± 1 S.E.

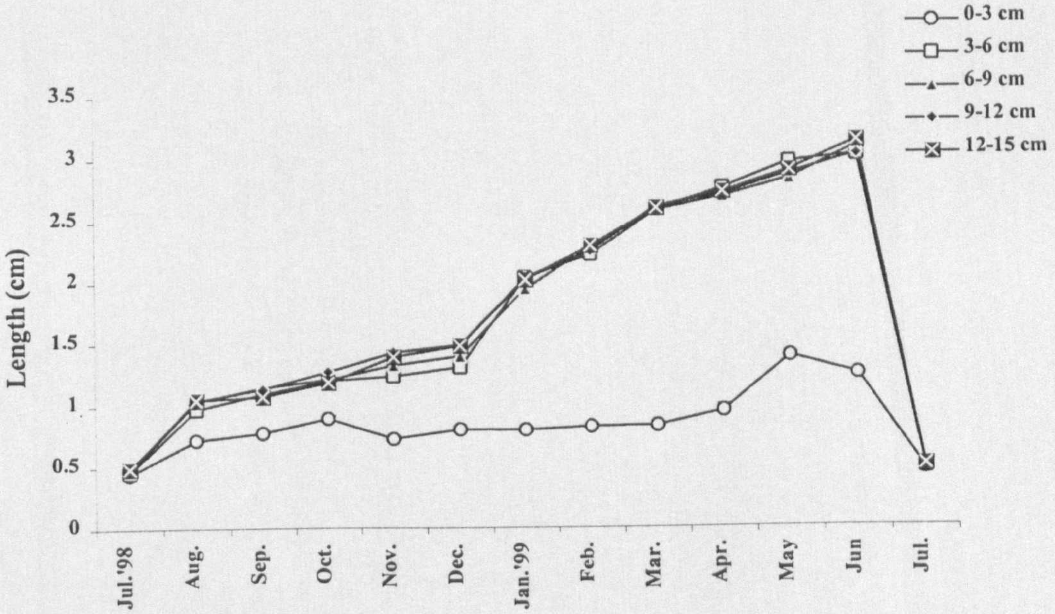


Figure 2.1b. The frond length of plants growing at various distance from the margin

of patches of turf. Bars = ± 1 S.E.

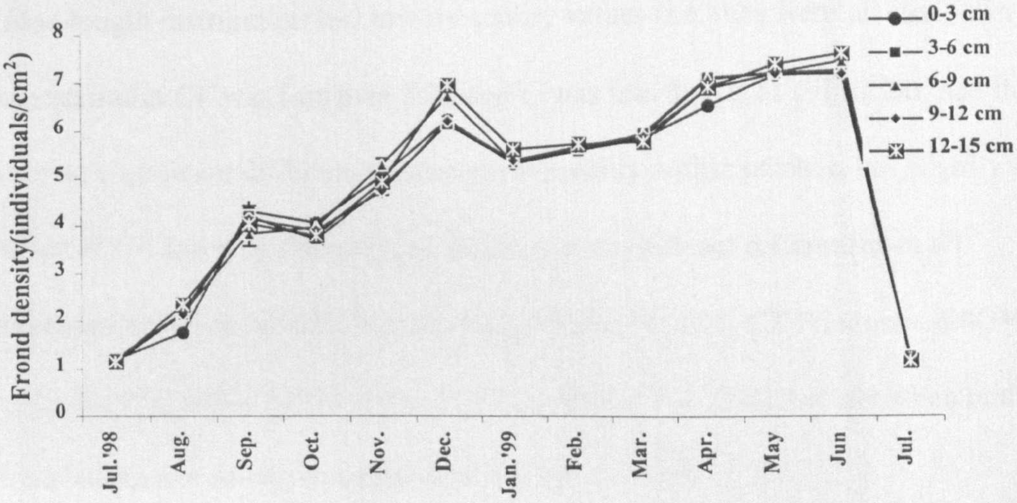


Figure 2.1c. The density of fronds growing at various distance from the margin of patches of turf. Bars = ± 1 S.E.

### 2.3.2 Temporal and spatial variations in population structure

Frond length distribution had low inequality values (i.e. they were all similar in size), the maximum *CV* was less than 0.22 and *G* was less than 0.11 (Fig.2.2a); and there were no significant differences in length inequality within patches, but slightly higher values of *CV* and *G* at the margins. There were significant differences in all coefficients with time (ANOVA *g1*, $F_{12,585}$=5.33, P<0.001, *CV* Friedman ANOVA $\chi^2$ = 413.93, P<0.0001, ANOVA log *G*, $F_{12,585}$=88.40, *P*<0.001), but not when both frond length and density reached their maxima.

Frond density inequality showed a similar pattern to frond length; and had low inequality values (Fig.2.2b). There were no differences in any of the coefficients between different areas in turfs, but there were differences in different months (ANOVA *g1*; $F_{12,585}$=1.93, *P*=0.03, Friedman ANOVA CV, $\chi^2$= 428.39, P<0.0001, ANOVA log *G*; $F_{12,585}$=134.03, *P*<0.0001). Skewness of frond density showed similar values throughout the year, but there was a significant difference between January and April.

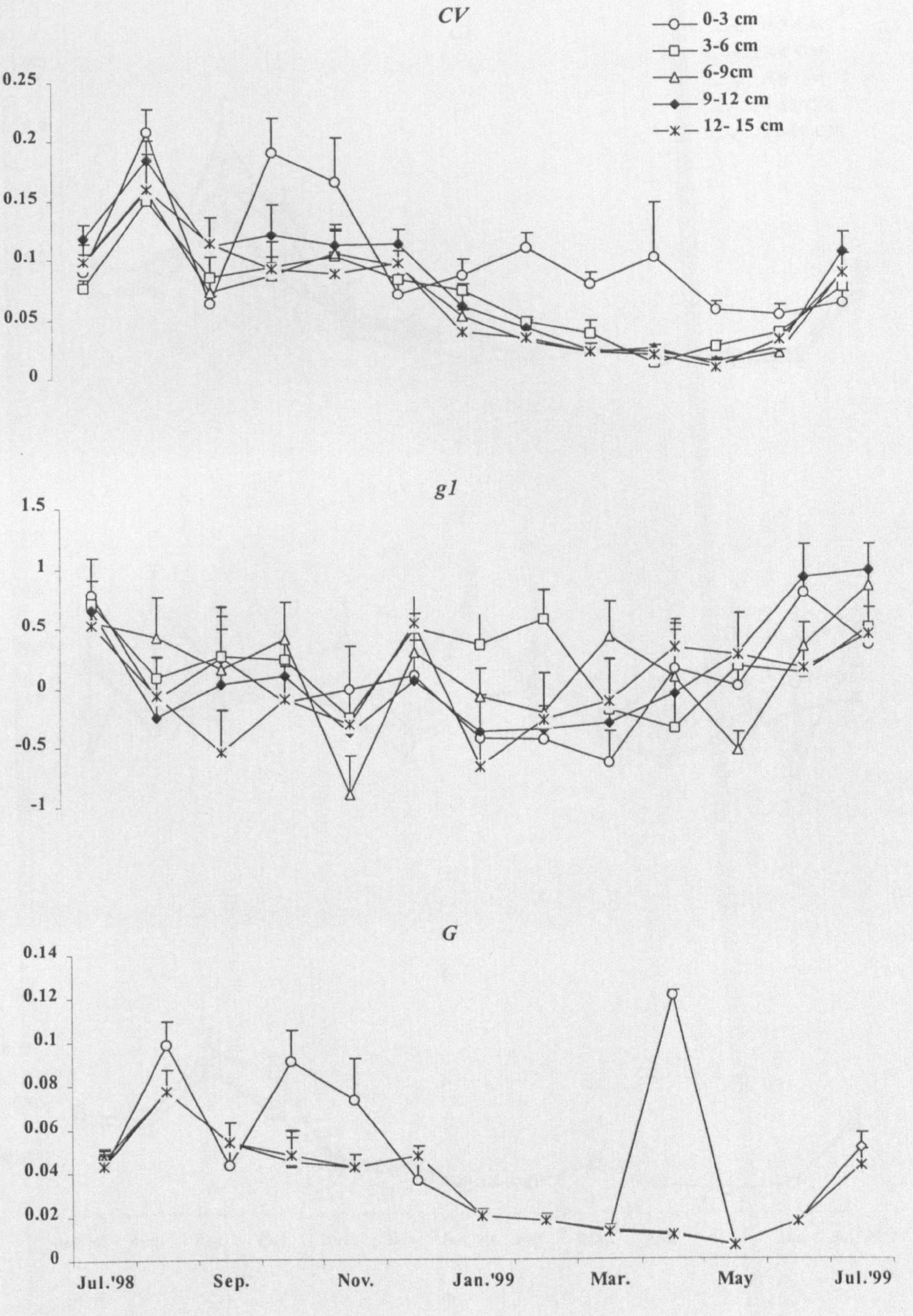


Figure 2.2a. Annual variation of *O. pinnatifida* frond length distribution at various distance from the margin of patches of turf. Bars = ± 1 S.E..

*CV*= coefficient variance, *g1*=skewness coefficient, *G*= Gini coefficient.

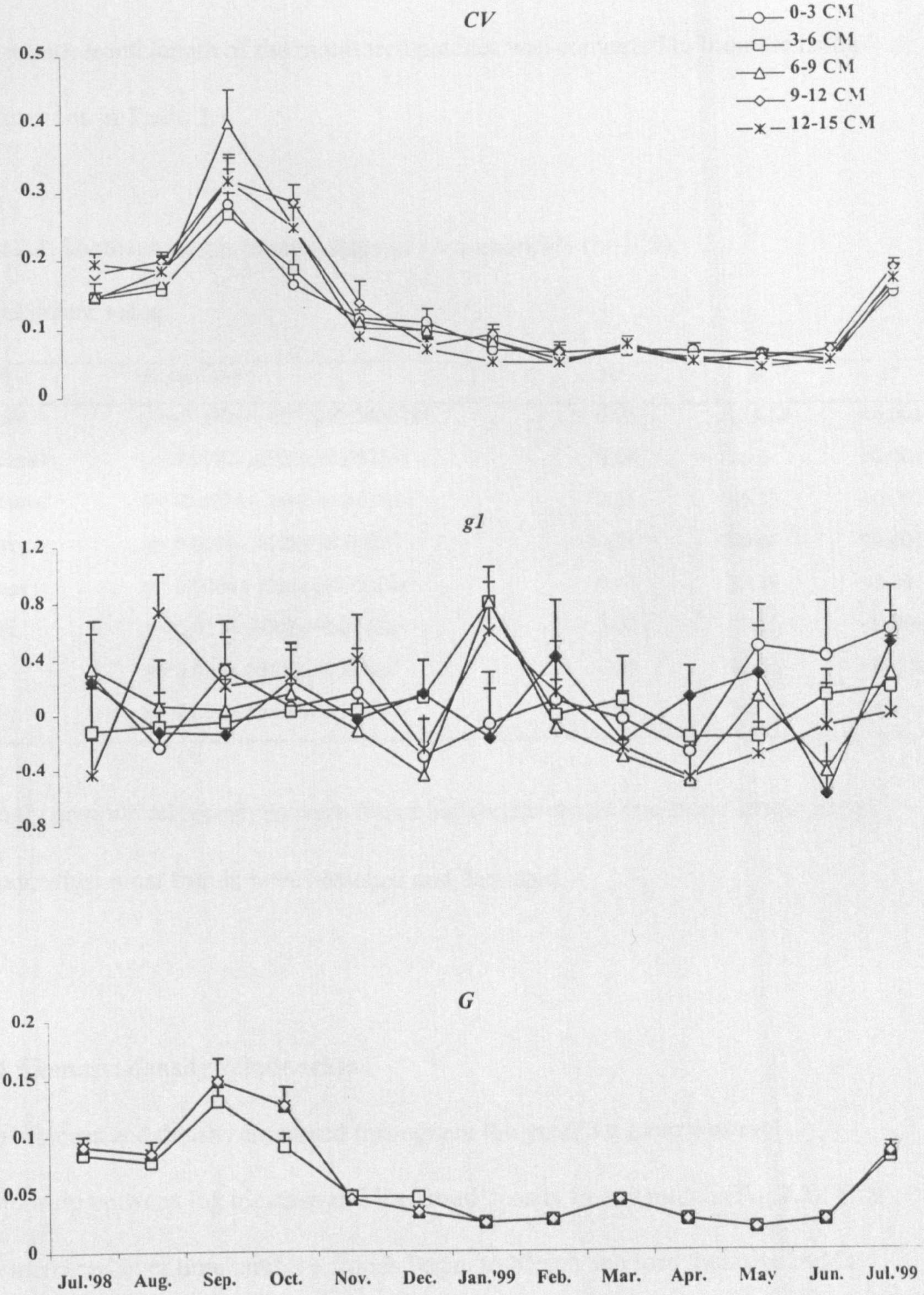


Figure 2.2b. Annual variation of *O. pinnatifida* frond density distribution at various distance from the margin of patches of turf. Bars = ± 1 S.E.

*CV*= coefficient variance, *g1*=skewness coefficient, *G*= Gini coefficient.

### 2.3.3 Biomass: length relationships

Each month frond length of the monitored patches was converted to biomass using the equations in Table 2.1.

Table 2.1. Biomass length relationships of *O. pinnatifida* (n=100), $r^2$: coefficient value

| Month | Equations | $R^2$ | F | *P* |
|---|---|---|---|---|
| **October** | $y= -0.0004+.0032x-0.00007x^2$ | 0.70 | 113.68 | <0.001 |
| **November** | $y= 0.0027-.0023x+0.0025x^2$ | 0.58 | 66.0 | <0.001 |
| **December** | $y= -0.0024+.0043x+0.0002x^2$ | 0.64 | 85.72 | <0.001 |
| **January** | $y= 0.0039-.0029x+0.002x^2$ | 0.55 | 60.06 | <0.001 |
| **February** | $y= 0.0004+.0004x+0.0016x^2$ | 0.63 | 83.14 | <0.001 |
| **March** | $y= 0.011+.0092x+0.0041x^2$ | 0.63 | 40.10 | <0.001 |
| **April** | $y= 0.039-.0248x+0.0079x^2$ | 0.50 | 48.83 | <0.001 |
| **May** | $y= 21.94-15.03x+2.58x^2$ | 0.07 | 3.6 | 0.07 |

Strongly positive relationships were found between biomass and frond length except in May, when most fronds were bleached and damaged.

### 2.3.4 Biomass: density relationships

Both biomass and density increased throughout the year, but there was no relationship between log biomass and log frond density in any month (Fig.2.3); they both increased over time until the fronds began to bleach and lose their tips in May. Pearson's product moment correlation revealed that the data were unsuitable for slope testing (e.g. Oct., $r = 0.04$, $P = 0.92$; Feb., $r = 0.33$, $P=0.35$ and Apr., $r = 0.19$, $P=0.60$). Thus, further slope fitting was not carried out.

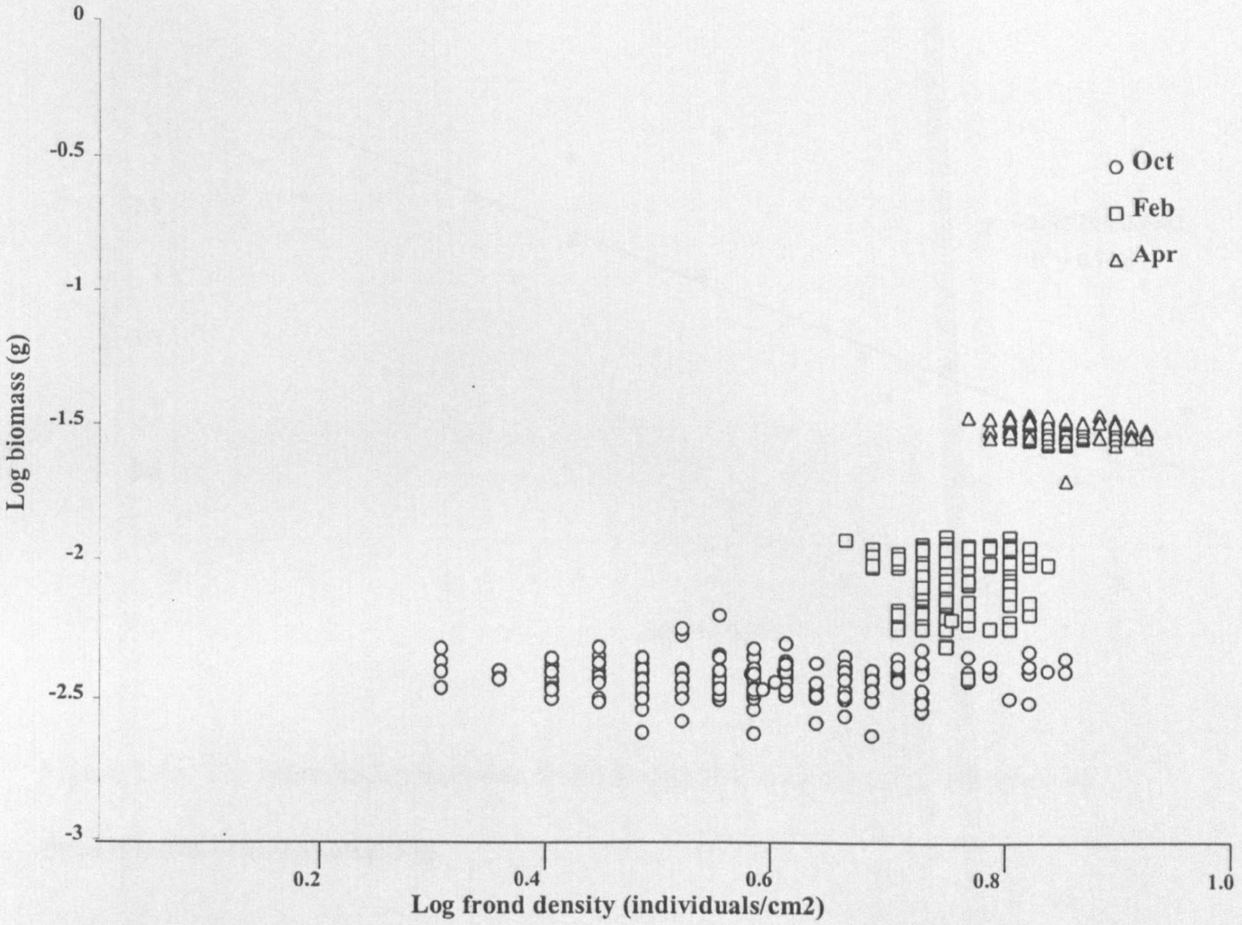


Figure 2.3. Self-thinning ($\log_{10}$ biomass-$\log_{10}$ density plots).

### 2.3.5 Relationship between plant growth and abiotic factors

Partial correlation and stepwise multiple regression showed that the only factor that influenced frond length and density was the sunshine hours three months prior to sampling. Further linear regression was applied to test the relationship between growth and sunshine hours. Increasing sunshine hours during spring and summer resulted in a reduction of frond length (Fig. 2.4a, $F_{1,11} = 25.78$, $P < 0.001$) and frond density (Fig. 2.4b, $F_{1,11} = 13.62$, $P < 0.01$).

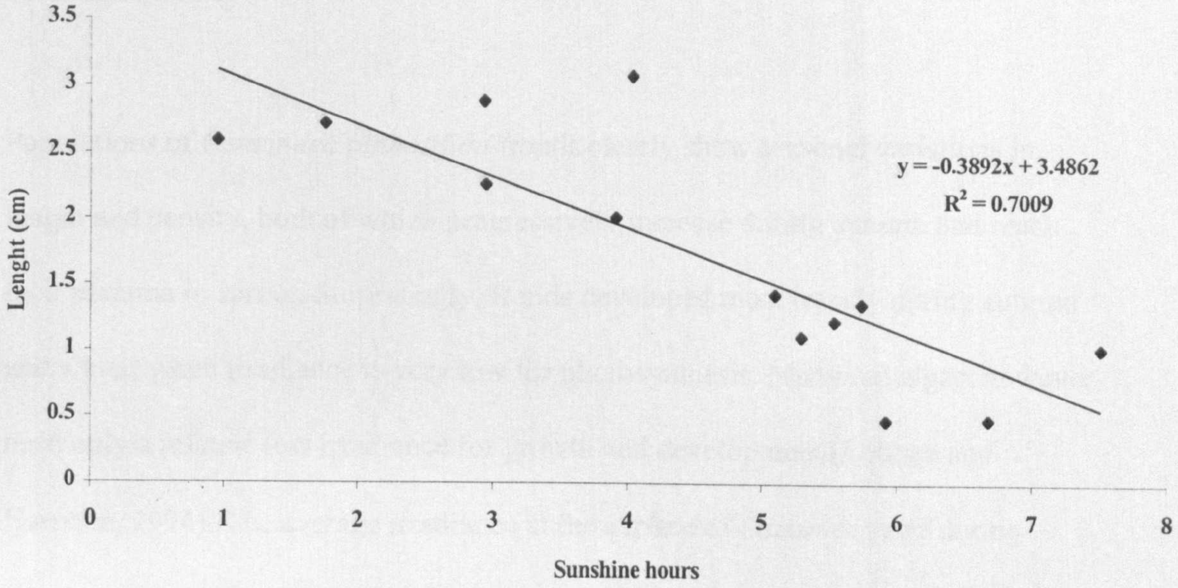


Figure 2.4a. The relationship between frond length and average sunshine hours of three months prior to sampling.

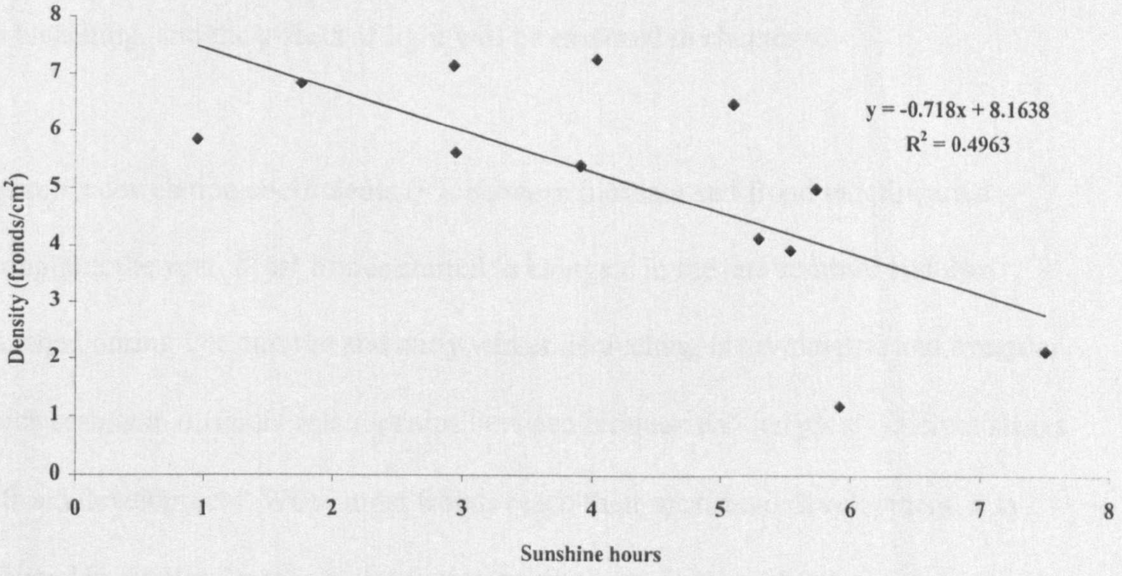


Figure 2.4b. The relationship between frond density and average sunshine hours of three months prior to sampling.

## 2.4 DISCUSSION

Populations of *Osmundea pinnatifida* fronds clearly show seasonal variations in length and density, both of which progressively increase during autumn and reach their maxima in spring. Surprisingly, fronds developed most rapidly during autumn and winter when irradiance is very low for photosynthesis. Many red algae, however, need only a relative low irradiance for growth and development (Lobban and Harrison, 1994). The average irradiance at the surface of *Osmundea* turf during winter was only 28 $\mu$mol. $m^{-2}$ $s^{-1}$. By contrast, during spring when fronds were exposed to greater irradiance of 1194 $\mu$mol. $m^{-2}$ $s^{-1}$, they became bleached. Most fronds then lost tissue and rapidly died back in summer. Frond loss both in length and density showed a negative relationship with sunshine hours in the previous three months when they were exposed to 7.5 hours sunshine/day, but bleaching was first noticed at beginning of April. This suggested that high irradiance is responsible for the bleaching, and the effects of light will be explored in chapter 4.

Pearson's correlation coefficients ($r^2$), between biomass and frond length varied throughout the year. Most fronds started to elongate in the late summer and then branched during late autumn and early winter. Branching is asymmetric and irregular which results in different relationships between biomass and length at different stages of frond development. When most fronds reach their maximum development, it is reflected in similar Pearson's correlation coefficients. Later, in May, when most fronds were suffering from bleaching and losing tissue, there was no relationship between biomass and length. Biomass: length relationships of *O. pinnatifida*, were therefore, influenced by the stage of frond development and bleaching of frond. In a stand of *O. pinnatifida* most fronds gradually arise vegetatively at the same time and seem to produce very few spores or are sterile, as is common in other turf-forming algae (Guiry and Womersley, 1993; Choi *et al.*, in press). *Osmundea* populations, therefore, would have no effects attributable to age or genetic differences or maternal effects between the plants, all of which can have great influence on size inequality in populations (Weiner and Thomas, 1986).

Plants within turfs are similar and uniform, but those at the periphery are more variable both in size and density. At the periphery, fronds are likely to be exposed to different conditions such as irradiance level, temperature and desiccation. In contrast, fronds within turfs are more protected from desiccation and herbivory than those at the periphery, and are likely to benefit from environmental homogeneity, all of which might influence the amount of variation between fronds. The environmental heterogeneity around the periphery might adversely influence photosynthesis at the edges and in consequence the fronds are smaller and less dense. This will be explored in chapter 3.

Monospecific stands of plants as diverse as trees and seaweeds usually conform to the self-thinning 'rule' (e.g. Harper, 1977; Cousens and Hutchings, 1983; Creed *et al.*, 1998). Surprisingly, *O. pinnatifida* does not seem to follow the rule even when in a crowded turf of 8-10 individuals/cm$^2$. In a dynamic dense stand of *O. pinnatifida*, each stage of frond development could have different demands for resources. At first, when most fronds arise in late summer they are less dense (Fig. 1.1c), thus it is unlikely that severe competition would occur at this stage. When the fronds reach their maximum length, they shade each other which may result in light limitation and increasing density might also influence nutrient circulation rates (Carpenter and William, 1993; Scrosati and DeWreede, 1997). However, through their stoloniferous holdfast, there is a physiological connection between many fronds in the turf and they may therefore be able to share nutrients and other substances as in some colonial species (Pitelka and Ashmun, 1985; de Kroon, 1993; Stuefer *et al.*, 1994; Alpert, 1996) *O. pinnatifida*, therefore, could avoid some of the effects of competition and self-thinning.

# CHAPTER 3

# THE EFFECT OF IRRADIANCE AND DESICCATION

## 3.1 INTRODUCTION

Seaweeds are aquatic plants, but intermittently experience aerial conditions. When the tide is out, they are exposed to much higher or lower temperatures depending on the season, desiccation, insolation and a different inorganic carbon source ($CO_2$ when emersed and $HCO_3^-$ when submerged). Such abiotic factors greatly influence the growth of intertidal algae (e.g. Johnston *et al.*, 1992; Matta and Chapman, 1995; Cheshire *et al.*, 1996). The physiologically resistant seaweeds survive under a variety of fluctuating conditions on the shore, but there are few studies that investigated their responses to several factors simultaneously which would be more ecologically relevant (Davison and Pearson, 1996; but see Dudgeon *et al.*, 1995; Matta and Chapman, 1995; Beach and Smith, 1997).

The stresses of desiccation and overheating during low tide can be so severe as to damage or kill plants, thus limiting their vertical distribution on the shore (Dring and Brown, 1982; Brown, 1987; Einav and Beer, 1993). Some reduction of stress may depend on aspect, or shading provided by living under a fucoid canopy or from the protection of growing in crowded stands. Closely packed turfs of low-growing seaweeds probably benefit greatly from mutual protection and the moist microclimate that develops within the turf. On the macroscale they cannot avoid the regular cycle of tidal inundation and emergence, which may adversely affect the growth of plants at the upper limits of their zone. However, on a microscale their growth may be substantially different from that of isolated individual plants, and little is known about variations in desiccation and irradiance within turfs.

The habitat of turf formation is known to moderate stressful conditions such as desiccation and herbivory, but to increase self-shading (Hay, 1981a; Taylor and Hay, 1984). Shading reduces photosynthesis, therefore results in slower growth of the individuals. However, the regime inside a turf is complex and the degree of mutual shading is probably very different at different depths within the turf and for plants close to the periphery of a patch compared to these in the middle. The variation of irradiance within turfs and its effects on photosynthesis between the top and under the canopy have been recently studied (Beach and Smith, 1997), but little is known of the difference in performance of plants at the periphery and centre of a patch.

There seem to be size differences between plants growing in different regions of algal turfs. For example, in turfs of the red alga *Osmundea pinnatifida* (Hudson) Lamouroux, fronds lower in the *Osmundea* zone and in the centre of turfs appear to be taller and denser than those higher on the shore and at the periphery (as shown in chapter 2). Such variations might result from differences in desiccation or irradiance within turfs or the plants' ability to use different carbon sources. Thus, the little-studied *Osmundea* turf provides an interesting system in which to examine the benefits and disadvantages of forming a turf and the effects of abiotic factors on intertidal seaweeds both on a macro and micro scale.

I therefore conducted experiments based on combinations of environmental factors that fronds experience on the shore, in order to investigate:

1) variations of irradiance and desiccation in different regions within turfs at the upper and lower limit of the *Osmundea* zone on the shore.
2) the effects of irradiance and desiccation on net photosynthesis when the alga is in air and in water.

I hypothesised that although turfs provide plants with mutual protection from desiccation, they still suffer from desiccation and self-shading which cause variations in frond length and density of the turf at different levels in the *Osmundea* zone and within individual turfs.

## 3.2 MATERIALS AND METHODS

### 3.2.1 Field study

The study site was on the southern shore of Port St. Mary Ledges, Isle of Man, British Isles (54°04'N, 4°46'W). Work was carried out within the *Osmundea* zone which extended from 2.0 m (lower limit) -3.5 m (higher limit) above the Lowest Astronomical Tide.

Irradiance was measured at different places above and within patches of turf (Periphery *VS* Centre) and at different times of the year (March *VS* May) with a Macam model Q102 light meter. Repeated measurements were made with six turfs on a sunny day when there was no cloud cover. These were later used as a basis for simulating natural light levels in the laboratory.

Desiccation of individual fronds was investigated on the shore with respect to differences in the location within a turf (Periphery *VS* Centre), shore level (High *VS* Low) and season (March *VS* May). These investigations were conducted during spring tides and dry weather when fronds experienced the most extreme drying conditions. Turfs were removed using a paint scraper, placed in a plastic bag and transferred to the laboratory.

### 3.2.2 Laboratory study

Thirty-five fronds from each patch were randomly selected and carefully removed and cleaned of any sediment, animals or attached epiphytes. Then they were weighed on a 4 digit balance (Desiccated weight) and re-dehydrated separately with filtered seawater until they became fully-hydrated, then re-weighed (Fully hydrated weight). Finally, they were oven-dried at 60°C until the weight became constant (Oven dry weight). Percentage desiccation was calculated as follows:

$$\% \text{ Desiccation} = 100 - \frac{(\text{Desiccated weight} - \text{Oven dry weight}) \times 100}{(\text{Fully hydrated weight} - \text{Oven dry weight})}$$

Fronds were cleaned thoroughly with seawater, placed in 250 ml of seawater in beakers and kept at 10°C in the dark for 24 hrs prior to measuring their rate of photosynthesis.

Three irradiance levels were chosen to simulate the light conditions of *Osmundea* turfs on the shore: 10 $\mu$mol.m$^{-2}$s$^{-1}$, 600 $\mu$mol.m$^{-2}$s$^{-1}$ and 1200 $\mu$mol.m$^{-2}$s$^{-1}$. These levels were chosen to approximate to those found in the field measurement in natural stands (Fig. 3.1).

Fronds were dried to three levels to simulate natural desiccation of turfs on the shore (Fig. 3.2): 0% (submerged), 50% (within turf, in the lower *Osmundea* zone, during winter) and 70% (peripheral turf, on the higher part of the zone, during spring).

Prior to manipulating desiccation, we investigated the relationship between water loss from the plant and time exposed in laboratory. Thirty individual fronds were dried at 16°C and 80% relative humidity in a controlled temperature room. Fronds were weighed hourly for 8 hrs. The best fit for the relationship between desiccation and exposed hours was the logarithmic model $Y=-8.51+38.54X-4.33X^2$ ($r^2 = 0.87$; $F_{2,88} = 382.54$, $P<0.001$). Subsequently, the fronds were dried for 2 hrs for 50% desiccation and 3.5 hrs for 70% desiccation.

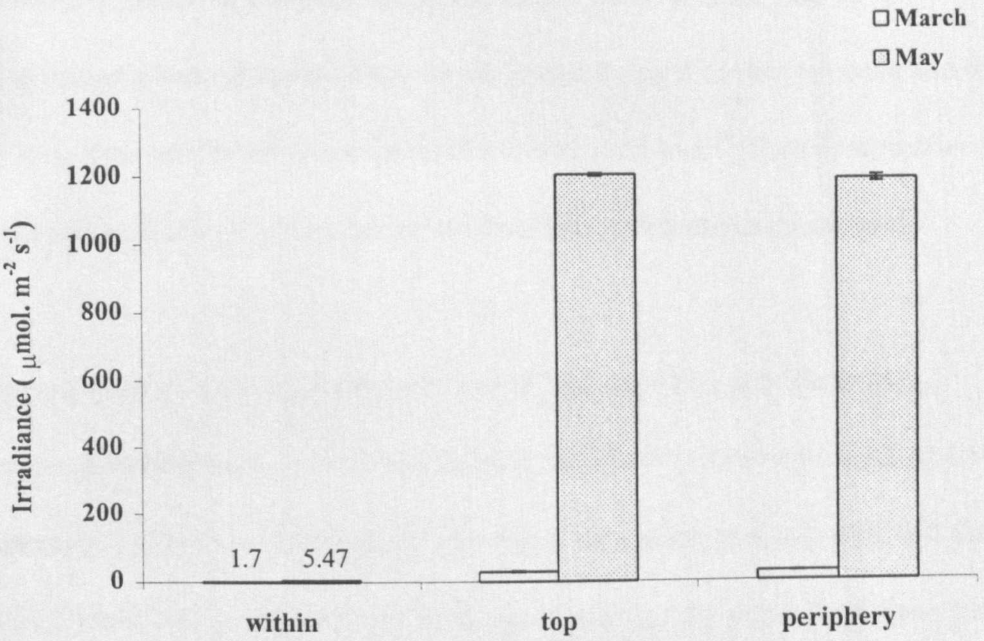


Figure 3.1. Irradiance at different area of turf between March and May.

Bars = ± 1 S.E.

### 3.2.3 Photosynthesis in air and water, and dark respiration

Photosynthesis of individual fronds in air was measured in a 150 ml temperature-controlled (12-15°C) chamber connected to an infra-red gas analyzer (IRGA Series 225). An open system was used with outside air flowing (ca. 100 $ml.l^{-1}$) both through the reference cell and the experimental chamber (differential mode). The air leaving the chamber passed into the analyzing cell of the IRGA and the rate of photosynthesis was calculated from the differential signal of the two cells and the flow rate. The outside air was calibrated and was used as a Carbon source after 15 minutes or until the $CO_2$ level became stable, before running each sample.

Photosynthesis in water was measured in a Clarke-type Oxygen Electrode (Hansatech Instruments, UK). A standard $O_2$ electrode vial mounted in a 12-15°C temperature-controlled water jacket was used. Preliminary trials showed that there was no Carbon limitation in the system when testing photosynthesis of five apical tips of *O. pinnatifida* under an irradiance of 600 $\mu molm^{-2}s^{-1}$ over 24 hrs. The rate of photosynthesis reached its maximum and became stable within an hour. Therefore we ran all the experiments for one hour. The system was left to become $O_2$ saturated before calibrating the $O_2$ in the system with the air (21% $O_2$) at 12 °C.

There were five replications for each treatment both in air and in water for each combination of irradiance and desiccation.

A Kodak slide projector was used as a light source for both systems, the irradiances were 10 $\mu mol.m^{-2}s^{-1}$, 600 $\mu mol.m^{-2}s^{-1}$ and 1200 $\mu mol.m^{-2}s^{-1}$. To measure dark respiration, sample chambers were covered with three layers of thick black plastic.

To compare the net photosynthesis and dark respiration between plants in air and water, photosynthesis quotients (PQ) were applied. It is assumed that 1 µmol$CO_2$ evolves 1 µmol$O_2$ (Rosenberg *et al.,* 1995). Therefore, the differential of $CO_2$ in the IRGA system could be converted and compared with $O_2$ evolved in an $O_2$ electrode system.

### 3.2.4 Data analyses

Friedman chi-square ANOVA was employed to test the desiccation of fronds with differences in the original location of individuals in the patch of turf, shore level and season as there was no homogeneity of variance after a series of transformations.

ANOVA was employed to test net photosynthesis and dark respiration of individuals when emersed or submerged. Log transformation was applied where there was no homogeneity of variance. Tukey multiple comparison was employed to test differences between conditions.

## 3.3 RESULTS

### 3.3.1 Desiccation of individuals

On the shore, the desiccation of individuals of *O. pinnatifida* varied greatly from 21.2%-81.7% following exposure to air during a single tide. The levels of desiccation experienced by the plants varied with season, and their position both on the shore and within the turf patches.

In May, the fronds experienced 32%-61% higher desiccation than in March. Desiccation of fronds was also influenced by their location within turfs ($\chi^2 = 88.84$, $P<0.001$, Fig. 3.2a). Fronds at the periphery of turfs experienced 82% desiccation in May but only 54% in March. However, plants within turfs were partially protected from desiccation, and lost only half as much water as peripheral plants (44% in May and 21% in March).

Shore level was also influential ($\chi^2 = 68.44$, $P<0.001$, Fig. 3.2b). At the higher level, fronds suffered more desiccation than lower down, 67% in May and 30% in March, compared to only 37% in May and 25% in March. However, there was no significant difference in percent desiccation between higher shore fronds in March and lower shore fronds in May. This confirmed that, as expected, plants growing low in the *Osmundea* zone are subject to less stress than those higher on the shore.

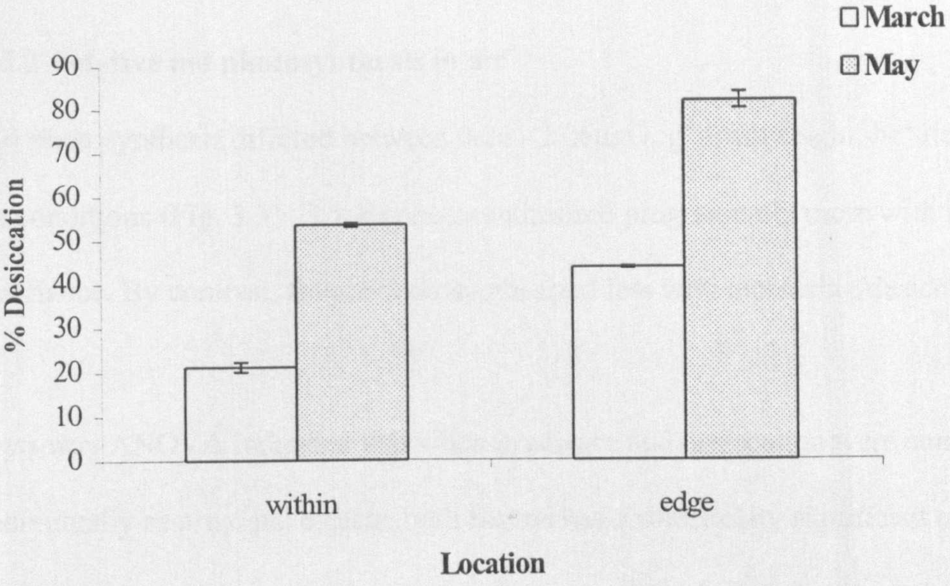


Figure 3.2a. Percent desiccation if individuals at different area within turf between March and May. Bars = ± 1S.E.

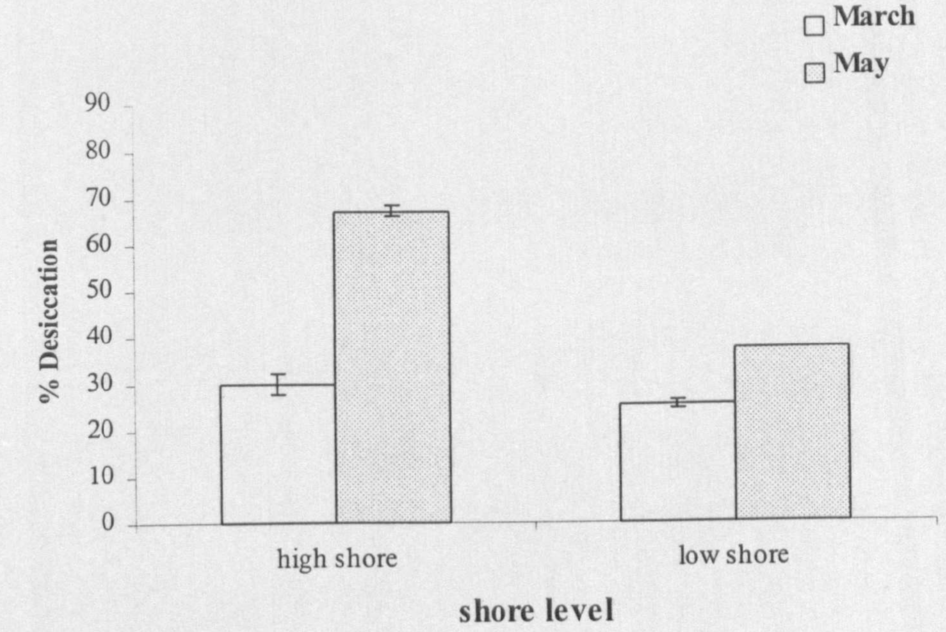


Figure 3.2b. Percent desiccation of individuals at different shore level between March and May. Bars = ± 1S.E.

### 3.3.2 Relative net photosynthesis in air

Net photosynthesis differed between 0.26 - 2.06$\mu gO_2.g^{-1}$ freshweight. $hr^{-1}$ depending on conditions (Fig. 3.3). Fronds photosynthesized progressively more with increasing irradiance. By contrast, fronds photosynthesized less with increasing desiccation.

Two-way ANOVA indicated that when irradiance and desiccation were considered individually as principal effects, both factors had a statistically significant effect ($P$ <0.001) on net photosynthesis and that there was an interaction between the factors ($F_{4,36}$=6.12, $P$<0.001). Under combinations of high light and no stress from desiccation, fronds had the highest levels of photosynthesis recorded.

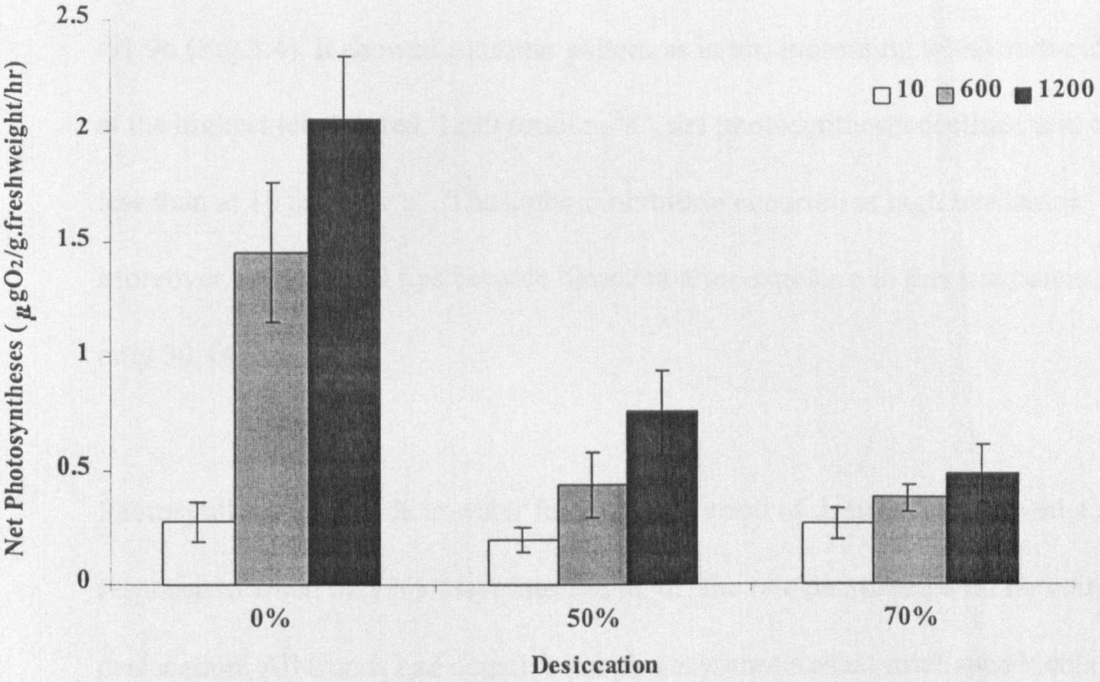


Figure 3.3. Net photosynthesis of individuals with combinations of irradiance and desiccation in the air. Bars = ± 1 S.E.

### 3.3.3 Relative net photosynthesis in water

The average relative net photosynthesis of submerged individuals varied from –0.94 to1.96 (Fig.3.4). It showed a similar pattern as in air, increasing with irradiance, but at the highest level tested, 1200 $\mu$mol.m$^{-2}$s$^{-1}$, net photosynthesis declined and became less than at 10 $\mu$mol.m$^{-2}$s$^{-1}$. Thus, photoinhibition occurred at high irradiance. Moreover, some apical tips became bleached after exposure to this irradiance for only 30 - 45 minutes. .

Photosynthesis of fronds in water following a period of desiccation showed a similar response to when they photosynthesised in air; the rate decreased with increasing desiccation. All fronds had negative net photosynthesis at all irradiance levels when resubmerged after exposure to 70% desiccation. By contrast, following 50% desiccation, submerged fronds had a positive net photosynthesis, indicating a recovery from desiccation and within an hour they reached the same photosynthetic rate as un-desiccation fronds.

Relative net photosynthesis of *O. pinnatifida* significantly increased over time ($F_{3,143} = 6.78$, $P<0.001$), slowly over the first 15 minutes and then accelerating with time. However, the net photosynthetic rate became stable and showed no significant difference after the first 15-30 minutes.

There was also an interaction between irradiance and desiccation ($F_{3,143} = 4.21$, $P<0.001$). At 600 $\mu$mol.m$^{-2}$s$^{-1}$ and 50% desiccation *O. pinnatifida* could increase its net photosynthesis to the same level as when there was no desiccation.

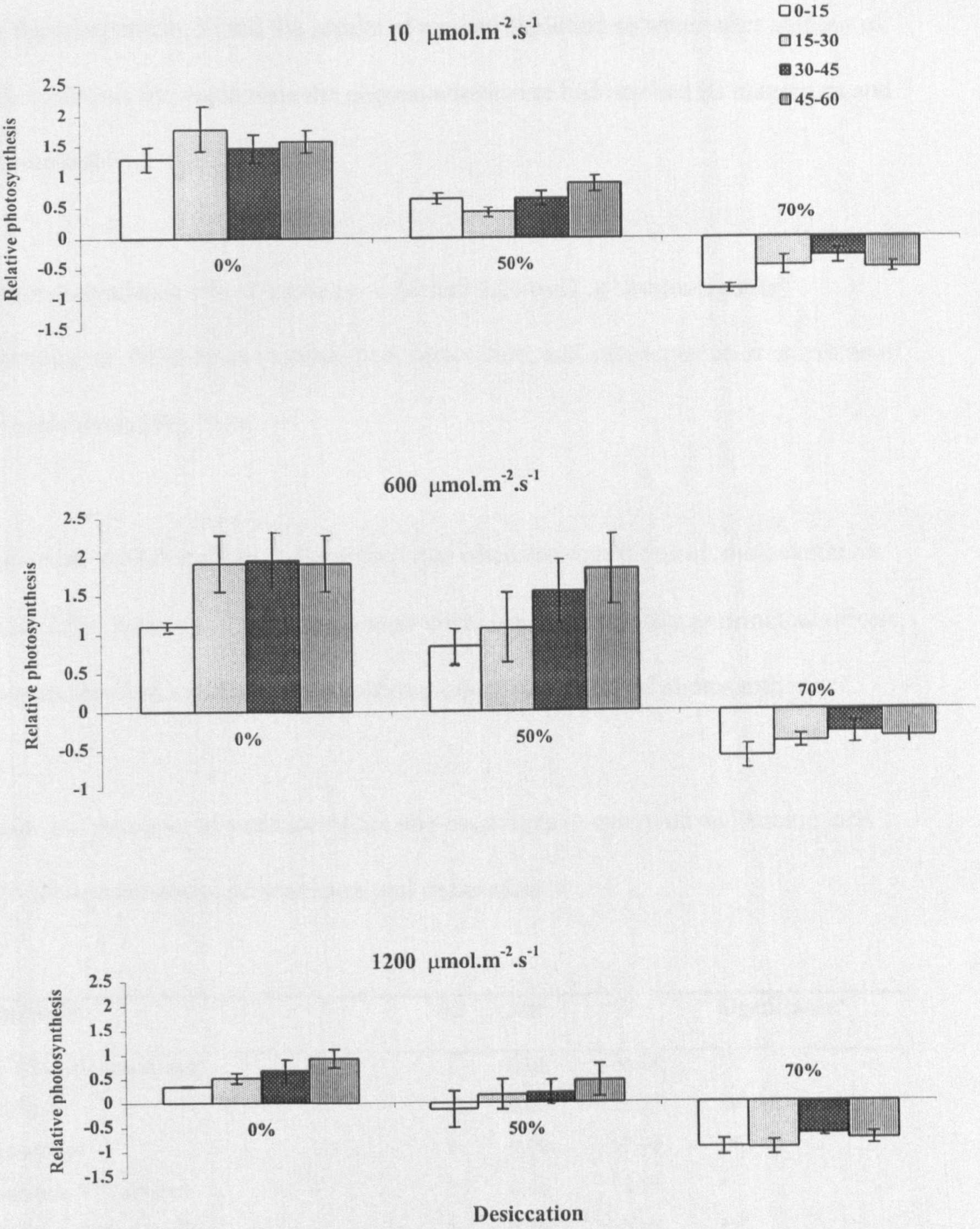


Figure 3.4. Relative photosynthesis rate of individuals with combinations of irradiance and desiccation every 15 minutes for an hour in the water. Bars = ± 1 S.E.

### 3.3.4 Comparison of photosynthesis when emersed and submerged

For the comparison, I used the results of oxygen evolution in water after an hour of photosynthesis by which time the photosynthetic rate had reached its maximum and become stable.

Net photosynthesis varied between –2.69 and 2.06 $\mu gO_2.g^{-1}$freshweight.$hr^{-1}$ depending on differences in irradiance, desiccation, and submergence or emersion of the individuals (Fig. 3.5).

Three-way ANOVA (Tab. 3.1) showed that when the conditions of photosynthesis (in air *VS* in water) and desiccation were considered individually as principal effects, those factors had a statistically significant effect on the rate of photosynthesis.

Table 3.1. Analysis of variance of net photosynthesis in emersion and submersion with the combinations of irradiance and desiccation

| **Treatment** | **df** | **MS** | **F** | **Significance**[a] |
|---|---|---|---|---|
| Air *VS* water (condition) | 1 | 0.05 | 4.14 | * |
| Irradiance | 2 | 0.02 | 1.37 | ns |
| Desiccation | 2 | 0.09 | 7.04 | ** |
| Condition X Irradiance | 2 | 0.46 | 3.77 | * |
| Condition X Desiccation | 2 | 0.49 | 3.97 | * |
| Irradiance X Desiccation | 4 | 0.29 | 2.32 | ns |
| Condition X Irradiance X Desiccation | 4 | 0.20 | 1.48 | ns |
| Error | 69 | 0.01 | | |

[a] Significance : *ns*= non-significance, * = $P \leq 0.05$, ** $P \leq 0.01$

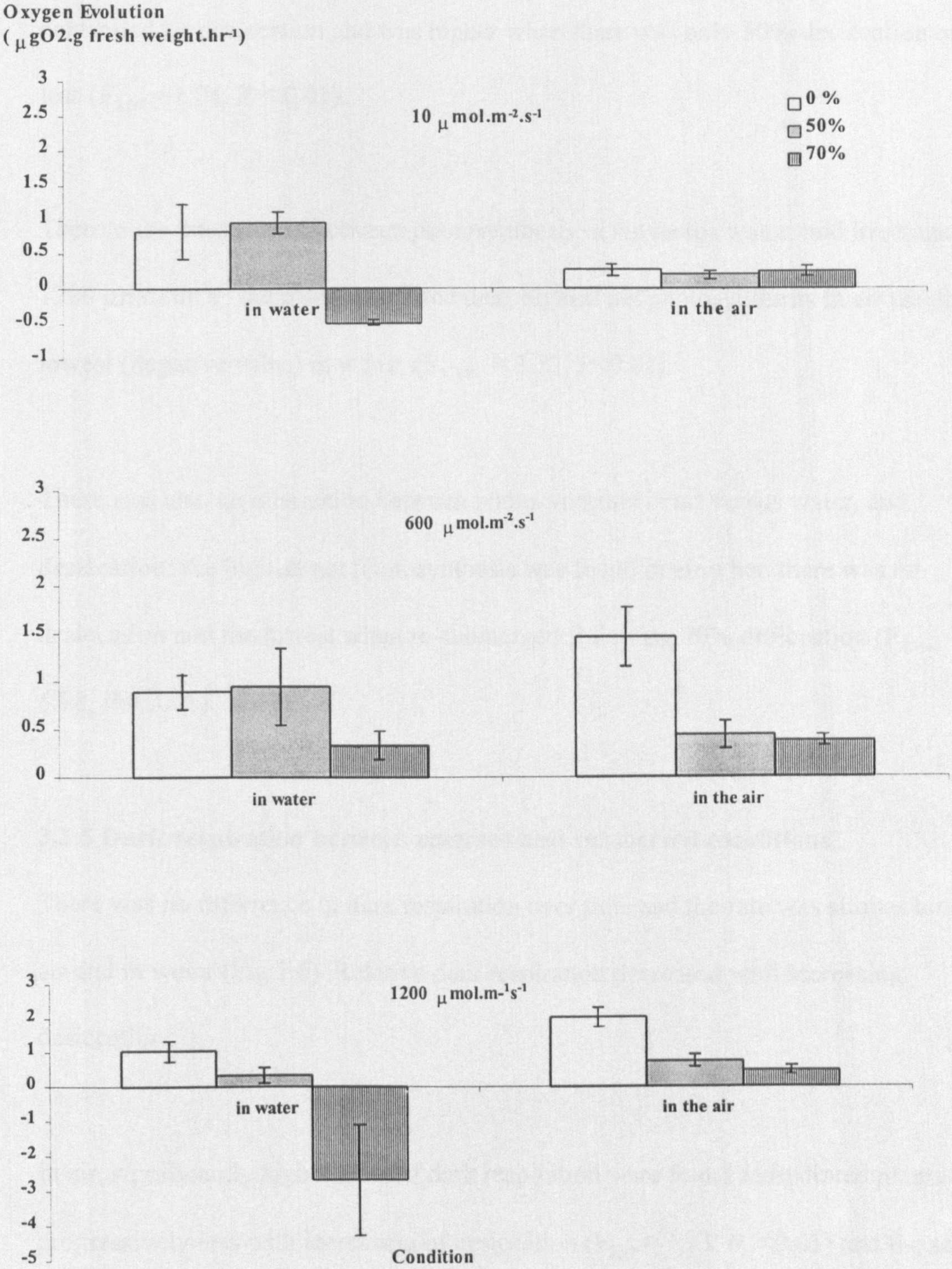


Figure 3.5. Comparison of net photosynthesis of individuals with combinations of irradiance and desiccation in emersion and submersion after an hour. Bars = ± 1S.E.

Higher net photosynthesis was found when fronds photosynthesized in air rather than in water but it was not consistent ($F_{1,69} = 4.14$, $P = 0.046$). Photosynthesis was controlled by desiccation and was higher when there was only 50% desiccation or less ($F_{2,69} = 7.04$, $P < 0.01$).

There were interactions between photosynthesis in air versus water, and irradiance: at 1200 $\mu$mol.m$^{-2}$s$^{-1}$ the plants exhibited their highest net photosynthesis in air and their lowest (negative value) in water. ($F_{3,143} = 3.77$, $P<0.01$).

There was also an interaction between photosynthesis in air versus water, and desiccation: the highest net photosynthesis was found in air when there was no desiccation and the lowest when re-submerged following 70% desiccation ($F_{3,143} = 6.78$, $P<0.001$).

### 3.3.5 Dark respiration between emersed and submersed conditions

There was no difference in dark respiration over time and the rate was similar both in air and in water (Fig.3.6). Relative dark respiration decreased with increasing desiccation.

In air, significantly higher rates of dark respiration were found in hydrated plants and progressively less with increasing of desiccation ($F_{2,12} = 7.23$, $P < 0.01$) and the same pattern was found in submersed condition ($F_{2,12} = 4.86$, $P < 0.01$).

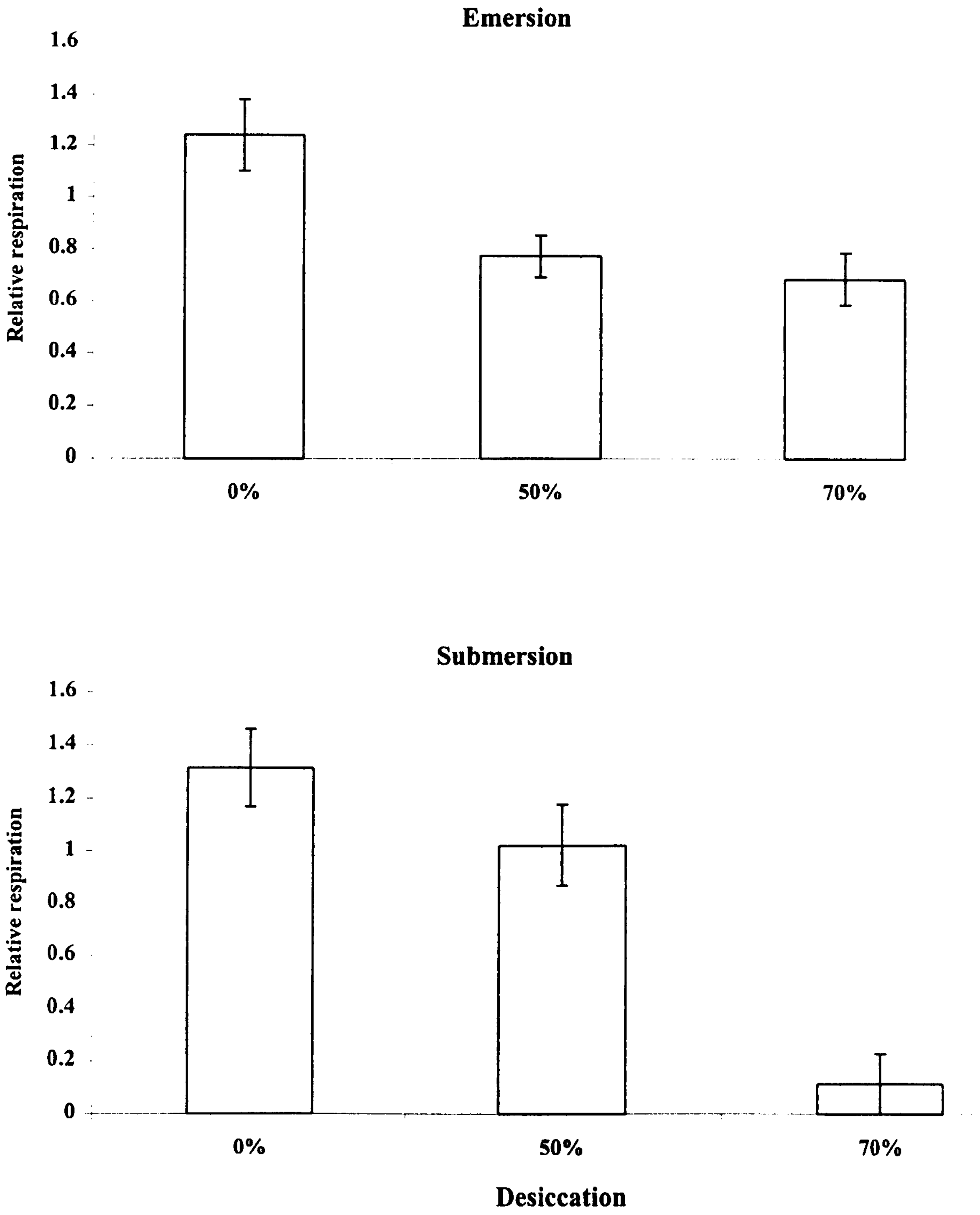


Figure 3.6. Relative respiration of individuals at different degrees of desiccation in emersion and submersion. Bars = ± 1 S.E.

## 3.4 DISCUSSION

To investigate the performance of *O. pinnatifida* with respect to net photosynthesis, we simulated in the laboratory the varied levels of desiccation and irradiance that fronds experienced on the shore. Dark respiration, therefore, must be carefully considered as it might show a different or inconsistent pattern in air and in water, thus influencing the outcome of net photosynthesis. However, unlike some brown algae (Oates and Murray, 1983), *O. pinnatifida* displayed a similar pattern of dark respiration both in air and in water.

Intertidal algae experience both submersion and exposure to the air as a consequence of the tidal cycle. When in air, they are subjected to high levels of irradiance and desiccation and if they are to continue to photosynthesise, they must switch from $HCO_3^-$ to $CO_2$ as their inorganic carbon source (Reiskind *et al.*, 1989; Madsen and Maberly, 1990). The efficiency with which they exploit these different sources of carbon can be different and this influences the outcome of net photosynthesis. The red algae *Acanthophora najadiformis* (Delile) Papenfuss and *Hypnea musciformis* (Wulfen) J. Ag., for example, showed a 4-5 fold greater rate of photosynthesis in air than in seawater (Einav and Beer, 1993). However, *O. pinnatifida* can use $HCO_3^-$ as efficiently as $CO_2$ (Johnston *et al.*, 1992). Thus, its ability to photosynthesise in air and water is not affected by the carbon source and our results showed that there was only slightly less net photosynthesis in water than in air ($P$=0.046).

Temperature is another important factor which influences photosynthesis and respiration of seaweeds. Increasing temperature results in increasing ratio of net photosynthesis and respiration of *Colpomenia peregrina* (Sauv.) Hamel (Matta and Chapman, 1995) but extreme high temperature (40 °C) results in decreasing net photosynthesis and leads to negative net photosynthesis in *Chondrus crispus* Stackh. (Dudgeon *et al.*, 1995). However, on a small scale within *Osmundea* turfs, there is little variation in temperature in different regions of turfs, e.g. 11.2 °C at the middle and 11.6°C at the periphery during late spring. Temperature within turfs is however much less than on the bare rock nearby which could rise to 16.0°C. I also found little difference in temperature between the limits of the *Osmundea* zone, 11.7°C at the upper limit and 11.1 °C at the lower limit. Thus, mutual protection within the turf significantly decreases stresses from temperature and the small differences in temperature in different regions of turfs would have minimal effect on the photosynthesis of the fronds.

The data suggest that fronds at the lower reaches of the *Osmundea* zone and within the turf suffered less desiccation than those higher up the shore and at the periphery of a patch. Probably as a result of this reduced stress, those fronds became longer and denser. Generally, intertidal seaweeds are known to have characteristics that enable them to avoid desiccation when the tide is out e.g. a low surface to mass ratio or by forming overlapping branches (Schonbeck and Norton, 1979; Dromgoole, 1980) or closely-packed turfs (Hay, 1981a; Taylor and Hay, 1984). Although *O. pinnatifida* forms extensive turfs on the shore, the individual fronds still suffered greatly from desiccation, especially at the periphery and in the upper level of the *Osmundea* zone.

While fronds at the periphery of a patch are directly exposed to air, those within turfs protect each other from exposure and thus reduce drying out. Furthermore, the most desiccated fronds were found on the upper limits of the zone where they were exposed to air for seven hours longer during spring tides than those at the lower limit of the zone.

Desiccation is known to reduce the rate of photosynthesis of many marine algae (Dring and Brown, 1982; Brown, 1987; Bell, 1993; Einav and Beer, 1993; Pearson and Davison, 1994; Matta and Chapman, 1995; Beach and Smith, 1997), but when fronds of some species lost only 10-20% of their water content, net photosynthesis increased (Johnson *et al.*, 1974; Quadier *et al.*, 1979; Dring and Brown, 1982; Beer and Eshel, 1983; Johnson and Raven, 1986). Until recently, Matta and Chapman (1995) argued that it might be a result from seawater slowing down $CO_2$ diffusion or from an overestimate of $CO_2$ in the IRGA system, rather than better photosynthesis mechanisms.

I found that even slight desiccation decreased net photosynthesis both in air and subsequently in water; and that there was clearly a significant and progressive decrease with increasing desiccation. However, when fronds had lost only 50% of their water content, but received 600 $\mu$mol.m$^{-2}$s$^{-1}$, the conditions found within turfs at the lower limit of the *Osmundea* zone during early spring, their net photosynthesis was not significantly different from that of un-desiccated plants. Therefore, fronds should be able to grow continuously at this time of year. By contrast, fronds at the upper reaches of the zone and at the periphery of turfs have reduced net photosynthesis and in consequence growth is limited.

When plants experience stressful conditions, they produce and accumulate reactive oxygen (Foyer *et al.*, 1994; Moran *et al.*, 1994; Collén and Pedérsen, 1994), which regulates or inhibits photosynthesis mechanisms (Kaiser 1979, Badger *et al.*, 1985). Thus, we would expect the same thing to occur in *O. pinnatifida* when it is stressed. Reduced photosynthesis with increasing desiccation, might therefore result from an accumulation of reactive oxygen. In some brown algae the reactive oxygen becomes active mainly after rehydration rather than during desiccation (Collén and Davison, 1999). This might also be the case with *O. pinnatifida*, as we found negative values of net photosynthesis only when fronds were resubmerged following severe (70%) desiccation. After such desiccation when fronds had rehydrated for 15-30 minutes, their net photosynthesis slightly increased, but still showed negative values even after an hour.

The ability of *O. pinnatifida* to recover from desiccation depends on the degree of desiccation, as in shown in some other algae (e.g. Pearson and Davison, 1994; Delgado *et al.*, 1995; Beach and Smith, 1997; Pfetzing *et al.*, 2000). *O. pinnatifida* experiences stress from desiccation when the tide is out, but could recover when the tide returns. Fronds lower on the shore would therefore recover more rapidly than those higher up. After 50% water loss, *O. pinnatifida* fully recovered and reached its maximum photosynthesis within an hour, but it took almost 5 hours to reach the same level following 70% desiccation.

The growth of *Osmundea* turfs on the shore is affected not only by desiccation, but also by irradiance. Plants in turfs are known to suffer from self-shading (Hay, 1981a; Taylor and Hay, 1984) and this is supported by our study. Irradiance within the *O. pinnatifida* turf was less than 10 μmol.$m^{-2}s^{-1}$ both in winter and late spring, a level which limits net photosynthesis. With higher irradiance fronds increased their net photosynthesis, but exhibited photoinhibition at 1200 μmol.$m^{-2}s^{-1}$. Generally, intertidal algae become light saturated at 400-600 μmol.$m^{-2}s^{-1}$ and red algae are known to grow at low light levels (Lobban and Harrison, 1994). Irradiance exceeding 600 μmol.$m^{-2}s^{-1}$ during late spring and summer may well result in photoinhibition perhaps followed by photooxidation of chlorophyll (Gantt, 1990). The bleaching was displayed both on the shore and in the laboratory when fronds were exposed to 1200 μmol.$m^{-2}s^{-1}$ irradiance. However, mechanisms of photoinhibition and bleaching are not clearly defined, but probably involve the interaction of several factors. Some studies have showed that photoinhibition occurs in algae with a combination of high irradiance and desiccation stress (Herbert and Waaland, 1988; Herbert, 1990) but also even when they are submerged (Huppertz *et al.* 1990). In *O. pinnatifida*, bleaching occurred following exposure to 70% desiccation and higher irradiance both in air and in water. Thus, fronds that are desiccated on the shore would suffer most during late spring and summer.

I conclude that *O. pinnatifida* fronds lower on the shore and within turfs experience less desiccation and recover more quickly, while those higher up and at the periphery of turfs desiccate more and take longer to recover, resulting in lower productivity. The combination of high desiccation and irradiance leads to photoinhibition and bleaching, severely stressful conditions that cause the die back of *O. pinnatifida* population and might curb turf expansion at the upper limit of the turf on the shore.

# CHAPTER 4

# THE EFFECTS OF DENSITY AND SHADE

## 4.1 INTRODUCTION

Algal turfs are known to be an adaptation that allows intertidal algae to persist under the stresses of desiccation and herbivory, but the accompanying self-shading is considered a disadvantage (Hay, 1981a; Taylor and Hay; 1984). However, *Ahnfeltiopsis concinna* (J.Ag) Silva *et* DeCew and *Laurencia mcdermidiae* (J. Ag.) Abbott, both form turfs and can adapt their pigmentation depending on the amount of irradiance (Beach and Smith, 1996a,b), thus probably increasing their ability to photosynthesise. Photoacclimation involving pigment adaptation is common in higher plants (e.g. Boardman, 1977), phytoplankton and macroalgae (e.g. Rosenberg and Ramus, 1982; Falkowski and LaRoche, 1991; Rmiki *et al.*, 1996; Weykam *et al.*, 1997; Stengel and Dring, 1998).

Red algae require relatively low irradiance for growth (Lobban and Harrison, 1994) and often require protection from the effects of insolation. *Iridaea cordata* (Turner) Bory, for example, increases its carotenoids in the summer when irradiant energy increases (Foltran *et al.*, 1996). Higher carotenoid: chorophyll ratios, which function most efficiently at higher irradiance, are a common adaptation for photoprotection that results in a wider vertical distribution in intertidal red algae than in subtidal species (Jones and Dent, 1971). Thus, self-shading within an algal turf might not be a severe disadvantage and could even be a benefit.

Increasing irradiance results in photoinhibition, which often is followed by photooxidation, seen as bleaching of the fronds (Gantt, 1990) as in *Osmundea*.

Experimental thinning of stands of *Mazzella cornucopiae*, a clonal intertidal red alga, leads to greater bleaching of the fronds than in natural stands, as a consequence of greater desiccation and higher insolation (Scrosati and DeWreede, 1998). Bleaching is, of course, symptomatic of pigment loss and has been well studied in reef corals (e.g. Glynn, 1993, 1996; Brown, 1997) where it is influenced by several factors including high temperature, desiccation and irradiance. It is also common in red algae (Dixon, 1970; Kain and Norton, 1990), but little attempt has been made to investigate its importance in limiting photosynthesis or to assess the extent to which it results in permanent damage to the plants.

Studies of algal turfs have focused on the differences in irradiance between the exposed top of a turf and the shaded proximal parts, and on individual fronds rather than regarding the whole turf as an 'organism' in which there is some physiological connection between fronds (Beach and Smith, 1997; Scrosati and DeWreede, 1998). At the centre of a turf, individual fronds have greater mutual protection than at the periphery as they are less exposed to the atmosphere. Similarly, plants in a big patch are more protected than those in a small patch. Such differences might influence the degree of bleaching and subsequent die back seen in several species of turf-forming red algae, and may even structure their populations.

I examined pigment adaptation of the plants of *Osmundea pinnatifida* and tested the effects of desiccation, irradiance, patch size and shore level on the bleaching of both individual fronds and whole turfs on the shore. I hypothesised that where there is less irradiance (or more self-shading) and/or desiccation, fronds would suffer less bleaching and persist longer.

## 4.2 MATERIALS AND METHODS

### 4.2.1 Index

Producing an index of the extent of bleaching damage and subsequent die back enabled me to monitor the extent and progression of the symptoms.

**Index of frond condition of individual fronds**

| Symptoms | Score |
|---|---|
| only tips bleached | 1 |
| Distal 1/4 of frond bleached | 2 |
| 1/2 frond bleached | 3 |
| Entire frond bleached | 4 |
| Tips of tissue lost | 5 |
| 1/4 frond lost | 6 |
| 1/2 frond lost | 7 |
| Entire fronds lost | 8 |

**Index of condition of whole patches of turf**

| Symptoms | Score |
|---|---|
| Beginning to bleach | 1 |
| 1/4 patch area totally bleached | 2 |
| 1/2 patch area totally bleached | 3 |
| 3/4 patch area totally bleached | 4 |
| Entire patch bleached | 5 |

Fifty individual fronds were randomly collected from Port St. Mary Ledges, on the south of Isle of Man (54°04'N, 4°46'W) in March - June 1999, closely examined and scored for symptoms of bleaching. The pattern of bleaching was also observed for thirty turfs of various sizes on the shore.

### 4.2.2 Effects of frond density, shore level and season on individual fronds.

*Osmundea* turfs were manipulated in various ways at the upper (3.5 m above LAT) and lower limits (2.0 m above LAT) of the *Osmundea* zone. They were trimmed using a paint scraper to remove some of the turf leaving one or more intact patches measuring 10 cm X 10 cm; none of which contained plants that had been peripheral. Within these patches, fronds were thinned to three densities, six replications each. In natural stands the density of fronds was 8-10 individuals/cm$^2$ which was left as 'high' density (100% density). Fronds were removed using forceps to leave a medium density (4-5-fronds/cm$^2$, 50% density) and a low density (1 frond/cm$^2$, 10% density). These densities were used in all the experiments

Five fronds in each patch (90 fronds in total) were selected randomly and tagged with "Twinglow" fluorescence tape cut into a very narrow (1 mm) strip. Their position was mapped and they were regularly monitored. All patches were marked by drilling into the rock nearby and plastic rawlplugs were used to secure steel ring-bolts, which were 'flagged' with yellow fluorescent tape. This method of tagging and marking was used in all the experiments. The marked patches and fronds were then monitored and scored for their condition monthly from 5 March -15 June 2000.

### 4.2.3 Effects of patch size, location of the individuals within a patch, and season

Thirty patches of *Osmundea* turf were randomly chosen near to the lower limit of the zone and were categorized into three size classes: small (<100 cm$^2$), medium (200-250 cm$^2$) and large (625-1000 cm$^2$), ten replications each. Size class categories were based on a survey of patch size distribution for 210 *Osmundea* patches. The selected patches were marked using the technique described above and were studied in two regions: periphery and centre. Five individual fronds were tagged in each region, a total of 300 fronds. The patches and individuals were then monitored and scored for condition monthly from 5 April-16 July 2000.

### 4.2.4 Effects of frond density and irradiance on bleaching of an individual frond

Thirty-six similar sized *Osmundea* turfs close to the lower limit of the *Osmundea* zone (2.2 m above LAT) were trimmed to 10 cm X 10 cm patches as above. These patches were at least 30 cm apart. They were arranged into 3 densities as above with combinations of three irradiance levels: natural (~1189 $\mu$mol.m$^{-2}$s$^{-1}$), 50% shading (~600 $\mu$mol.m$^{-2}$s$^{-1}$) and 96% shading (~45 $\mu$mol.m$^{-2}$s$^{-1}$). There were four replications of each treatment.

To produce different levels of irradiance the patches were covered with a 15 cm X 15 cm shade which was fixed to the rock. The shades were 10 cm high above the top of the turf and were open - sided to allow good ventilation and water circulation, thus minimising additional effects on the fronds underneath. The shades were made from chicken wired wrapped with black nylon mesh for 50% shading and with thick black plastic bin liners for 96% shading. Air temperature and relative humidity were measured underneath these shades at the surface of turfs and on open rock both on sunny and overcast days. Five fronds at the centre of patches were tagged to avoid edge effects at each treatment, a total of 180 fronds. The experiment ran from 15 April- 15 May 2000, after which the tagged fronds were collected and scored for their condition back at the laboratory using the index of frond condition.

### 4.2.5 Effects of frond density, shore level and season on the desiccation of individuals

Similar sized *Osmundea* turfs were trimmed to 10 cm X 10 cm patches as above, fifteen at both the upper and lower limits of their zone. Fronds were manipulated into three densities as above, five replications each. They were left on the shore for 2-3 days and then collected on a clear dry day after they had been exposed to air for 7 hours on the upper limit and 4 hours on the lower limit of the *Osmundea* zone. Seven individuals from each treatment were randomly selected, 210 fronds in total. All sediment, animals and epiphytes were removed from the fronds, which were weighed (Desiccated weight) on a 4 digit balance, then re-hydrated separately with filtered seawater and re-weighed when fully-hydrated (Fully hydrated weight). Finally, they were oven-dried at 60°C to constant weight (Oven dry weight). This experiment was set up on 14 March and terminated on 16 March 2000; and repeated on 23 May terminating on 25 May 2000.

$$\text{\% Desiccation} = 100 - \frac{(\text{Desiccated weight} - \text{Oven dry weight}) \times 100}{(\text{Fully hydrated weight} - \text{Oven dry weight})}$$

### 4.2.6 Pigment analyses

Fronds were randomly collected from the periphery and centre of big patches (30-35 cm in diameter) on the shore, and brought into the laboratory on 10 April 2000. Some healthy fronds were cleaned with filtered seawater and blotted. Pigment analyses, for chlorophyll *a*, carotenoids, R-phycoerythrin and R-phycocyanin, were carried out on crude extracts using 0.8-1.0 g fresh weight samples, ten replications each following the methods in Evans (1985). Pigment concentrations were determined in a spectrophotometer, Philips PU 8670 VIS/NIR.

### 4.2.7 Data analyses

Friedman ANOVA was employed to analyse the data from experiments where bleaching was assessed, as the measured parameter (condition index) was a ranked variable. The Friedman ANOVA was also employed to test the effects of density, shore level and season on percentage desiccation as there was no homogeneity of variance after a series of transformations. Multiple comparisons were also tested when there were significant differences between treatments, following Zar (1984, p230.)

One-way ANOVA was used to compare pigment composition of fronds in different regions of the turfs, where the data displayed homogeneity.

## 4.3 RESULTS

### 4.3.1 Effects of frond density, shore level and season on individual fronds

Bleaching and damage to the fronds followed a consistent pattern, changing colour from dark red to pale yellow, first at the distal tip then progressively down the fronds, followed by loss of their tissue.

There were significant differences in frond bleaching at different frond densities, shore levels and with season ($\chi^2 = 541.85$, $P < 0.001$; Fig. 4.1). Frond tips began to bleach during March and this gradually spread down the frond during spring, with most fronds having died back completely by June. I also noticed that plants growing on unshaded rock tended to die back earlier than others in more shaded positions at the same level.

Fronds near their upper limit suffered more at all densities and seasons (Fig. 4.1). Decreasing frond density accelerated bleaching, but had less effect low in the *Osmundea* zone.

There was little difference in the condition of plants at different densities in March, but by May fronds in low density stands were 30% more damaged than at natural density. Most fronds were rotting and lost by June so, of course, densities plummeted, but there were still a few healthy fronds left on the lower shore in the (initially) 50% and natural density treatments.

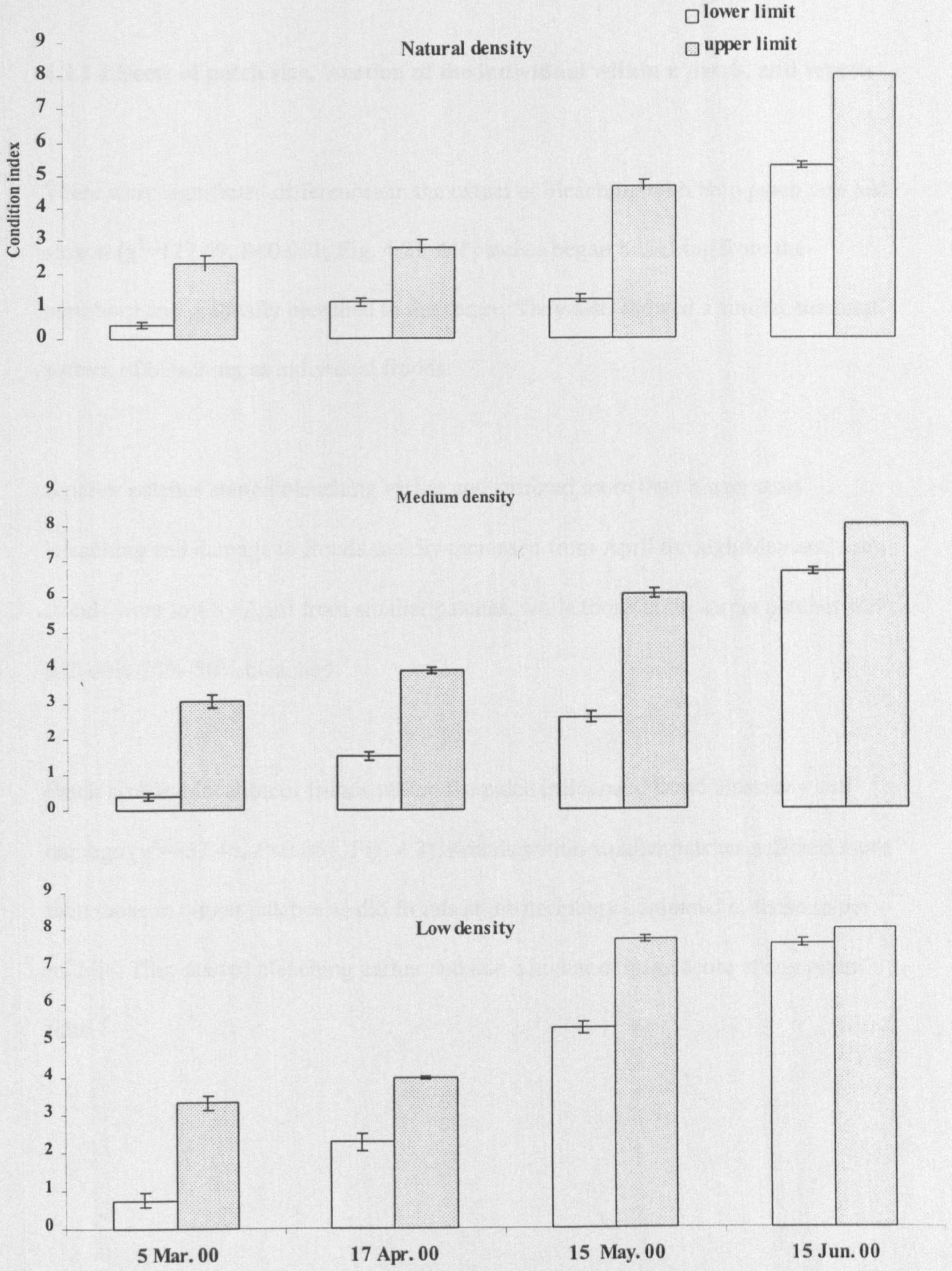


Figure 4.1. The condition of *O. pinnatifida* fronds at different densities in patches at the upper and lower limits of their zone. Bars = ± 1S.E.

### 4.3.2 Effects of patch size, location of the individual within a patch, and season

There were significant differences in the extent of bleaching with both patch size and season ($\chi^2$=127.69, P<0.001; Fig. 4.2). All patches began bleaching from the periphery and gradually bleached to the centre. They also showed a similar seasonal pattern of bleaching as individual fronds.

Smaller patches started bleaching earlier and suffered more than bigger ones. Bleaching and damage to fronds rapidly increased from April through May and some fronds were lost by April from smaller patches, while those in the larger patches were still only 25%-50% bleached.

Patch size and location of fronds within the patch influenced frond bleaching and damage ($\chi^2$=833.45, *P*<0.001, Fig. 4.3). Fronds within smaller patches suffered more than those in bigger patches as did fronds at the periphery compared to those in the middle. They started bleaching earlier and had a higher damage score at any given time.

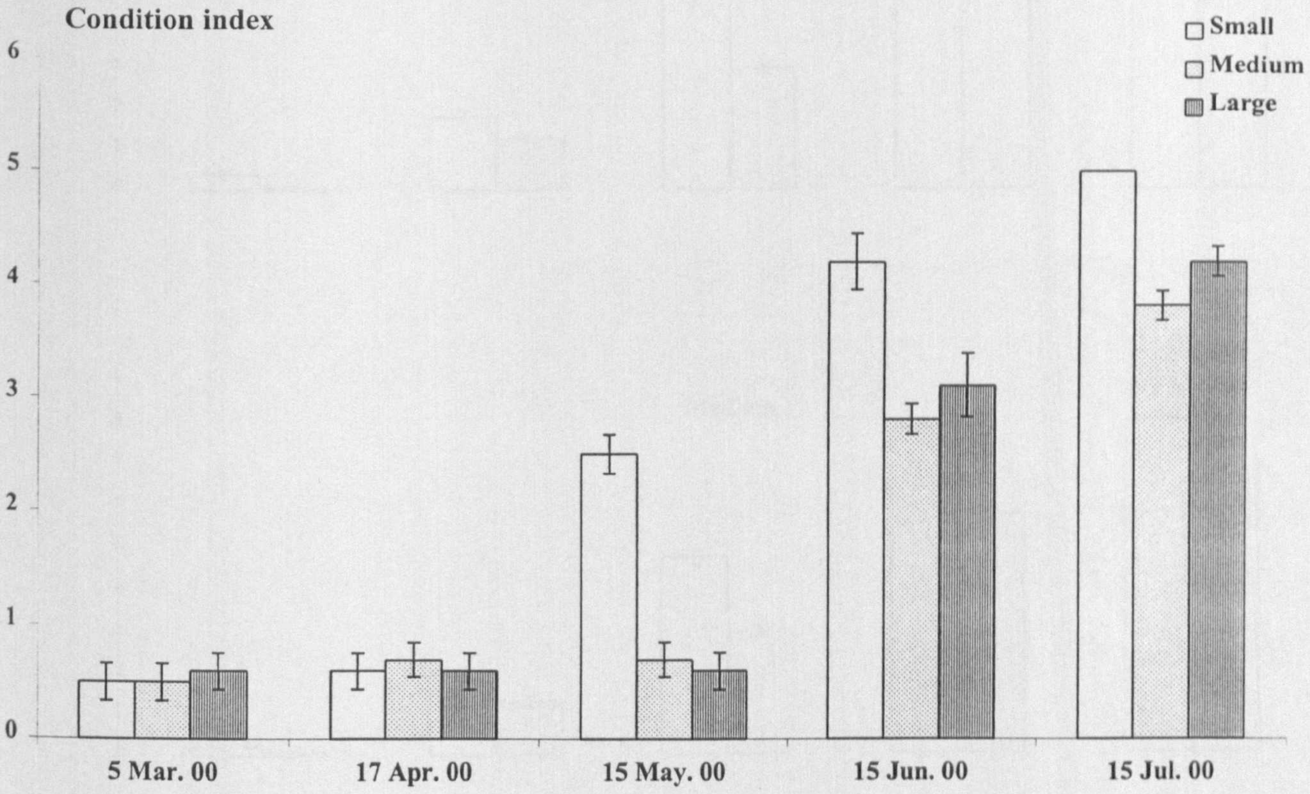


Figure 4.2. The condition of *O. pinnatifida* turf patches of different size: small (<100 cm$^2$), medium (200-250 cm$^2$) and large (>625-1000 cm$^2$). Bars = ± 1S.E.

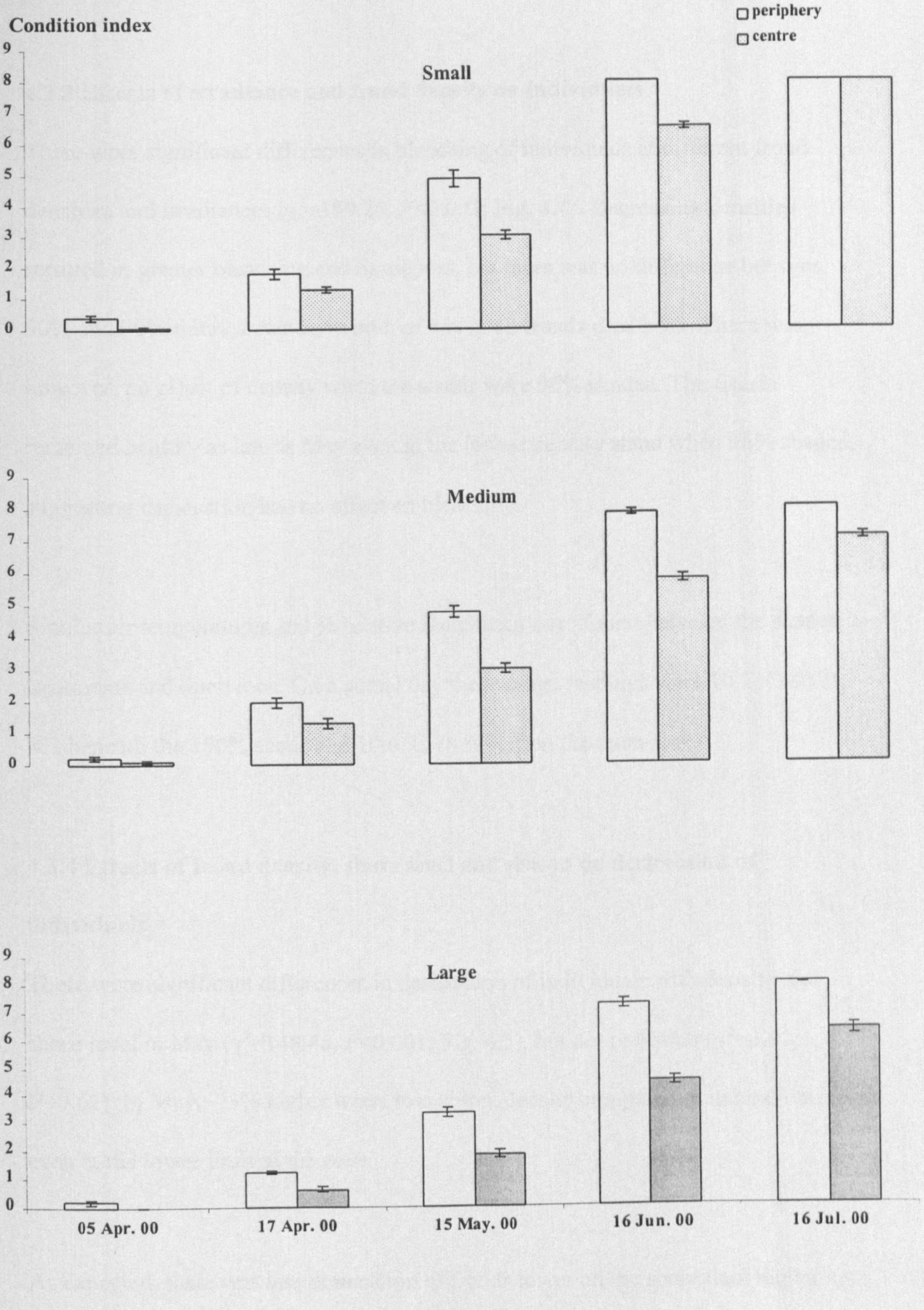


Figure 4. 3. The condition of *O. pinnatifida* fronds at the periphery and centre of turfs of three size classes. Bars = ± 1S.E.

### 4.3.3 Effects of irradiance and frond density on individuals

There were significant differences in bleaching of individuals at different frond densities and irradiances ($\chi^2$=159.25, *P*<0.001; Fig. 4.4). Decreasing densities resulted in greater bleaching and tissue loss, but there was no difference between 50% and 90% thinned stands, in both of which all fronds died back. There was, however, no effect of density when the stands were 96% shaded. The fronds remained healthy as late as May even in the lowest density stand when 96% shaded, suggesting desiccation had no effect on bleaching.

Similar air temperatures and % relative humidities were found between the shaded treatments and open rock. On a sunny day the average readings were 10.2 C 80 % RH beneath the 100% shade and 10.6 C 78 % RH on the open rock.

### 4.3.4 Effects of frond density, shore level and season on desiccation of individuals

There were significant differences in desiccation of individuals with density and shore level in May ($\chi^2$=148.46, *P*<0.001; Fig. 4.5), but not in March ($\chi^2$=3.52, *P*=0.62). In May, 43% higher water loss at low density compared to natural density even at the lower limit of the zone.

As expected, there was less desiccation of fronds lower on the shore than higher up. Moreover, the combination of low frond density and higher shore level during spring resulted in plants losing up to 85% of their water content on a single tide, whereas plants at natural density lost only 37%.

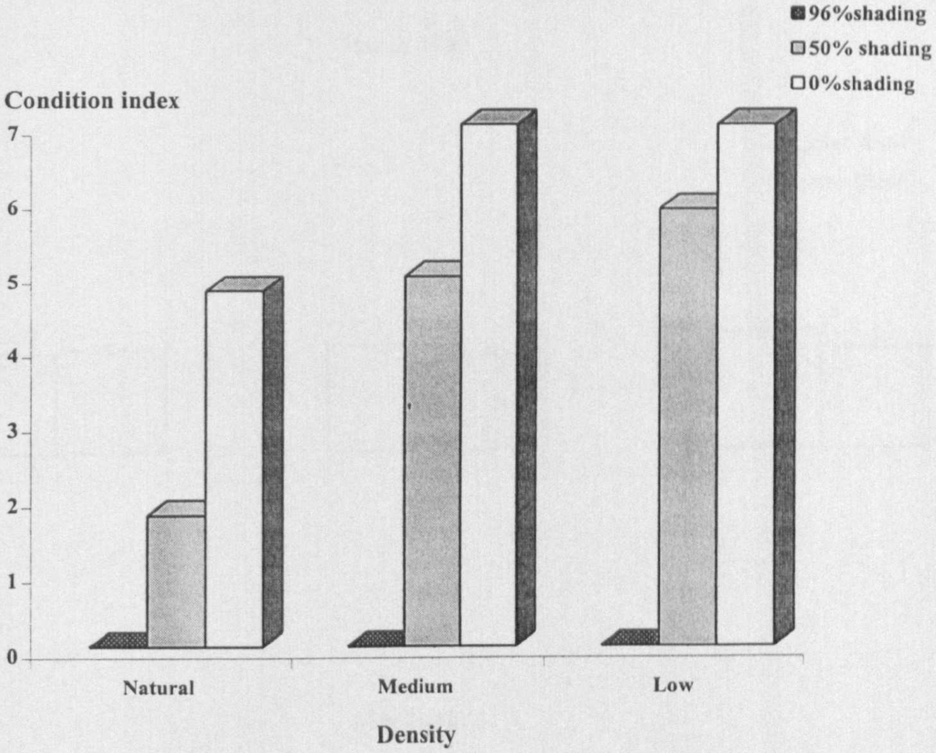


Figure 4.4. The condition of *O. pinnatifida* fronds in the field at different irradiance and densities between 15 Apr. –15 May 2001. Bars = ± 1S.E.

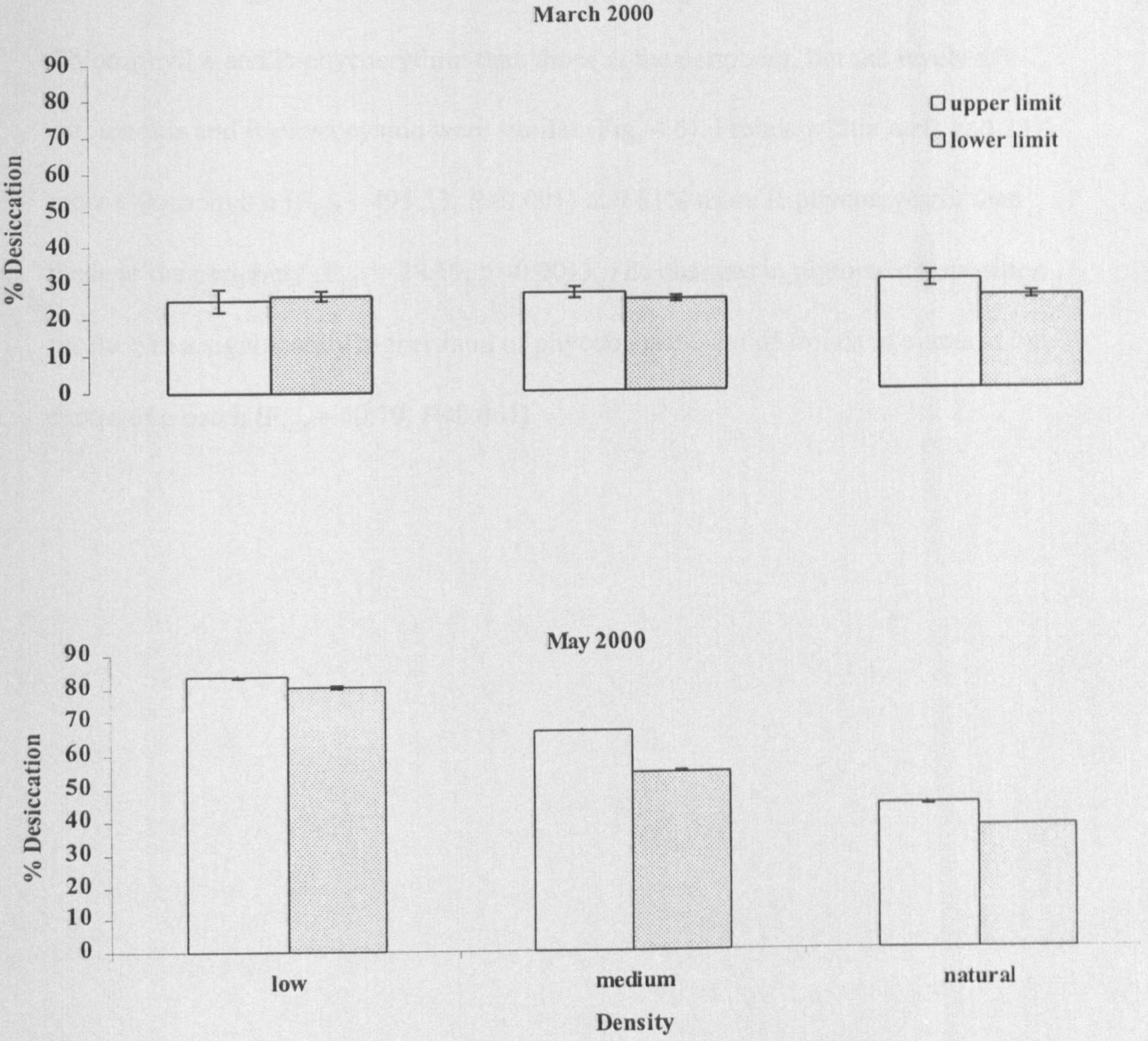


Figure 4.5. The degree of desiccation of fronds in the field at different densities at the upper and lower limits of their zone. Bars = ± 1S.E.

### 4.3.5 Pigment composition

Prior to bleaching, fronds at the centre of turfs had higher concentrations of Chlorophyll *a* and R-phycoerythrin than those at the periphery, but the levels of carotenoids and R-phycocyanin were similar (Fig. 4.6). Fronds within turfs had 23% more chlorophyll *a* ($F_{1,18} = 495.33$, $P<0.001$) and 61% more R-phycoerythrin than those at the periphery ($F_{1,18} = 28.19$, $P<0.001$). The changes in pigment composition resulted in a significantly higher ratio of phycobilins: chl *a* of fronds in plants at the centre of a patch ($F_{1,18} = 40.79$, $P<0.001$).

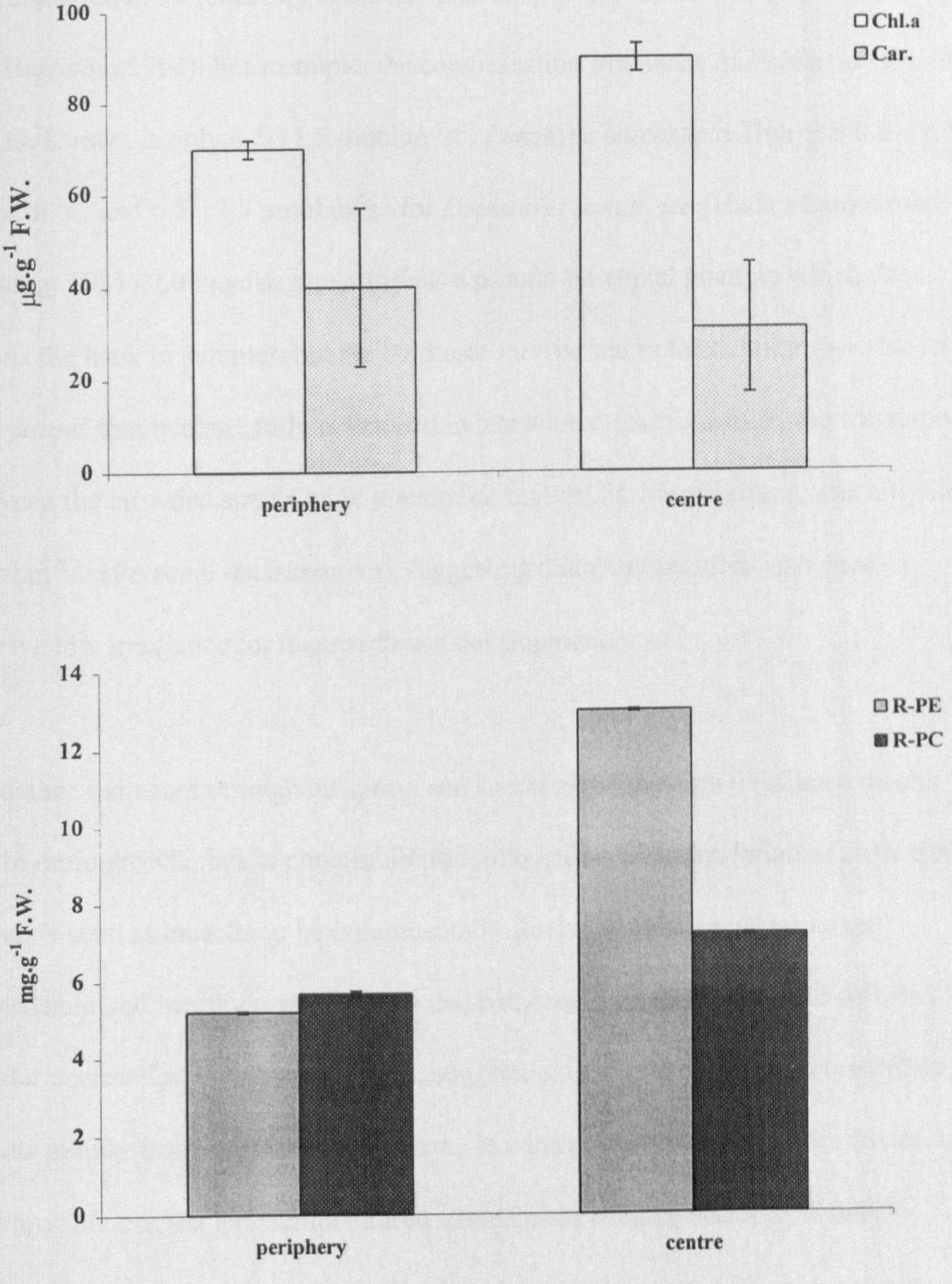


Figure 4.6. The pigment composition of fronds from the periphery and centre of turfs. Bars = ± 1S.E. Chl. *a* = chlorophyll *a*, Car. = carotenoids, R-PE = R - phycoerythrin and R-PC = R- phycocyanin

## 4.4 DISCUSSION

Red algae require a relatively low irradiance for photosynthesis and growth (Lobban and Harrison, 1994). For example, the compensation irradiance of *Palmaria palmata* (L.) O. Kuntze is only 8.5-11.5 $\mu$mol.m$^{-2}$s$^{-1}$, *Porphyra leucosticta* Thuret is 6.0-11.5 $\mu$mol.m$^{-2}$s$^{-1}$ and 6.5-17.5 $\mu$mol.m$^{-2}$s$^{-1}$ for *Delesseria sanguinea* (Huds.) Lamouroux (Lüning, 1981). *Osmundea pinnatifida* is a pseudo-perennial plant, in which the fronds die back in summer, but the holdfasts survive and in the autumn give rise to new fronds that become fully developed in late winter. During winter, the irradiance between the crowded stands of *O. pinnatifida* on Port St. Mary Ledges, was only 28 $\mu$mol.m$^{-2}$s$^{-1}$ (Personal measurement), suggesting that *O. pinnatifida* also needs a relative low irradiance for its growth and development.

Irradiance increases throughout spring and summer and the high irradiance results not in rapid growth, but in photoinhibition followed by photooxidation of chlorophyll which is seen as bleaching. In experimentally shaded stands, fronds remained unbleached and healthy even in stands that had been thinned by 90% and suffered greater desiccation than natural stands, suggesting that bleaching of *O. pinnatifida* results mainly from high irradiance. Even, in winter, when there was little desiccation and low, but not freezing temperatures, some fronds became bleached if fully insolated. Moreover, turfs on a nearby shore beneath a canopy of fucoids remained fully pigmented in winter, but when the canopy was removed they rapidly became bleached (Jenkins *et al.*, 1999).

Unlike other turf-forming species, in which self-shading appears to be a disadvantage (Hay, 1981a; Taylor and Hay, 1984; Beach and Smith, 1997), *O. pinnatifida* may benefit from self-shading. The most adversely affected fronds were found in the most thinned stands in which individuals fronds were directly exposed to almost full sunlight. In contrast, within naturally dense stands where fronds were crowded together, the irradiance levels within the turf were over two orders of magnitude less than I measured late in spring. Crowded stands of *O. pinnatifida* that suffer less bleaching, persist for a month longer on the shore. This is paralleled by the pattern of bleaching seen in individual fronds where bleaching and later decay begin at the brightly illuminated tips and gradually spread downward through the dimly lit proximal regions. Similarly, the turf patches started to bleach from the periphery where the plants are exposed to higher irradiance, and then spread inward to the centre of patches. Comparable 'bleaching gradients' are also displayed by a clonal alga, *Mazzaella cornucopiae* (Scrosati and DeWreede, 1998).

Most plants, including red seaweeds, have mechanisms to protect themselves from high irradiance e.g. chloroplast movement, photorespiration and carotenoid quenching, which all are found in *Porphyra* spp. (Herbert and Waaland, 1988). In *Gracilaria lichenoides* (L.) Harvey and *G. verrucosa* (Huds.) Papenfuss, an increase in carotenoids protects them from photodamage (Vershinin and Kamnev, 1996). I found no studies on physiological photoprotection of *Osumundea pinnatifida* and our results showed that there was no difference in carotenoids between plants occupying the periphery and centre of the turf in April. Also, its tendency to bleach indicates that it has little or no protection from high irradiance. In contrast, I found more phycobilins: chl.*a* ratio in fronds in plants within turfs than in those at the periphery - a common form of photoacclimation in red algae which increases their ability to capture light (Boney and Corner, 1960; Rosenberg and Ramus, 1982; Beach and Smith, 1996a). This adaptation would compensate for self-shading and may enable *O. pinnatifida* to benefit from growing in a turf without suffering from its major potential disadvantage.

*Osmundea* turfs occur in patches of different sizes on the shore and smaller patches bleach more rapidly than bigger ones, presumable because their constituent fronds are exposed to greater irradiance. Surface area: biomass has been used to investigate the amount of irradiance that algae intercept. The higher the ratio of surface area: biomass the greater irradiance a plant receives for its size (Littler and Littler, 1980; Littler, 1980; Littler and Arnold, 1982). When this ratio was applied to patches of turf as opposed to individual fronds, there is a higher surface area: biomass for the smaller patches, suggesting that their individual fronds are exposed to greater irradiance. Moreover, the number of more vulnerable peripheral fronds/ area of a small patch is also greater. Bleaching starts from the periphery and might quickly spread to other individuals through the stoloniferous holdfast which connects adjacent fronds, and results in the rapid total bleaching of a smaller patch.

The *Osmundea* zone occupies a vertical range of 1.5 m. on the shore at Port St. Mary Ledges. The difference in emergence time of turfs at the upper and lower limits of the zone is about 4 hours longer during neap tides and 7 hours longer during spring tides, which must influence the degree of bleaching of fronds. When emersed, fronds are exposed directly to full sunlight and, of course plants at their upper limit are exposed for longer. By contrast, when submerged, turfs receive less irradiance because of absorbtion and scattering by seawater and reflection from the surface (Lobban and Harrison, 1994). The submergence depth of turfs during spring tides is 2.0 m-2.5 m., which cuts down the amount of irradiance received by turfs at their lower limit. Not surprisingly, turfs on the upper limit exhibited earlier bleaching and a faster progression of bleaching than those lower downshore.

The pseudo-perennial and turf-forming habit of *O. pinnatifida* may be an evolutionary strategy by which it survives high irradiance on the shore. Crowded fronds protect each other from high irradiance, thus increasing their seasonal longevity. As summer progresses persistence is no longer tenable, but although the fronds die back the holdfast remains to produce new thalli in the autumn. The perennial holdfast is critical to the long - term persistence of such stands.

# CHAPTER 5

# DISTRIBUTION, EXPANSION AND RECRUITMENT

## 5.1 INTRODUCTION

*Osmundea* forms patches of turf which vary greatly in size, but neither isolated plants nor very small clusters of plants are common on the shore. So how do new patches arise? Also, how do patches expand or repair gaps that occur within them following storm damage?

Several mechanisms may be available to *O. pinnatifida*. Like most red algae, they can produce both asexual tetraspores and gametes. The resultant zygotes form spore-producing cystocarps. Both their carpospores and the tetraspores facilitate dispersal and recruitment of new plants.

There is also the possibility of vegetative growth that is an important means of propagation and expansion in many higher plants, for example grass or strawberries. In such plants the individual shoots (ramet) of a single clonal plant (genet) are connected through runners (as in strawberries) or roots, rhizomes or stems (Pitelka and Ashmun, 1985). Clonal plants are hierarchically organised in ramets and genets. Demographic processes at the level of the ramet are fundamental for the dynamics of genets (Eriksson and Jerling, 1990; Eriksson, 1992). Ramets within populations vary considerably across successional stages and between habitats (Brewer, 1996).

Many Rhodophyta are also clonal plants, for example species of *Mazzaella*, *Chondrus*, *Mastocarpus*, *Gracilaria* and *Gelidium* (Scrosati and De Wreede, 1997), but studies have been focused only at the level of the ramet (see Santos, 1995;

Scorsati, 1998). *O. pinnatifida* is also a clonal alga, and grows in 2 directions with creeping stoloniferous holdfasts and upright fronds. The turfs inhabit a wide range on the shore at 2.0 -3.5 m above the Lowest Astronomical Tide (LAT) with a lower frond density at the upper limit of the *Osmundea* zone. The difference in frond density (ramet) could influence patch size (genet) and the consequence is different patch size distribution between shore level.

*O. pinnatifida* maintains and propagates itself in mature stands by vegetative growth (Godin, 1981), but the extent to which spores or sexual reproduction give rise to new patches is unknown. Temperature, photoperiod, irradiance quantity and nutrient levels, for example, are known to influence reproduction of many seaweeds (Murray and Dixon, 1992); and limpets are known to graze on algae spores and occasionally also on adult fronds of many seaweeds (e.g. Hawkins and Hartnoll, 1983; Johnson *et al.*, 1997; Burrows and Hawkins, 1998; Jenkins *et al*, 1999), thus inhibiting their growth and recruitment.

The aims of this study were to investigate 1) the population structure (patch size and frond density) and reproduction of *Osmundea* turfs with relation to differences in degrees of wave exposure, shore levels and season, and 2) the expansion rate of different patch sizes. I hypothesised that limpets limit patch size and inhibit the recruitment of this population by grazing on the plants and spores.

## 5.2 MATERIALS AND METHODS

### 5.2.1 Patch size distribution and frond density

Port St. Mary Ledges ( PSM, 54° 0′ N; 4° 44′ W) is a moderately exposed shore and Scarlett Point (SP, 54° 0′ N; 4° 39′ W) is a very exposed shore in terms of the biological exposure scale in Lewis (1964). Permanent markers were made using yellow bright fluorescence tapes that were fixed with rawplugs on the upper (3.5 m. above LAT) and lower (2.0 m. above LAT) limits of *Osmundea* zonation. The permanent marks were used as reference points for horizontal line transects across the shores. This marking technique was also used for all the experiments. Thirty-five randomly selected patches of *Osmundea* turf were photographed using a digital camera (Kodak DC 120) at each site during winter 1998 and spring and summer 1999. The photographs were converted into patch area by image analysis software (Scion Image Beta 3b) in the laboratory.

Frond density in each patch was investigated by counting fronds randomly in 2 cm X 2 cm quadrats, three replicate counts for each patch.

### 5.2.2 Patch expansion

To measure their expansion, patches were categorized into 3 size classes using frequency table based on size distribution of turfs on the shores (Fig. 5.1): small (79-235cm$^2$), medium (266- 769 cm$^2$) and large (842-1472cm$^2$), ten replications each. This monitoring was carried out on Port St. Mary ledges where *Osmundea* turfs were abundant. Patches were marked, monitored and their size measured monthly from

August 1999- July 2000.

### 5.2.3 Limpet grazing

To assess limpet grazing on the turfs, turfs were manipulated by excluding limpets for each of three patch size classes, ten replications each. Limpets were excluded from the periphery of each patch with a micro fence size 5 cm X 5 cm, thus 25 $cm^2$ of bare rock were monitored. The fences, made from chicken wired, were fixed at the periphery of turf patch using ring-bolts screwed into holes drilled in the rock; and the same was done on the opposite side of the patch but without the chicken wire. Those areas were then monitored and photographed monthly from August 1999- July 2000. The outward growth rate of the patches was calculated thus:

$$\text{Relative patch expansion} = \frac{\text{Log}_e\, L2 - \text{Log}_e\, L1}{t2 - t1}$$

Where L2 and L1 are area cover (mm) at time interval from patch expanding

t2 and t1 are the time interval (one month)

### 5.2.4 Reproduction and recruitment

To assess seasonal reproduction of frond, five *O. pinnatifida* turfs were randomly collected from each site (Port St. Mary Ledges and Scarlet Point) during June 1998 - July1999 at both the upper and lower limits of *Osmundea* zone. Thirty fronds from each patch (a total of 150 fronds), were randomly chosen and examined for reproductive spores under a dissecting microscope and any spores were measured. Percent reproduction of fronds was calculated for each site.

On each sampling occasion, twenty tips of reproductive fronds were cleaned and placed in petri dishes in various conditions to stimulate spore release, five replications (Personal communication Kain (Jones), J. M. and Holt, T.):

1) desiccated and kept in the dark for 24 hours at 12-15 °C

2) desiccated for 24 hours under 60 $\mu$mol.m$^{-2}$.s$^{-1}$ irradiance at 12-15°C

3) submerged for 24 hours under 60 $\mu$mol.m$^{-2}$.s$^{-1}$ irradiance at 12-15°C

4) submerged for 24 hours under 60 $\mu$mol.m$^{-2}$.s$^{-1}$ irradiance at 5°C

5) the fronds were squashed using a spatula after being submerged for 24 hours under 60 $\mu$mol.m$^{-2}$.s$^{-1}$ irradiance at 12-15°C

When the spores were released, the fronds were removed. Then the spores were cultured in 10 ml of filtered seawater changed every 2-3 days. Spores were kept at 12-15°C controlled room temperature under 60 $\mu$mol.m$^{-2}$.s$^{-1}$ supplied by Thorn EMI 100 W polylux 3500 fluorescent tubes situated 40 cm above the shelf. Light was measured with a LI-COR Quantum photometer (Model LI-250 Light meter).

Spores were cultured for 3 weeks; they were monitored and counted daily under a microscope. Their survivorship in each condition was calculated and spore development was observed.

To assess recruitment of new patches, a 1m X 1m area within the *Osmundea* zone (five replications at each site) was marked using the technique above. These areas were observed and searched monthly from April 1999- March 2000 for newly-arisen juvenile plants.

### 5.2.5 Data analyses

Analysis of variance (ANOVA) was employed to test the effects of seasons, degree of wave exposure and shore level on patch size and frond density within the turfs. If necessary, data were transformed to meet assumptions of the parametric test.

Friedman ANOVA was employed to compare expansion rate of patches at different seasons, in different patch sizes and with or without limpets as there was no homogeneity of these data sets after a series of transformations.

The Kolmovgorov Smirnov test, a frequency analysis, was employed to test the distribution of population patch size.

Binary Logistic Regression using MINITAB Statistical Software (Minitab Inc., PA. USA) was applied to test the difference in percentage reproduction of fronds between season, degrees of wave exposure and shore levels.

## 5.3 RESULTS

### 5.3.1 Patch size population and distribution

There were various sizes of *Osmundea* patches on the shores, the smallest (28 $cm^2$) was found on the upper limit of the zone on the more exposed shore during winter and the biggest (7479 $cm^2$) on the same shore but at the lower limit.

Most patches were smaller than 1000$cm^2$ (Fig. 5.1; d=0.15, $P<0.01$) and the average patch size varied from 420 $cm^2$ – 1122 $cm^2$ (Fig. 5.2). Patches became significantly smaller during spring and summer ($F_{2,408}=5.31$, $P<0.01$).

Average patch size was significantly smaller at the upper limit of the *Osmundea* zone ($F_{1,408}$ - 5.12, $P<0.05$), and there was also an interaction between shore level and the degree of wave exposure. The smallest patches were found on the upper limit of the more exposed shore ($F_{2,408}=4.55$, $P<0.01$), surprising as I expected a greater wave action would decrease stress from desiccation on the upper limit.

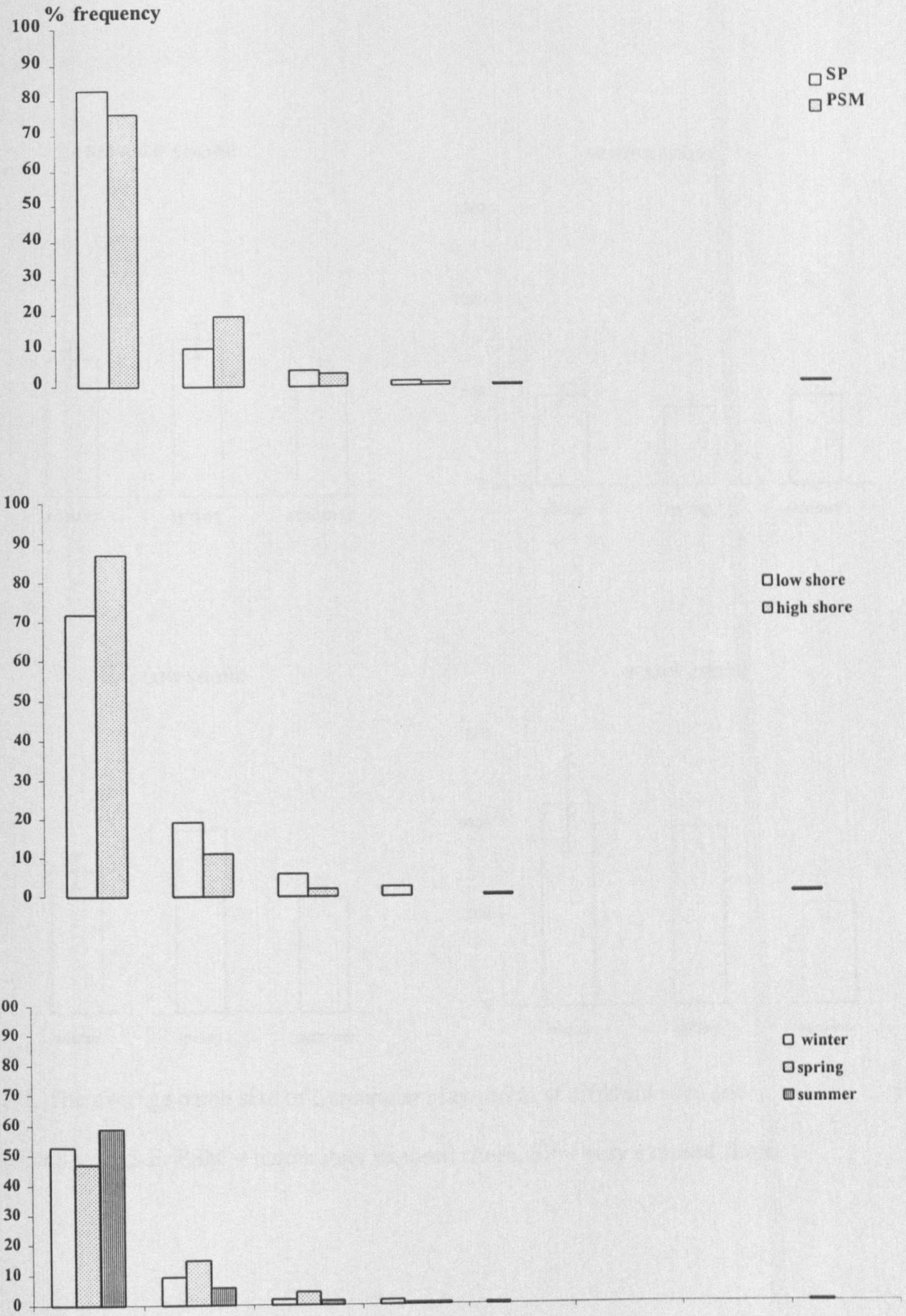


Figure 5.1. The distribution of *Osmundea* patch size at different sites and season.

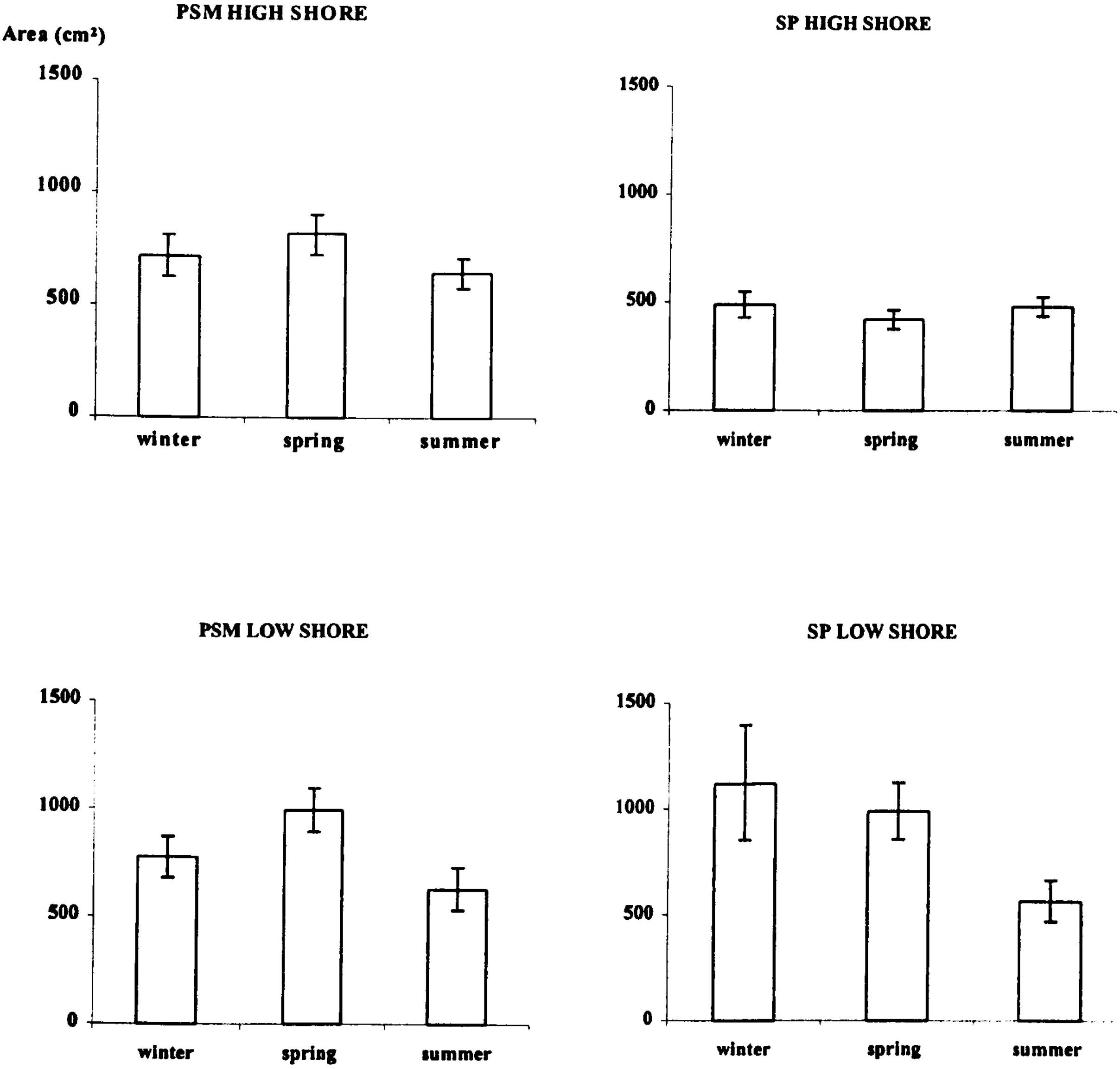


Figure 5.2. The average patch size of *Osmundea pinnatifida* at different sites and seasons. Bars = ± 1S.E. PSM = moderately exposed shore, SP = very exposed shore

### 5.3.2 Frond density

The average frond density varied from 1.14 to 9.53 individuals/ $cm^2$ (Fig. 5.3). Frond density also displayed a similar seasonal pattern to that of patch size. The greatest density was in winter, it declined during spring and most fronds were lost during summer ($F_{2,408}$=604.05, $P<0.001$).

Frond density was significantly less higher up the shore ($F_{1,408}$=717.74, $P<0.001$), 50% less at the upper limit. There was no difference between average densities with different degrees of wave exposure. The density of the fronds was not constant over the year. Loss began at the margin of the patch, but later shoots within the turfs were progressively lost. The density of fronds during spring on the very exposed shore was not different from that of the fronds on the moderately exposed shore in summer ($F_{2,408}$=6.21, $P<0.01$), suggesting that fronds were lost earlier on the less exposed shore.

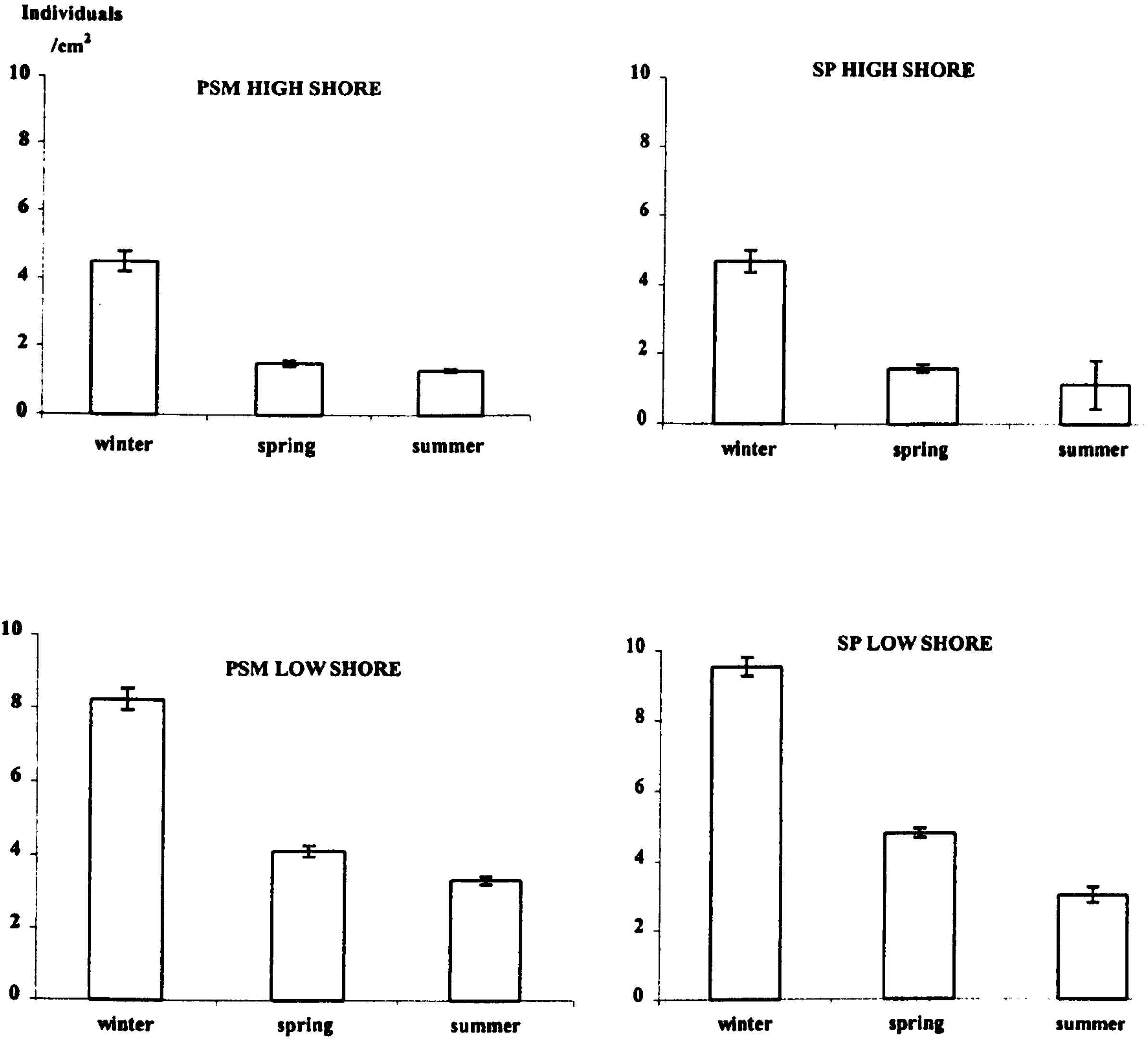


Figure 5.3. The average frond density within *Osmundea* patches at different sites and seasons. Bars = ± 1S.E.. PSM = moderately exposed shore, SP = very exposed shore

### 5.3.3 Patch expansion and limpet grazing

All patches displayed a similar pattern of seasonal expansion, increasing in size in late summer through autumn (Fig. 5.4), but there were some losses during winter which resulted in smaller patches. Patch size decreased again the following spring through to the beginning of summer.

There were significant differences in the relative expansion of turfs at different seasons, with patch size and limpet factors ($\chi^2 = 161.24$, $P<0.001$; Fig. 5.5). Smaller patches had a smaller expansion rate than bigger ones, and there were wide variations among patches of this size. Medium and large patches also showed very slight expansion throughout the year and there was no significant difference between the rates for medium and large patches.

There was a significant difference in the expansion of patches with and without limpets but the expansion rates were very small, for example 0.015 mm/ month without limpets and 0.003 mm/ month with limpets, in small patches during August. So even without limpet grazing patch expansion is exceedingly slow.

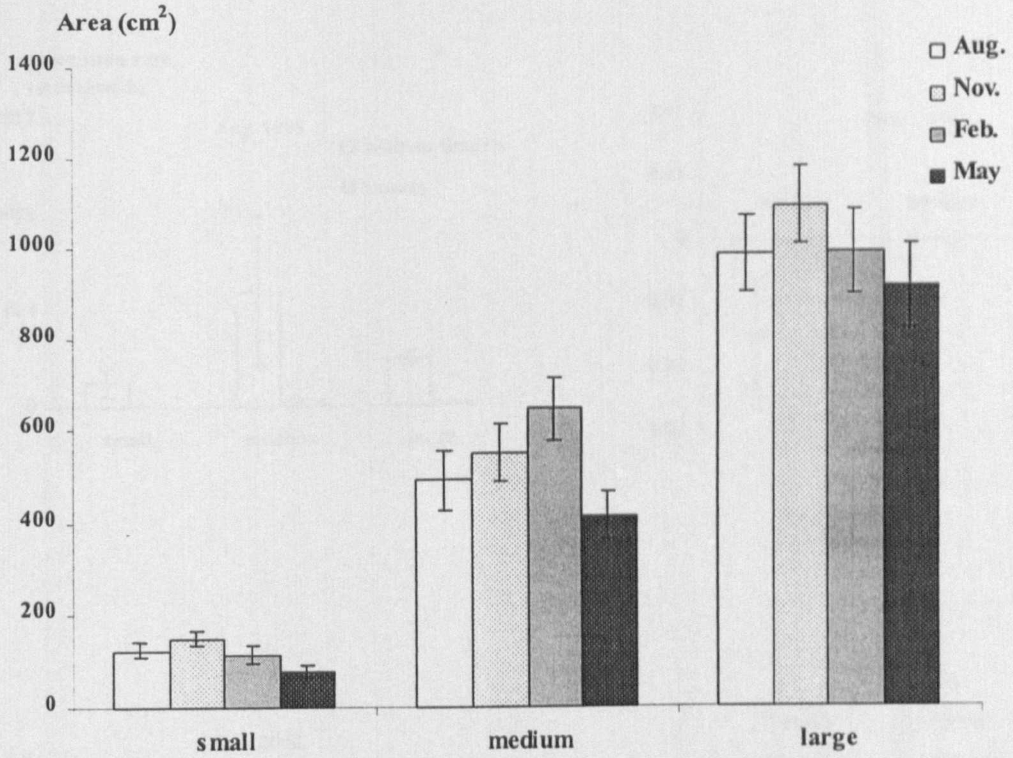


Figure 5.4. Seasonal variations in the average patch size of three size classes.

Bars = ± 1S.E.

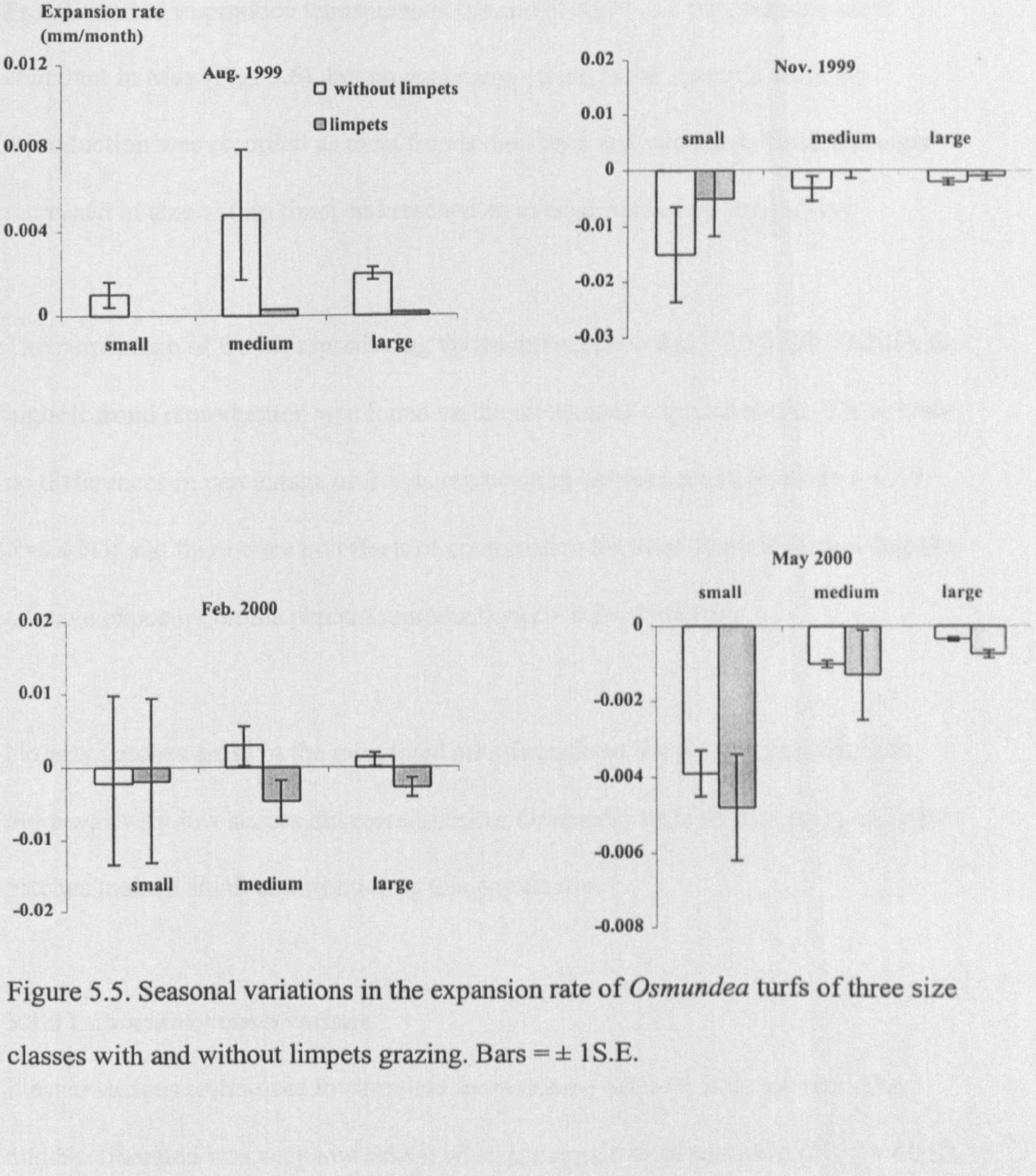


Figure 5.5. Seasonal variations in the expansion rate of *Osmundea* turfs of three size classes with and without limpets grazing. Bars = ± 1S.E.

### 5.3.4 Reproduction variation of fronds and recruitment on the shore

Fronds started to produce tetraspores at the end of April and they became more abundant in May (Fig. 5.6), but no gametangia were found. Later in June, no reproduction was recorded as most fronds died back and were lost. Tetrasporangia increased in size within time, and reached an average size of 98 μm in May.

The percentage of fronds reproducing varied among shores ($z = 10.33, P < 0.001$), the highest frond reproduction was found on the moderately exposed shore. There were no differences in percentage of fronds reproducing between shore levels ($z = 0.69$, $P = 0.491$); and there were no effects of combination between shore level and degrees of wave exposure on the percent reproduction($z = 0.84$, $P = 0.403$).

No new patches arose in the monitored area throughout the year, suggesting that there was very low successful recruitment of *Osmundea* turfs on the shore; and new patches make a small contribution to this population.

### 5.3.5 Laboratory observations

I tested various techniques to stimulate spore release but with little success. The number liberated was very low except when the fronds were squashed ($F_{2,12} = 40.32$, $P < 0.001$), but this can hardly be considered a natural release of mature spores. The spores took 2-3 days to settle and stick on to the petri dishes. The development and growth of the spores was very slow, the maximum size of tetraspore germlings was 20 mm tall after 3 weeks.

The mortality of tetraspores increased with time irrespective of the conditions (Fig.5.7a). However, at the end of experiment some spores survived especially those released under desiccated and submerged conditions ($F_{2,12} = 11.31$, $P < 0.01$; Fig. 5.7b).

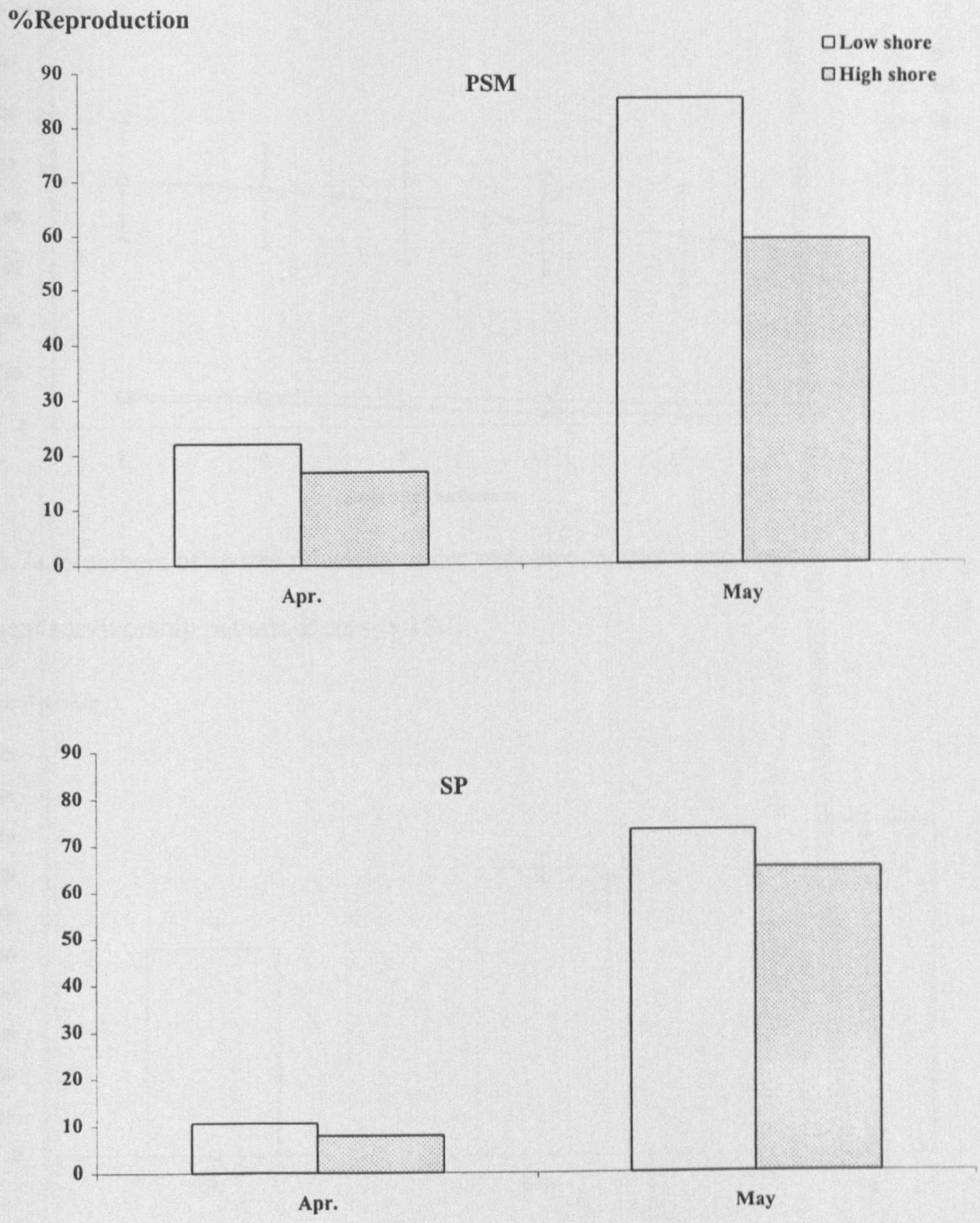


Figure 5.6. Seasonal variations in percentage reproduction of *Osmundea* turfs at different sites and seasons. PSM = moderately exposed shore, SP = very exposed shore

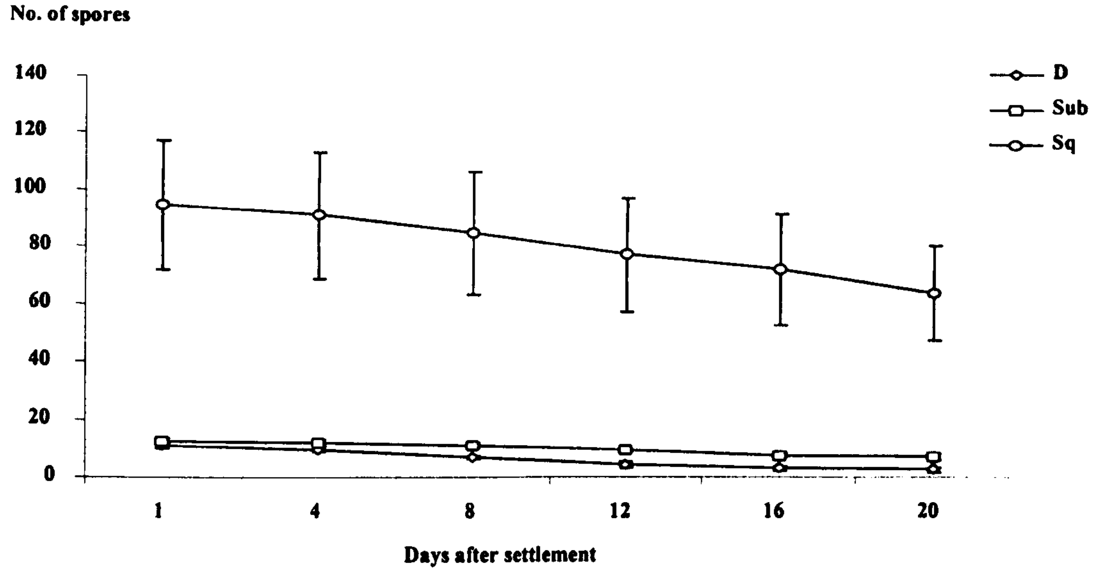


Figure 5.7a. Numbers of spores releasing under various conditions and their subsequent survivorship pattern. Bars = ± 1S.E.

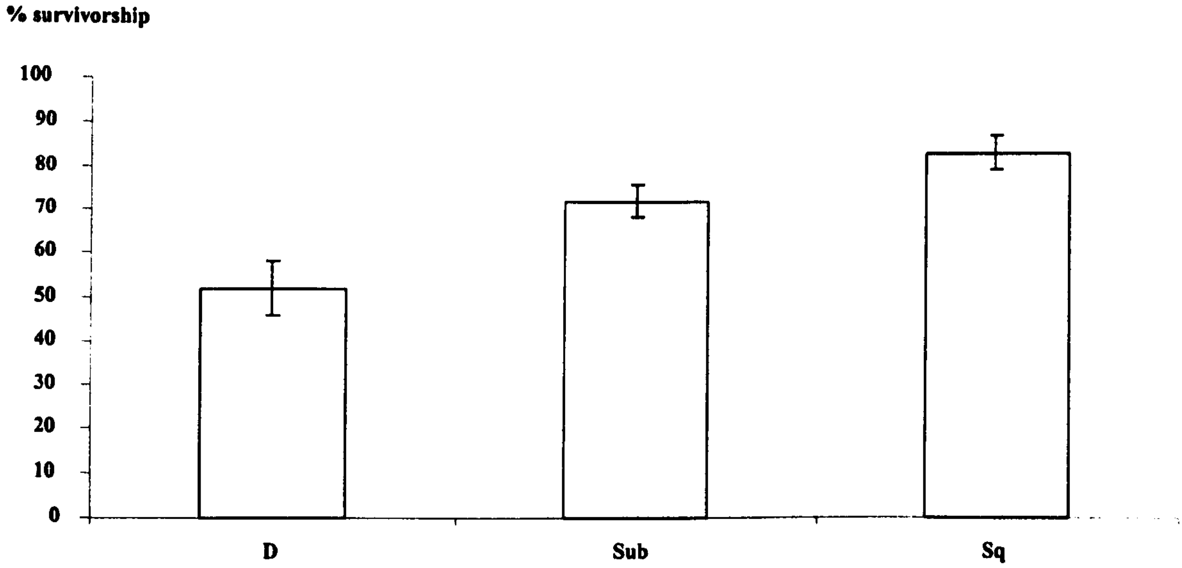


Figure 5.7b. Percent survivorship of tetraspores after 21 days in culture after release. Bars = ± 1S.E. D= desiccated, Sub = submerged for 24 hours at 12-15°C and Sq = Squashed fronds.

## 5.4 DISCUSSION

In the temperate zone, many algae show two periods of fertility, the first in spring and the second during autumn, and in most cases reproduction follows maximum growth (Hoffmann, 1987). The results showed that *Osmundea pinnatifida* produces tetraspores only in April- May just before they die back in June. The mature tetrasporangia are 75-125 m ( Maggs and Hommersand, 1993), a similar range found to that in late May shortly before most fronds die back on the shores of the Isle of Man. Also, the results showed that the numbers of spores releasing were very low with high mortality (32% - 46%) even in favourable laboratory conditions. High mortality in early stages, however, is a common phenomenon in many seaweeds, for example more than 70% of *Fucus serratus* died at the zygote stage on the shore (Creed *et al.*, 1996). A combination of a very short reproduction period, high mortality and harsh conditions on the shore, result in poor recruitment success; thus new cohorts of juvenile *Osmundea* are rarely found. Spore release, therefore, does not seem to lead to a remarkable success in establishing new populations.

The sinking rate of propagules is influenced by their size, large ones tending to settle faster than smaller ones (Okuda and Neushul, 1981). Smaller spores, therefore, are likely to disperse a greater distance. Tetraspore size in red algae ranges from 15 –120 μm in diameter (Ngan and Price, 1979), and those of *O. pinnatifida* fall into the higher part of this range at the average of 98 μm in May. The large spore size, and low stature of the plants and their close proximity in dense turfs would conspire to ensure the spores will settle close by (Santelices, 1990). Indeed many spores may drop between the parent plants and are less likely to develop in the dark within the turf, or interfered by accumulated sediment (Devenny and Volse, 1978), thus limiting their recruitment elsewhere.

If some spores disperse further and survive in the harsh conditions of the open shore, they might still be grazed by some herbivores. Limpets are known to limit seaweed recruitment on many intertidal rocky shores (e.g. Hawkins and Hartnoll, 1983). We have never found new recruitment on the mapped area where limpets could invade, but a few new patches were recorded in crevices where limpets could not reach them. Moreover, we noticed that most older patches are associated with rock crevices in the rock or crustose algae where presumably spores had successful established and later developed into a fully grown patch. Such microtopography could be an important refuge for algal propagules not only where there are grazing limpets, but also when stressful abiotic conditions occur in spring and summer.

On the Manx shores, *Patella vulgata* was 35% denser at Scarlett Point than on Port St. Mary ledges (Jenkins *et al.*, 1999). Limpets exert their effect on exposed shores by grazing on the epilithic microbial film (Hill and Hawkins, 1990) but rarely feed on the mature stages of macroalgae. However, Hawkins and Hartnoll (1983) have observed small limpets climbing up fronds of *Osmundea* feeding either upon *Osmundea* itself or its epiphytes. Also, they pointed out that if limpets can manage to eat an alga which is available, then they will, provided that no higher preference species is present. *O. pinnatifida*, however, contains halogenated secondary metabolites that are known to repel potential grazers (Erickson, 1983; Hay and

Fenical, 1988). Thus, limpets are unlikely to graze on *Osmundea* or will have less effect on the turfs.

Shore level influences the degree of desiccation of *Osmundea* fronds, which could indirectly influence patch size through frond density. On the upper limit of the *Osmundea* zone, turfs have 50% less frond density than lower down (see Fig. 5.3). This results from higher desiccation as shown in Chapter 3.

The vegetative expansion of *Osmundea* turf results from two or more fronds coming into contact, one becomes inert and forms rhizoids, and bends over to creep on the substratum (Godin, 1981). Therefore, in the lower zone during winter when upright fronds become fully grown and much denser, more frequent frond contact might result in greater expansion, resulting in larger patches. Indeed, the bigger *Osmundea* turfs were found on the lower limit of the exposed shore where there is less desiccation because of longer hours spent submerged and the increased spray from waves.

In a big patch, fronds have greater mutual protections than those in a smaller patch as shown in chapter 4, and have a higher rate of photosynthesis as shown in chapter 3. Thus, fronds suffer less from stressful conditions and have a greater productivity resulting in a higher expansion rate. During winter small patches were severely damaged and some portions of the turf matrix were removed, compared to big patches which have dense stoloniferous holdfasts of many generations of creeping fronds, thus increasing their tenacity and ability to withstand strong wave action.

Throughout the following year, those patches slowly repaired but never recovered to the same size as the previous year. During spring and summer, however, all patches are curbed by bleaching and die back of fronds resulting in a smaller patch area.

Once established, *Osmundea* turfs are extremely stable. Seasonal variations in environmental conditions have a strong influence on the growth and distribution of this population while limpets probably inhibit the appearance of new patches. Patch initiation might require a "recruitment window", perhaps cool and cloudy weather as proposed as a requirement for *Pelvetia fastigiata* (L.) Dcne. et Thuret (Brawley and Johnson, 1991) and a temporary absence or inactivity of limpets. Such conditions might also encourage an increase in patch size, extending the growth season by delaying the onset of annual die back.

# CHAPTER 6

# SEDIMENT AND TURF COMMUNITY

## 6.1 INTRODUCTION

Extensive turfs of algae are a feature of the lower reaches of rocky shores in many parts of the world (Myers and Southgate, 1980; Kain and Norton, 1990). The crowded fronds create a labyrinth, which traps sediment (Scoffin, 1970; Stewart, 1983; Airoldi *et al.*, 1996), and is often inhabited by a rich and varied fauna (Neumann *et al.*, 1970; Myers and Southgate 1980). The accumulation of sediment within turfs varies in time and space, both horizontally and vertically on the shore (Whorff *et al.*, 1995), and seasonally, largely as a consequence of wave action (Lewis 1964; Stephenson and Stephenson 1972; Stewart 1983; Airoldi *et al.*, 1996). Terrestrial sources of sediment washing down on to the shore as a result of deforestation and erosion may also be important in some regions (Airoldi *et al.*, 1996).

The effects of sediment on the intertidal and subtidal zones have been well studied, but rarely with respect to turf communities. Sediment is known to scour or occlude the substratum, as well as smothering organisms or cutting off the light to juvenile attached plants (Norton, 1978). Thus, it interferes with the recruitment, growth and survival of algae (Neushul *et al.*, 1976), as well as zonation patterns and species diversity (Daly and Mathieson, 1977; Little and Smith, 1980; Taylor and Littler, 1982; Littler *et al.*, 1983). Sediment can also regulate the respiratory metabolism in some common shore gastropods (Marshall and McQuaid, 1989; Chandrasekara and Frid, 1998), clog the feeding mechanism of suspension feeders (Elethriou and Basford, 1989; Aller and Stupakoff, 1996) and inhibit the settlement of a variety marine invertebrates (Stewart, 1989).

In turf communities, studies have mostly focused on the effect of sediment on algae themselves rather than the fauna harboured by the turfs (but see Whroff *et al.*, 1995). For example, the amount and type of sediment may structure both the species composition and diversity of the algal flora (Stewart, 1982; Kendrick, 1991; Airoldi *et al.*, 1995), but there is only one report of the effects on fauna (Whroff *et al.*, 1995). It is well known that algal turfs can trap sediment on shores where otherwise it would be absent, but little is known about the relationships between turf communities, sediment accumulation and the interaction between physical factors, sediment supply and fauna. In an attempt to investigate these relationships, I report the results of a study of turfs of *Osmundea pinnatifida* (Hudson) Lamouroux on rocky shores of the Isle of Man. *O. pinnatifida* was chosen as a model system because it forms discrete patches of short turf, with irregular branches that trap sediment. These patches represent small 'islands' of favourable habitat in an otherwise adverse terrain of open rock and within them there is a greater animal diversity than on the adjacent rock.

I measured the amount and types of sediment within patches of *O. pinnatifida* in two contrasting seasons, on shores with different degrees of wave exposure and at different levels on the same shore. The associated fauna within the turfs was examined at the same time.

I hypothesized that (1) the *Osmundea* turf harbours a fauna whose composition, distribution and diversity will vary between sites and seasons, and (2) the nature of the associated fauna will be determined chiefly by the amount and type of sediment that accumulates within the turf.

## 6.2 MATERIALS AND METHODS

### 6.2.1 Study site and sampling

The study sites were all located in the South of the Isle of Man, in the Irish Sea. Three shores were selected with different degrees of wave exposure: sheltered (S) Port Erin (54° 06′ N; 4° 46′ W), moderately exposed (M) Port St. Mary Ledges (54° 0′ N; 4° 44′ W), and exposed (E) Scarlet Point (54° 04′ N; 4° 39′ W). Exposure was assessed using the biological exposure scale indicator method of Lewis (1964). Each shore was sampled at two shore levels within the turf zone: upper limit (h) - 3.5 m above Lowest Astronomical Tide (LAT) and lower limit (l) - 2.0 m above LAT. Samples were taken in two seasons: late autumn (November 1998) and summer (August 1999). Thirty patches of turf were chosen randomly at each shore level and in each season. Areas of turf measuring 10cm x10cm were removed using a paint scraper. This was done carefully to prevent the loss of associated organisms and sediment. Samples were immediately placed in plastic bags and transferred to the laboratory for processing.

Samples were washed with filtered seawater to remove both sediment and animals. The sediment was then filtered using distilled water and gentle suction, and dried at 60°C to constant weight. The dry sediment was then sieved into seven size fractions; >2.00 mm, 1.00-2.00 mm, 500 μm-1.00mm, 250-500 μm, 125-250 μm, 63-125 μm and < 63μm and each fraction was weighed.

The animals were stained using Rose Bengal which was helpful for distinguishing small animals from sediment during sorting. Animals were preserved with 10% formalin and subsequently identified to species.

### 6.2.2 Data analyses

The species diversity (H') and equitability (J) of each sample were calculated for each site, level and season. The data for each variable (count of species abundance, H', J and total weight of sediment and of each size fraction separately) was analyzed using ANOVA for each season using a nested design with degree of exposure (shore) as the main factor and shore level nested within the main factor. To test for temporal change, repeated measures were used; this was interpreted as a first approximation of seasonal effects. Seasonal effects were assessed using repeated measures. This analysis was done using untransformed and transformed data (species numbers = $\sqrt{x}$; sediment amounts = $\ln x$) with PROC ANOVA (SAS 1990). Statistical results are presented based on the transformed analyses, but for clarity graphical output is based on the untransformed means.

The potential relationships between species abundance and site factors, season and sediment were then assessed using stepwise multiple regression (PROC GLM; SAS 1990). Here degree of exposure, shore elevation and season were treated as categorical variables and sediment values as an ordinal variable. The aim was not to develop predictive models, but rather to select those combinations of variables that were associated with the abundance of individual species, to give information on the types of factors that might be controlling their distribution. The univariate approach was used to generate hypotheses for individual species which could be tested experimentally in future work. Transformed data were used throughout.

Multivariate analysis was carried also out using CANOCO for WINDOWS (ter Braak and Smilauer 1998). The dataset (24 species x 60 samples) was analysed using a sequence of techniques; in all multivariate analyses the species data were transformed (ln x+1) and the downweighting option for rare species was not used. Initially the species x plot data were analysed with DECORANA (DCA) to measure the gradient lengths. The gradient length on the first axis was 2.9, suggesting that the linear model should be used. Thereafter, two constrained ordinations were run using environmental variables in which wave exposure, shore elevation and season were considered as using categorical information and the different sediment fractions were treated as ordinal data. The first constrained ordination was a Redundancy Analysis (RDA), where the Forward Selection procedure was used with a Monte Carlo test with 499 permutations, to determine which environmental variables were important in explaining the variation in the species in each data set. The following variables were selected ($P<0.05$) in order: season, shore elevation and amount of sediment in 125-250 μm fractions. In the final RDA the eigenvalues for the four axes were 0.141, 0.125, 0.029 and 0.366, and the Monte Carlo tests with 999 permutations were significant, $P = 0.001$ (first canonical axis, $F = 9.207$, $P<0.01$; overall model, $F = 7.835$, $P<0.001$).

## 6.3 RESULTS

### 6.3.1 Sediment trapped in algal turfs

The total amount of sediment trapped varied greatly between 1126 and 4628 g/m$^2$, and the amount present differed with seasons, wave exposure and shore elevation. During the winter, greater amounts of sediment were found especially on the sheltered shore, and higher on the shore compared to the lower level (Fig. 6.1, Tab.6.1). During the summer, there was less sediment on all shores.

Total sediment load was greater, and tended to be composed of the larger -sized particles, at the higher level than lower on the shore, but there were no clear seasonal or spatial patterns between fractions (Fig.6.1, Tab.6.1).

Table 6.1. Summary of significant results (F-ratio) from analyses of variance

| **Sediment fraction** | **Winter** | | **Summer** | | **Repeated measures** | | |
|---|---|---|---|---|---|---|---|
| | **Degree of exposure** | **Shore level** | **Degree of exposure** | **Shore level** | **Season** | **Season x Degree of exposure** | **Season x Shore level** |
| Total sediment | 8.08*** | 8.61*** | 2.33ns | 12.92*** | 11.77** | 9.20** | 6.94** |
| >2.00 mm | 7.61** | 2.90ns | 3.29ns | 6.27** | 10.78** | 8.27** | 1.94ns |
| 1.00-2.00 mm | 4.66* | 4.32* | 3.66* | 11.06*** | 1.70ns | 7.25** | 2.99ns |
| 500 μm-1.00 mm | 1.18ns | 4.05* | 5.62* | 11.53*** | 1.89ns | 3.22ns | 2.19ns |
| 250-500 μm | 0.14ns | 5.19** | 6.97** | 15.07*** | 3.36ns | 2.32ns | 2.42ns |
| 125-250 μm | 27.53*** | 15.96*** | 5.21* | 2.83ns | 18.03*** | 16.00*** | 15.64*** |
| 63-125 μm | 10.35*** | 4.45*** | 2.20ns | 0.90ns | 67.89*** | 12.35*** | 10.28*** |
| <0.63μm | 0.71ns | 5.11*** | 1.99ns | 7.97*** | 11.83** | 1.11ns | 3.23* |

Significance : ns= non-significance, * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.01$

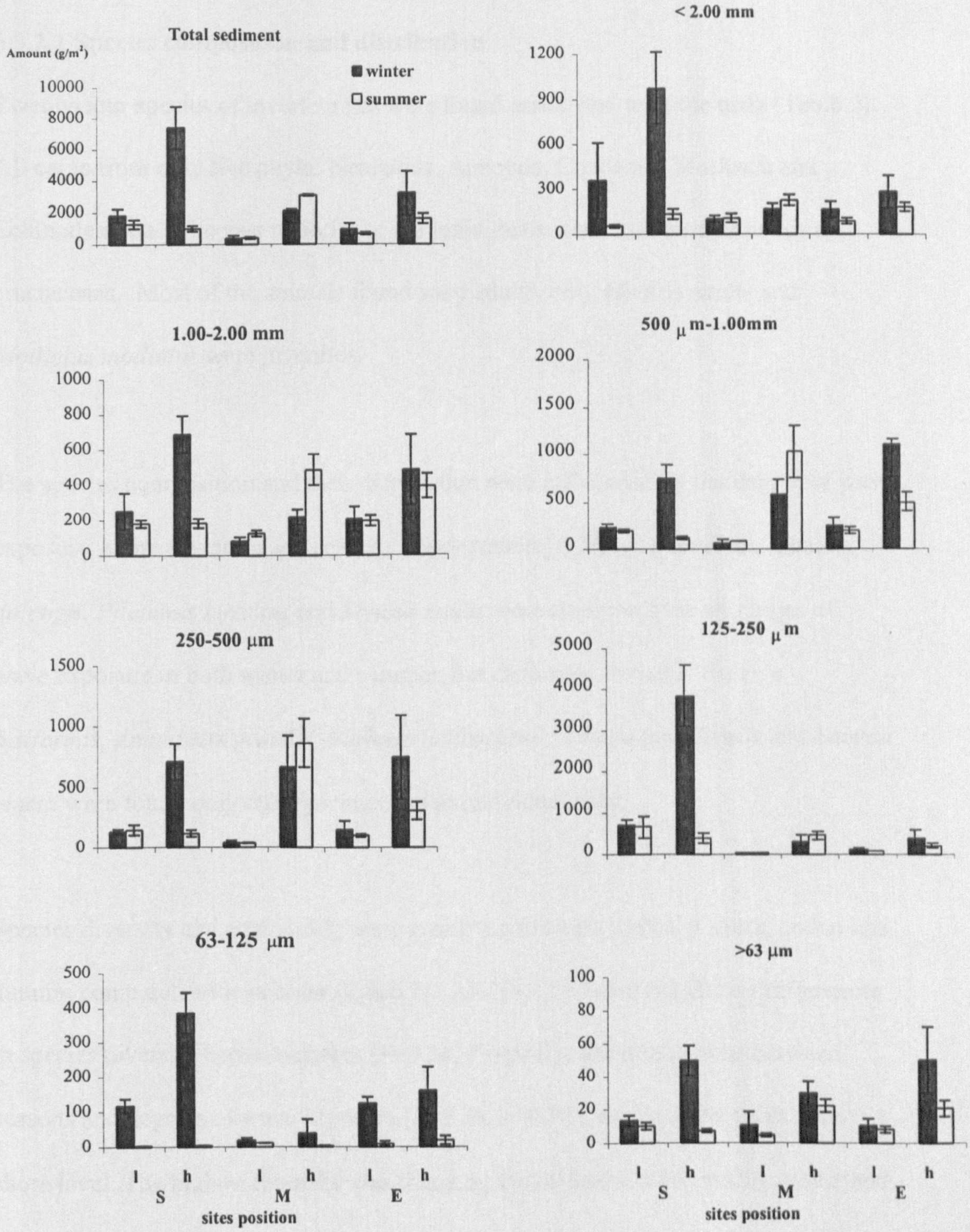


Figure 6.1. Effects of degrees of wave exposure; sheltered (S), moderately exposed (M) and exposed (E) shore at low (l) and high (h) shore levels on associated sediment within turfs in two seasons.

### 6.3.2 Fauna of algal turfs

#### 6.3.2.1 Species composition and distribution

Twenty-four species of invertebrates were found associated with the turfs (Tab.6.2). All came from only five phyla: Nematoda, Annelida, Crustacea, Mollusca and Echinodermata. The vast majority of the individuals were molluscs, annelids and crustaceans. Most of the animals found were adults, only *Mytilus edulis* and *Modiolus modiolus* were juveniles.

The species composition and their distribution were influenced by the degree of wave exposure, shore elevation and season. *Hyale stebbingi*, *Idotea granulosa, Tanais dulongii*, *Pilumnus hirtellus* and *Mytilus edulis* were common over all ranges of wave exposure in both winter and summer, but *Oerstedia dorsalis*, *Owenia fusiformis*, *Amphitrite gracilis, Barleeia unifasciata*, *Gibbula umbilicalis* and *Lacuna vincta* were found only during winter and at individual sites.

Species diversity and equitability were greater on the most exposed shore, and in late autumn compared with summer (Tab.6.2). ANOVA revealed significant differences in species diversity between shores (F=9.34, $P$<0.001), and interactions between seasons and degrees of wave exposure (F=5.25, $P$<0.01), but no differences with shore level. The highest diversity was found on the exposure shore during winter and the lowest was found on the shelter shore in summer. Equitability showed similar, significant differences with degrees of wave exposure (F=5.84, $P$<0.01) and interaction between season and degrees of wave exposure (F=4.28, $P$<0.05), but not with season (F=0.05, $P$=0.819).

Table 6.2. Summary species list and its distribution of associated animals within turfs species diversity and equitability at 3 degrees of wave exposure, sheltered (S), moderately exposed (M) and exposed (E) shores at low (L) and high (H) shore levels within the turf zonation in winter and summer.

| **Phylum** | **Species** | **Winter** | | | | | | **Summer** | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | S | | M | | E | | S | | M | | E | |
| | | **L** | **H** | **L** | **H** | **L** | **H** | **L** | **H** | **L** | **H** | **L** | **H** |
| **Nematoda** | *Oerstedia dorsalis* | | | | X | | | | | | | | |
| **Annelida** | *Amphitrite gracilis* | | | | | | X | | | | | | |
| | *Capitella* sp I | | | | | X | X | | | | | | |
| | *Cirriformia tentaculata* | | | | X | X | | | X | | | | |
| | *Nephtys caeca* | | | | X | | | | X | | | | X |
| | *Nereis pelagica* | | X | | X | | | | X | | | | |
| | *Owenia fusiformis* | | X | | | | | | | | | | |
| **Crustacea** | *Hyale stebbingi* | X | X | X | X | X | X | X | X | X | X | X | X |
| | *Tanais dulongii* | X | X | X | X | X | X | | X | X | X | X | X |
| | *Idotea pelagica* | X | X | X | | X | X | X | | X | | X | X |
| | *Idotea granulosa* | X | X | X | X | X | X | X | | X | | X | |
| | *Pilumnus hirtelluss* | X | X | X | X | X | X | X | X | X | X | X | X |
| **Mollusca** | *Gibbula umbilicalis* | X | | | | | | | | | | | |
| | *Barleeia unifastica* | | | | | | X | | | | | | |
| | *Cingula trifasciata* | | | | | | X | | | | | | |
| | *Lacuna vincta* | X | | | | | | | | | | | |
| | *Littorina littorea* | X | X | | | | X | | | | | | |
| | *Littorina obtusata* | | | | | X | X | | | | | | |
| | *Littorina saxtilis* | | | | | | | | X | | X | | |
| | *Nucella lapillus* | X | X | X | | X | X | | | | | | |
| | *Rissoa parva* | | X | | | | | X | X | | X | X | X |
| | *Modiolus modiolus* | | | X | | X | X | | X | | | X | |
| | *Mytilus edulis* | X | X | X | | X | X | | X | X | X | X | X |
| **Echinodermata** | *Acrocnidia brachiata* | | X | X | | | | | X | | | | |
| **Community structure** | Species diversity | 2.04 | 1.77 | 1.42 | 1.08 | 2.85 | 2.72 | 0.99 | 2.18 | 1.68 | 1.82 | 2.54 | 1.50 |
| | Equitability | 0.44 | 0.39 | 0.31 | 0.24 | 0.62 | 0.60 | 0.22 | 0.48 | 0.37 | 0.40 | 0.56 | 0.33 |

### 6.3.2.2 Spatial and temporal variations in populations

Eight species showed significant differences in their abundance with respect to degree of wave exposure, shore elevation, seasons and their interactions (Tab.6.3). *Mytilus edulis* was the most abundant species on the sheltered shore and *Hyale stebbingi* on the moderately exposed shore respectively during winter, but there was no dominant species on the very exposed shore. Most of the associated fauna inhabited the turfs both in winter and summer, but *Littorina obtusata* was only found during winter. The abundance of most animals decreased during summer, but *Rissoa parva*, *Modiolus modiolus* and *Tanais dulongii* greatly increased in summer (Fig.6.2).

Table 6.3 Summary of significant results (F-ratio) from analyses of variance.

| **Species** | **Winter** | | **Summer** | | **Repeated measures** | | |
|---|---|---|---|---|---|---|---|
| | **Degree of exposure** | **Shore level** | **Degree of exposure** | **Shore level** | **Season** | **Season x Degree of exposure** | **Season x shore level** |
| ***H. stebbingi*** | 26.34*** | 4.43* | 11.01*** | 4.72* | 63.23*** | 15.06*** | 0.70ns |
| ***I. granulosa*** | 10.32*** | 16.07*** | 2.59 | 4.77** | 88.52*** | 7.72** | 11.49*** |
| ***L. obtusata*** | 10.77 *** | 17.39 ns | ns | ns | 42.26*** | 10.77*** | 17.38*** |
| ***M. modiolus*** | 5.19 * | 0.29 ns | 0.70 ns | 1.03 ns | 1.23 ns | 2.34 ns | 0.1 ns |
| ***M. edulis*** | 1.87*** | 3.67** | 0.80 ns | 3.97* | 40.19*** | 11.81*** | 3.19* |
| ***P. hirtellus*** | 6.60** | 2.21ns | 3.12ns | 8.40*** | 25.41*** | 6.56** | 3.36* |
| ***R. parva*** | 3.49* | 3.49* | 6.43** | 3.81* | 0.01ns | 6.07** | 3.36* |
| ***T. dulongii*** | 1.52ns | 2.59ns | 10.78*** | 9.10*** | 15.38*** | 1.08ns | 1.98ns |

Animals species which are not presented showed no significant relationship, otherwise ns = non-significance, * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$

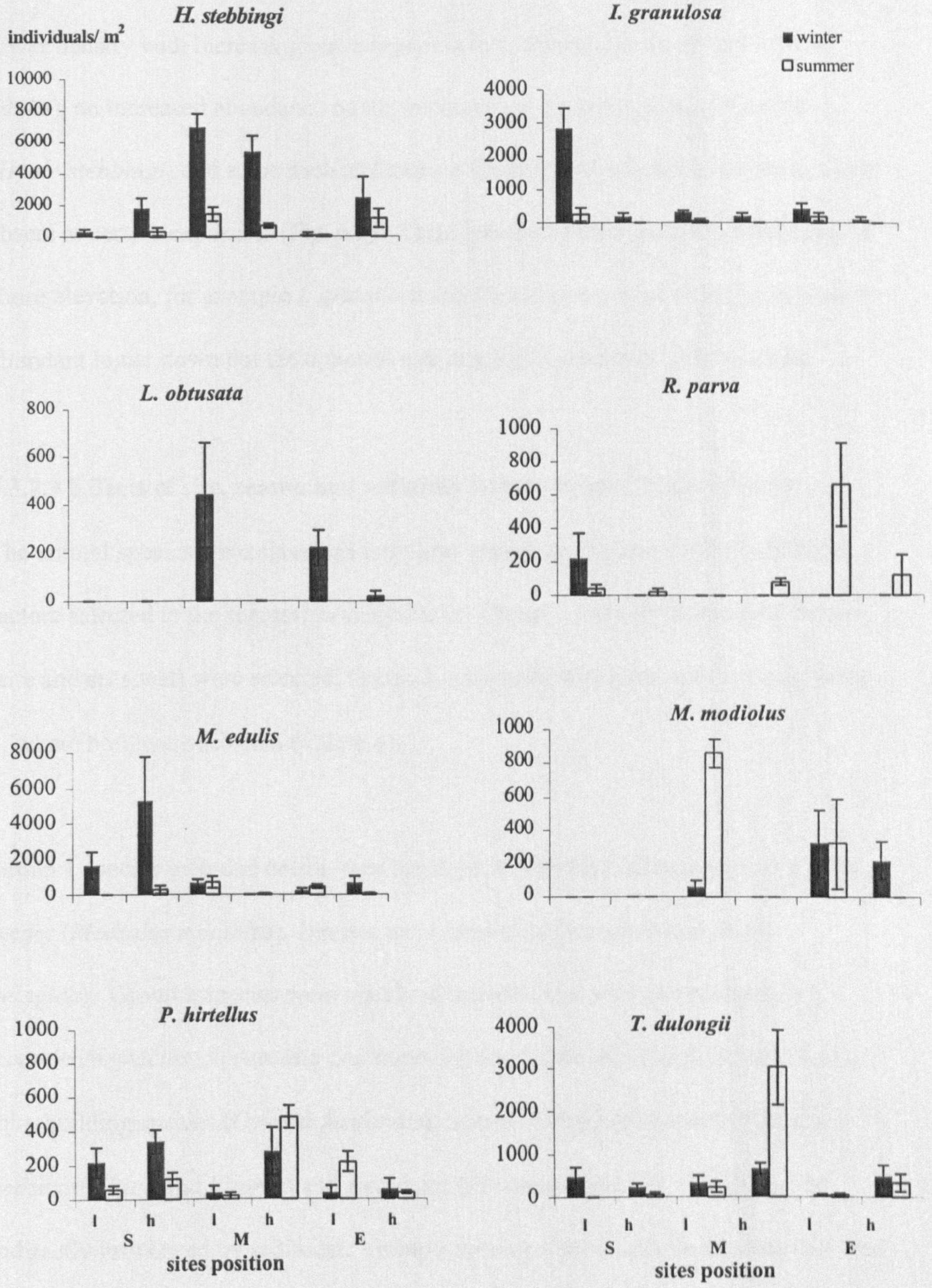


Figure 6.2. Effects of degrees of wave exposure; sheltered (S), moderately exposed shore (M) and exposed (E) shores in two seasons on species density of associated animals which showed significant relationships.

Three patterns of density were found with respect to degree of wave exposure: a lower density with increasing wave exposure (e.g. *Idotea granulosa* and *Mytilus edulis*), an increased abundance on the intermediate moderately exposed shore (*Hyale stebbingi*) and some such as *Littorina obtusata* and *Modiolus modiolus* were absent at certain exposures (Fig. 6.2). There was no uniform pattern with respect to shore elevation, for example *I. granulosa* and *Rissoa parva* were significantly more abundant lower down but the opposite was true for *H. stebbingi* and *M. edulis*.

### 6.3.2.3 Effects of site, season and sediment factors on species distribution

The animal species were classified into three groups on the basis of the significant factors selected in the regression analyses, i.e: Group 1, only environmental factors (site and seasonal) were selected; Group 2, only sediments were selected and Group 3, where both were selected (Tab. 6.4).

Group 1 species included detritivores that feed on sediment (*Rissoa parva*), a filter feeder (*Modiolus modiolus*), and two carnivores (*Nepthys caeca* and *Nereis pelagica*). Group 2 species were mainly detritivores that feed on sediment (e.g. *Amphitrite gracilis*, *Acrocnidia brachiata*, *Mytilus edulis* and *Capitella* sp I) and a tube-building species (*Owenia fusiformis*). However, this group also included a herbivore (*Littorina littorea*) and a predator (*Pilumnus hirtellus*), which may be indirectly influenced by sediment. Group 3 species were mostly herbivores that feed on epiphytes of *O. pinnatifida* (e.g. *Hyale stebbingi*, *Idotea pelagica*, *I. granulosa*, *Gibbula umbilicalis*, *Barleeia unifasciata*, *Littorina obtusata* and *Lacuna vincta)*, a detritivore (*Tanais dulongii*) and a carnivore (*Nucella lapillus*).

Table 6.4 Summary of results from the stepwise multiple regression, separating species responses into three types: (a) species where only site and seasonal factors were selected, (b) species where only sediment factors were selected and (c) site, seasonal and sediment factors were selected. Final equations are presented and significance of individual variable are denoted as : - = no significant relationship, otherwise + = $P<0.10$, * =$P<0.05$, ** = $P<0.01$, *** = $P<0.001$.

| | **Species** | $r^2$ | **Significant variables selected** | **Parameter** | **F-ratio** | **Probability** |
|---|---|---|---|---|---|---|
| **(a) Site and seasonal factors** | *R. parva* | 0.142 | $b_0$ | 0.0169 | 0.13 | - |
| | | | Exposure | -0.0365 | 2.96 | + |
| | | | Season | 0.0540 | 6.47 | * |
| | *M. modiolus* | 0.1287 | $b_0$ | 0.0311 | 0.30 | - |
| | | | Shore | 0.041 | 5.62 | * |
| | | | Exposure | -0.047 | 2.8 | + |
| | *N. caeca* | 0.0466 | $b_0$ | -0.0026 | 0.90 | - |
| | | | Season | 0.003 | 2.83 | + |
| | *N. pelagica* | 0.1198 | $b_0$ | 0.0632 | 12.63 | *** |
| | | | Season | -0.0316 | 7.89 | ** |
| **(b) Sediment factors** | *A. brachiata* | 0.0797 | $b_0$ | -0.0046 | 0.52 | - |
| | | | Sediment 125µm – 250µm | 0.0086 | 5.02 | * |
| | *P. hirtellus* | 0.3688 | $b_0$ | -0.1002 | 8.03 | ** |
| | | | Sediment < 63µm | -0.1517 | 4.87 | * |
| | | | Total Sediment | 0.0847 | 25.66 | *** |
| | *A. gracilis* | 0.3566 | $b_0$ | 0.0073 | 1.95 | - |
| | | | Sediment 1 - 2 mm | 0.0101 | 2.90 | + |
| | | | Sediment < 63µm | 0.0458 | 20.54 | *** |
| | | | Total Sediment | -0.0103 | 7.41 | ** |
| | *L. littorea* | 0.2617 | $b_0$ | -0.015 | 5.12 | * |
| | | | Sediment > 2mm | 0.0166 | 4.98 | * |
| | | | Sediment 63µm – 125µm | 0.0233 | 2.59 | + |
| | *O. fusiformis* | 0.1279 | $b_0$ | -0.0062 | 2.86 | + |
| | | | Sediment 125µm – 250µm | 0.0064 | 8.50 | ** |
| | *M. edulis* | 0.4710 | $b_0$ | 0.7266 | 12.90 | *** |
| | | | Sediment > 2mm | 0.2086 | 10.08 | ** |
| | | | Sediment 500 µm – 1mm | 0.2116 | 2.34 | - |
| | | | Sediment 125µm – 250µm | 0.3026 | 11.23 | ** |
| | | | Sediment 63µm – 125µm | 0.3357 | 10.61 | ** |
| | | | Total Sediment | -0.5894 | 8.59 | ** |
| | *C.* sp. I | 0.3326 | $b_0$ | 0.042 | 3.01 | + |
| | | | Sediment 1 - 2mm | 0.0450 | 2.63 | - |
| | | | Sediment < 63µm | 0.2090 | 19.74 | *** |
| | | | Total Sediment | -0.0495 | 7.80 | ** |

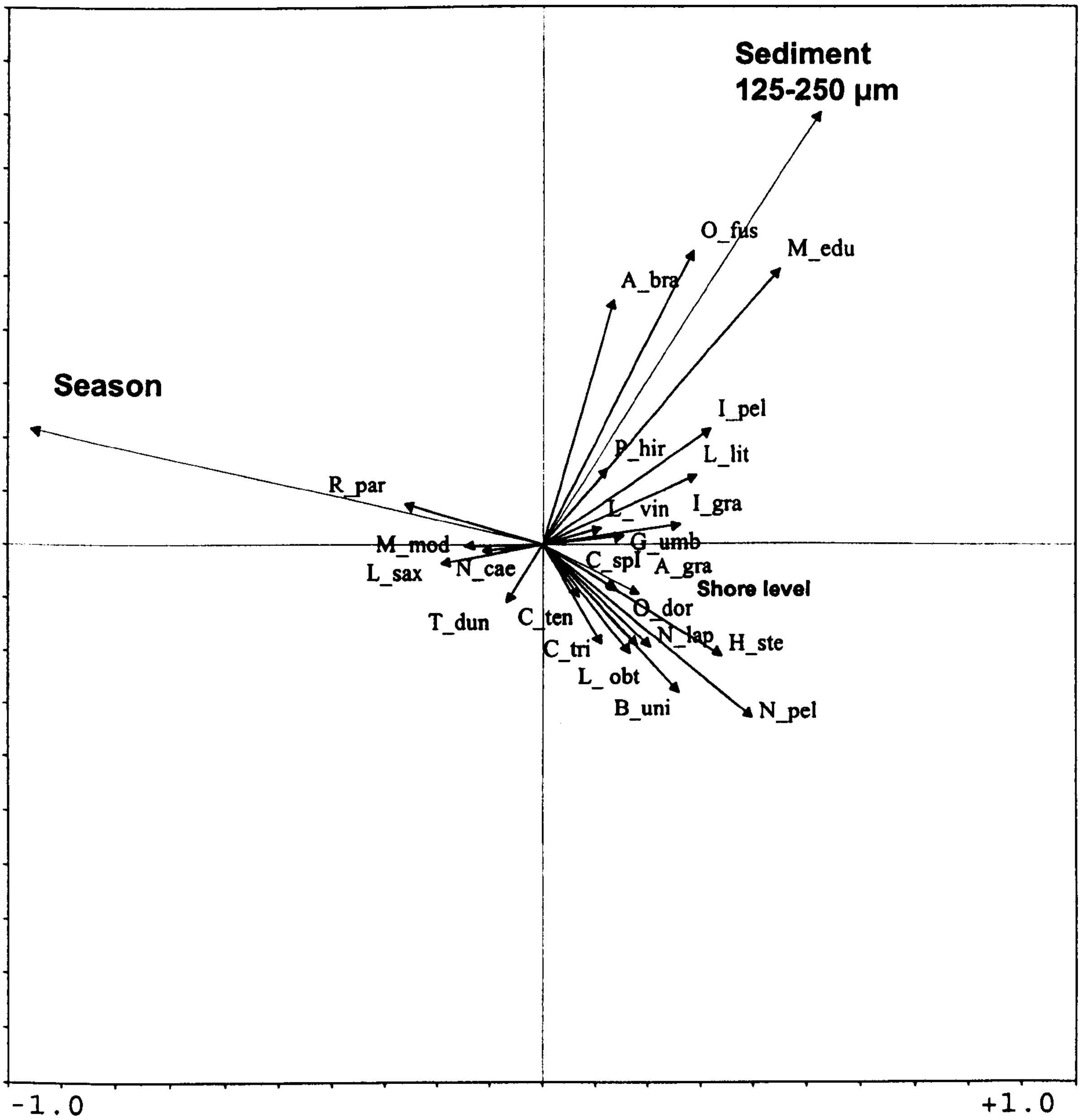
|  | Species | $r^2$ | Significant variables selected | Parameter | F-ratio | Probability |
|---|---|---|---|---|---|---|
| **(c) Site, seasonal and sediment factors** | *H. stebbingi* | 0.5450 | $b_0$ | 1.11227 | 38.85 | *** |
|  |  |  | Sediment 125µm – 250µm | 0.13614 | 2.55 | + |
|  |  |  | Sediment 250µm – 500µm | -0.3295 | 33.21 | *** |
|  |  |  | Sediment < 63µm | 0.5856 | 6.31 | ** |
|  |  |  | Shore | -0.213 | 17.32 | *** |
|  |  |  | Exposure | 0.1165 | 2.650 | + |
|  |  |  | Season | -0.2576 | 19.75 | *** |
|  | *I. pelagica* | 0.3310 | $b_0$ | 0.1333 | 6.85 | * |
|  |  |  | Sediment > 2mm | 0.0619 | 7.48 | ** |
|  |  |  | Shore | 0.0238 | 4.61 | * |
|  |  |  | Exposure | -0.0463 | 4.53 | * |
|  |  |  | Season | -0.0343 | 3.42 | * |
|  |  |  | Total Sediment | -0.02645 | 2.44 | + |
|  | *I. granulosa* | 0.5973 | $b_0$ | 0.3322 | 16.49 | *** |
|  |  |  | Sediment 63µm – 125µm | 0.1865 | 3.07 | + |
|  |  |  | Sediment < 63µm | -0.4861 | 17.13 | *** |
|  |  |  | Exposure | -0.181 | 27.05 | *** |
|  |  |  | Season | -0.1013 | 5.01 | * |
|  |  |  | Total Sediment | 0.0974 | 10.45 | ** |
|  | *T. dulongii* | 0.4198 | $b_0$ | 0.2755 | 6.97 | * |
|  |  |  | Sediment 250µm – 500µm | 0.2906 | 37.39 | *** |
|  |  |  | Sediment 125µm – 250µm | -0.1042 | 8.07 | ** |
|  |  |  | Sediment < 63µm | -0.4960 | 10.82 | ** |
|  |  |  | Shore | -0.0573 | 3.02 | + |
|  |  |  | Season | -0.0685 | 3.35 | + |
|  | *G. umbilicalis* | 0.2700 | $b_0$ | 0.0068 | 1 | - |
|  |  |  | Sediment > 2mm | 0.0180 | 18.04 | *** |
|  |  |  | Sediment < 63µm | -0.0236 | 3.70 | + |
|  |  |  | Exposure | -0.0109 | 5.30 | * |
|  | *B. unifasciata* | 0.2953 | $b_0$ | -0.0372 | 1.45 | - |
|  |  |  | Sediment 500µm – 1mm | 0.1539 | 17.82 | *** |
|  |  |  | Sediment 250µm – 500µm | -0.1455 | 15.76 | *** |
|  |  |  | Exposure | 0.0308 | 2.95 | + |
|  |  |  | Season | -0.0272 | 4.01 | + |
|  | *L. obtusata* | 0.545 | $b_0$ | 0.2975 | 75.05 | *** |
|  |  |  | Sediment > 2mm | 0.0253 | 3.15 | + |
|  |  |  | Sediment 63µm – 125µm | -0.1848 | 26.49 | *** |
|  |  |  | Exposure | -0.0313 | 4.76 | * |
|  |  |  | Season | -0.1286 | 48.19 | *** |
|  | *L. vincta* | 0.3063 | $b_0$ | 0.0011 | 0.06 | - |
|  |  |  | Sediment > 2mm | 0.0143 | 23.33 | *** |
|  |  |  | Sediment < 63µm | -0.0212 | 6.19 | * |
|  |  |  | Exposure | -0.0062 | 3.50 | + |
|  | *N. lapillus* | 0.5346 | $b_0$ | 0.2645 | 55.10 | *** |
|  |  |  | Sediment > 2mm | 0.057- | 14.77 | *** |
|  |  |  | Sediment 63µm – 125µm | -0.1466 | 15.48 | *** |
|  |  |  | Exposure | -0.0432 | 8.43 | ** |
|  |  |  | Season | -0.1168 | 36.94 | *** |

### 6.3.3 Faunal communities within the algal turfs

The RDA biplot (Fig. 6.3) showed the distribution of species with respect to the three significant ($P<0.05$) environmental variables; season, sediment fraction (125-250 m) and shore level. Season and sediment fraction (125-250 m) had a greater influence than shore level, and the three variables were almost orthogonal. The species were generally distributed in the direction of one or other of these environmental variables, forming three groups (1) associated with season- *Rissoa parva*, *Modiolus modiolus*, *Littorina saxtilis* and *Nephyts ceaca*; (2) associated with sediment (125-250 m)- *Acrocnidia brachiata*, *Owenia fusiformis*, *Mytilus edulis*, *Pilumnis hirtellus*, *Idotea pelagica*, and *Littorina littorea*; and (3) associated with shore level –*Capitella* sp I, *Cirriformia tentaculata*, *Amphitrite gracilis*, *Cingula trifasciata*, *Littorina obtusta*, *Nucella lapillus*, *Oerstedia dorsalis*, *Barleeia unifastica*, *Hyale stebbingi* and *Nereis pelagica*. A few species showed intermediate distributions –*Tanais dulongii* between seasons and shore elevation and *Lacuna vincta*, *Idotea granulosa* and *Gibbula umbilicalis* between sediment (125-250 m) and shore elevation.

Figure 6.3. RDA result shows distribution of associated animals and relationship between the animals and environmental conditions.

Species code: *Ampitrite gracilis* (A_gra), *Barleeia unifastica* (B_uni), *Capitella* Sp I (C_Sp I), *Cirriformia tentaculata* (C_ten), *Gibbula umbilacus* (G_umb), *Hyale stebbingi* (H_ste), *Idotea pelagica* (I_pel), *Idotea granulosa* (I_gra), *Lacuna vincta* (L_vin), *Littoina littorea* (L_lit), *Littorina obtusata* (L_obs), *Littorina saxtilis* (L_sax), *Modiolus modiolus* (M_mod), *Mytilus edulis* (M_edu), *Nephtys caeca* (N_cae), *Neris pelagica* (N_pel), *Nucella lapillus* (N_lap), *Oerstedia dorsalis* (O_dor), *Owenia fusiformis* (O_fus), *Pilumnus hirtellus* (P_hir), *Cingula trifasciata* (C_tri), *Rissoa parva* (R_par), *Tanais dulongii* (T_dul).



## 6.4 DISCUSSION

In contrast to the adjacent rock, *Osmundea* turf sustains an abundant fauna of small and juvenile animals. Although 33% of these are herbivores, they do not often consume the *Osmundea* plants. Like most of its close relatives, *O. pinnatifida* contains halogenated secondary metabolites that are known to repel potential grazers (Erickson,1983; Hay and Fenical, 1988). Indeed *Littorina littorea*, one of the commonest grazers on the intertidal zone, is known to shun *O. pinnatifida* in preference to other algae (Watson and Norton, 1985). However, since the turf-dwelling herbivores are not found outside the turf even when the tide is in, they must feed on microalgal epiphytes or diatoms that colonise the *Osmundea* fronds or on the sediment.

Unlike most intertidal microhabitats such as crevices, overhangs, and pools, which are permanent features of the topography, algal turfs are living habitats that vary seasonally in their structure. *O. pinnatifida* fronds develop during the late summer to form dense turfs by October then bleach and die-back early in the following summer. Thus, the seasonal changes in the turf structure influence the diversity and abundance of animals. Greater complexity of an algal stand supports a greater diversity of associated animals (Myers and Southgate, 1980; Davenport *et al.*, 1999). It is, therefore, not surprising that most of the species that inhabit the turf are more abundant in late autumn when the turf is at, or near, maximum development. However, *Rissoa parva* and *Modiolus modiolus* were the only exceptions because they reproduce and reach their maximum number during summer which explains their isolated position in the RDA result (Fig.6.3). *R. parva* favours a silty habitat, it breeds throughout the year but reaches its peak in summer; it could be washed from the turfs in the winter months (Fretter and Graham, 1962; Wigham, 1975; Southgate, 1982). Similar to *R. parva*, *M. modiolus* spawns continually throughout the year but the recruitment of small spats correspond to the increase in feeding condition in the spring and summer months (Jasim and Brand, 1989). Moreover, the juvenile has a higher growth rate in complete darkness or subdued light, compared with those in direct sunlight (Mohammed, 1987).

Physical factors such as exposure to desiccation are related to shore elevation and wave action and are known to control the distribution of the most abundant species on the shore (Lewis, 1964), but much less is known about the action of such constraints upon small or juvenile organisms where the microhabitat may be influential.

Although the fauna was sampled across the lower and upper limits of the *Osmundea* zone, only four animal species exhibited any significant effect attributable to shore level. This is probably because the effects of desiccation are greatly reduced within the turf, which even at its upper limit remains damp throughout the low tide period. When the tide is out, limpets cluster around the margin of the turf patches, presumably to benefit from the proximity to moisture. Even juvenile *Modiolus*, which as adults are confined to the sublittoral zone and suffer greatly when exposed to the air (Coleman and Trueman, 1971; Gillmor, 1982), colonise and, at least temporarily, survive within the turfs. Other turf dwellers such as *Nucella lapillus*, a common intertidal carnivore, are also found in rock crevices, which also provide a damp haven when the tide retreats, but they forage for barnacles on the open rock when submerged.

Animals on intertidal rocky shores are often controlled by the degree of wave exposure and may even be washed away by the surf (Lewis, 1964). However, within the microhabitat of algal turfs they are protected to some extent from wave action. It could, however, influence them indirectly through the amount of sediment accumulated within turfs. Greater water turbulence on more exposed shores (Denny 1988) can have conflicting effects. On the one hand wave action resuspends bottom sediment thereby increasing sediment supply, but on the other hand it can prevent sediment from settling, or even flush out previously trapped sediment from the turf. Once sediment is resuspended by turbulence, the larger particles will sink more rapidly than smaller ones and are therefore more likely to be trapped by the turf. Although the effects of water turbulence are complex, I found a greater abundance of sediment on the sheltered shore, which is likely to be supplied by an adjacent sandy beach, and much less sediment accumulation on exposed shores and at the lower shore levels, where there is greater water movement.

Sediment accumulation is not only influenced by wave action but also by season. On the shore, stormy weather during winter increased sediment loads five-fold in the water over the intertidal zone compared with summer loads (Jenkins, 1995). The interaction between the greater sediment supply and the longer and bushier fronds in winter explains the abundance of sediment trapped within the turfs. The great variations of sediment accumulation indicated substantial sediment movement within turfs. Sediment movement is a disturbance factor which reduces stability and limits the diversity of the animals both on rocky shores and in soft-bottom communities (Littler *et al.*, 1983; Snelgrove and Butman, 1994) as well as in *Osmundea* turfs.

Most the species found in the present study showed less relation to shore elevation and degree of wave exposure, than to sediment accumulation, which influenced 67% of the associated animal species. Generally, localised patches of sediment induce a spatial heterogeneity which increases species diversity within rocky shore communities (McQuaid and Dover, 1990). The sediment within *Osmundea* turfs provides a habitat suitable for a range of animals that require sediment, which is otherwise scarce elsewhere on the rocky shores we studied. I found that 46% of such animals are detritivores, including the polychaetes *Capitella* sp I and *Cirriformia tentaculata*, which are normally found in soft-sediment rather than on seaweeds.

Not surprisingly, we found most of the detritivores showed a strong correlation with sediment accumulation. An exception was the snail *Rissoa parva* which might be more influenced by its reproduction during summer and resulted in its greater density. Sediment provides food source for filter feeders and building material for tube-dwellers. The abundance of *T. dulongii*, a tube-building species, showed a strongly positive relationship with the abundance of the sediment fraction in the 250-500 μm range, which it uses for constructing its tube (White, 1987), and a tube-building polychaete *Owenia fusiformis* with the 125- 250 μm range.

Surprisingly, all the herbivores within the turfs also showed a strong relationship with sediment accumulation. Most herbivores were associated with coarse sediment (>2mm) and had a negative correlation with finer sediment (< 63-125 μm) except *Hyale stebbingi*. The coarser sediment might be expected to damage or even scour away the epiphytes that are a food source for the herbivores (D'Antonio, 1986). It is also possible that the sediment encourages the growth of microorganisms that serve as a food source for the mesograzers, which are unlikely to feed on *O. pinnatifida* itself. For example, some littorinid snails prefer to feed on microorganisms on the surface of rock, mud, sand or gravel if edible seaweeds are unavailable (Norton *et al.*, 1990). However, coarser sediment is likely to contain less nutrients for microorganisms (Snelgrove and Butman, 1994). Therefore, it is still unclear why such coarse sediment showed a positive relationship to the herbivores. Finer sediment reduces light and oxygen levels (Devinny and Volse, 1978), and I found anoxic conditions where very fine sediment had accumulated, creating an unfavourable habitat for most animals.

However, there must also be biotic interactions between the animals in this microcommunity. *Rissoa parva*, for example, is scarce in turfs on the sheltered shore where its predator *Pilumnius hirtellus* is present, and abundant on the wave exposed shore where turbulence eliminates *P. hirtellus*.

I conclude that the main structuring factors for most intertidal communities, desiccation and wave exposure, have less influence on the turf fauna, except in so far as they affect sediment accumulation. As for the biotic factors that are known to be influential on the shore, e.g. competition and predation, we have little knowledge of the conflicts within the crowded micro-world of algal turfs.

# CHAPTER 7

# GENERAL DISCUSSION

Turfs of red seaweeds are ubiquitous especially in warmer waters e.g. California, Brazil, Caribbean, West Africa and the tropical shore of Northern Australia (Kain and Norton, 1990). Clearly the mutual protection from desiccation and insolation provided by congested stands of low plants allows them to be more successful than individual plants. The same genera and even the same species of red algae are typical of turfs worldwide e.g. *Laurencia* (=*Osmundea*) spp., *Gelidium* spp, *Jania* spp., *Centroceras clavulatum* (C. Ag.) Montagne and *Hypnea musciformis* (Wulf) Lamouroux. I have attempted to investigate what properties these species have in common that might explain why they are successful turf dwellers. They seem to share similar characteristics such as the ability to regenerate after dying back, and a reliance on vegetative propagation. It is possible, however, to conclude that the success of *Osmundea* turfs results from the possession of organic halogen-containing compounds (Fenical, 1975; Erickson, 1983) which discourage herbivory, and a perennial stoloniferous holdfast system that can tolerate highly stressful conditions each year then regenerate upright branches when conditions are more favorable.

An excellent ecological strategy is to occupy space as low spreading turfs do. It is also seen in organisms as diverse as corals (e.g. Highsmith, 1980, Wallace, 1985), bryozoans (Winston and Jackson, 1984), sponges ( Wulff, 1986), encrusting red algae (Stewart, 1989) and some higher plants (Lovett Doust, 1981). It has two benefits: it pre-empts space thus excluding competitors (e.g. Hruby and Norton, 1979; Sousa, 1979; Lubchenco, 1980; Chapman, 1984; Dayton *et al.*, 1984; Keser and Larson, 1984; Benedetti-Checchi and Cinelli, 1992), and presents a surface that is unsuitable for the settlement of other species (Deysher and Norton, 1982;

Figueiredo *et al.*, 1997 and references therein). Indeed, the ability to 'repel-boarders' is an essential requirement for space-occupiers if they are not to become infested with epiphytes and rival species.

*Osmundea* can be so adept at monopolising space that it may form extensive turfs, but on many shores it occurs instead discrete patches. These turfs represent small 'islands' that provide a shelter for marine organisms and increase habitat diversity on rocky shores. Ecologists are interested not just in islands in the ocean but also 'islands' of distinct communities such as lakes or tide pools separated from similar communities (Begon *et al.*, 1986). The larger an island habitat the greater the species diversity it should have. This prediction has been tested for a variety of situations e.g. the diversity of fish in lakes (Tonn and Magnusson, 1982), birds on oceanic islets (Johnson, 1975), insects on mangrove islands (Simberloff, 1976) and various intertidal systems (Heck and Thoman, 1981; Orth *et al.*, 1984; Summerson and Peterson, 1984; Nelson and Bonsdorff, 1990; Thompson *et al.*, 1996). In all these cases it was found that species diversity is generally higher in habitats with high complexity compared to simpler habitats, rather than by size alone. This is because large areas are likely to have a greater variety of habitats, thus increasing exploitable resources such as space, food and refugia from predation. The *Osmundea* turfs are a complex matrix of irregular branching fronds with trapped sediment and low desiccation level, thus high species diversity is to be expected.

The species-area relationship (MacArthur and Wilson, 1967) that is found in seagrass habitats (Irlandi, 1997), and in terrestrial systems (Brittingham and Temple, 1983;

Andrén *et al.*, 1985; Small and Hunter, 1988; Adrén, 1992) might also fit the communities found in these monospecific turfs. Because there are little variations of frond length and density within these dense stands, different-sized turfs are unlikely to have heterogeneous microhabitats. There are, however, 'edge effects'. Smaller patches have a greater edge to area ratio than large patches, theoretically making prey more accessible to external predators, and thus decreasing the abundance and/or diversity of the resident fauna. Indeed, there was a higher faunal diversity in big patches of *Osmundea* than small ones (Stones, 2000).

Patch size not only influences animal diversity, but also expansion rate. Generally, the expansion rate of *Osmundea* patches is very small and is limited by seasonal factors and limpet grazing. Hughes (1989) suggested that in clonal organisms a big patch has slower growth than a smaller patch due to intraspecific-competition. This, however, is not always true if there is physical disturbance. My results showed that parts were commonly removed from smaller patches by severe wave during the autumn and winter more than from the bigger patches, also the smaller patches were more severely curbed by desiccation than the bigger ones in summer. Thus, the bigger patch has indirectly benefits from its size. However, Hughes' claim could be tested by monitoring the growth of *Osmundea* turfs of different sizes in laboratory conditions free from limiting factors. This might also provide some data that would allow the likely ages of the patches to be predicted.

So far, there are only two species in the closely related genus *Laurencia* whose life cycle has been completed in culture, *Laurencia brachyclados* Pilger and *L. pinnata*

Yamada (McDermid, 1990). McDermid attempted to study the life histories of all the *Laurencia* spp. in Hawaii, but only *L. brachyclados* was cultured successfully. She suggested that maybe *Laurencia* species must live for many years before reaching a reproductive state, or need specific requirements for reproductive development such as a shock or a particular change in environmental conditions. A combination of culturing *Osmundea* patches and monitoring their spore reproduction in the laboratory under a variety of conditions would provide a better understanding of their reproduction e.g. when do the plants first start to produce spores and is there a relationship between age and the ability to reproduce?

The laboratory work on the effects of irradiance and desiccation on photosynthesis and respiration was not merely relevant to the current study, *Osmundea* may provide a useful subject for general physiological and ecological investigations. Unlike many seaweeds, *Osmundea* fronds are small, and therefore easy to handle and manipulate experimentation. Pieces of larger plants are habitually used in laboratory experiments, but mutilating them in this way is likely to alter their physiological responses (Littler and Littler, 1985). Because of their small size, *Osmundea* fronds could be used whole.

Also, I noticed that there are few epiphytes associated with the *Osmundea* fronds. Epiphytes are known to retard photosynthesis by shading the 'host' fronds and competing for their nutrients (Pickering *et al.*, 1993; Friedlander and Levy, 1995; Friedlander *et al.*, 1996). The lack of epiphytes would be useful in field experiments were it would be difficult or even impossible to remove epiphytes completely.

Furthermore, because of the reliance on vegetative reproduction, there is a replication of genotype, as in other clonal organisms (Silander, 1985); in other words there is no genetic variation among fronds and, probably, some turfs. All these characteristics indicate that *O. pinnatifida* would be ideal material for studies on the physiology of algae in particular and plants in general.

*Osmundea* turfs are a fascinating system which is well adapted to the harsh world of the rocky shore. It is an intertidal organism but could be utilised to study ecology both in terrestrial and marine ecosystems.

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