# Spatial variability in the epiphytic algal assemblages of *Zostera marina* seagrass beds

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ABSTRACT: Within-bed variation of epiphytic algal assemblages was studied in 3 *Zostera marina* beds around Plymouth Sound (Devon, United Kingdom) in order to determine if distance from edge of bed affected the assemblage composition. Replicate seagrass samples were taken at 0, 1, 3 and 6 m along a transect running from the edge of each bed. Individual epiphytes were enumerated and placed into 6 'functional' groups: filamentous, foliose, corticated filamentous, corticated foliose, saccate and coralline. The abundance of each functional group did not vary with distance into each bed, nor was it related to measures of seagrass architecture or potential grazing pressure from gastropods. A positive relationship between amphipod abundance and total epiphytes suggest these crustaceans are influenced by epiphytes as an available substrate rather than exerting a grazing effect. Differences amongst beds, however, were evident for filamentous, corticated filamentous and coralline functional groups. These groups comprised 99% of all epiphytes, resulting in the total algal abundance being different amongst beds. Similarly, the assemblage composition of the epiphytes was consistent within each bed, but differed amongst all 3 beds. Overall, therefore, epiphytic abundance and composition was not affected by distance from the edge of the bed, seagrass architecture or grazing pressure within the bed, but existence of within-bed variation cannot be completely ruled out due to the comparatively low power of the analysis. The only significant variation occurred at the amongst-bed level, probably due to variations in large-scale factors.

KEY WORDS: Epiphytes · Algae · Assemblage composition · Functional groups · Edge effects · Algal community

## INTRODUCTION

Epiphytic algae utilise the surface of seagrass blades as a substrate for growth, the seagrass providing a habitat for increased light availability and water flow that allows optimum growth and supply of nutrients (Nelson & Waaland 1997). Epiphytic algae can comprise between 24 and 67% of the total biomass of a seagrass bed (Penhale 1977, Kitting et al. 1984, Morgan & Kitting 1984, Nelson & Waaland 1997); primary production by epiphytes can be as low as 18% of the total bed (Penhale 1977), but can be so high that it exceeds that of the seagrass (Fry 1984). The epiphytic assemblage on seagrasses often consists of a large number of species displaying a variety of morphologies (Milchakova 2000, Vanderklift & Lavery 2000), so consequently epiphytic algal assemblage composition can be highly variable on both spatial (Kendrick & Burt 1997, Lavery & Vanderklift 2000a,b, Milchakova 2000, Vanderklift & Lavery 2000) and temporal (Alcoverro et al. 1997, Kendrick & Burt 1997, Reyes & Sanson 1997, Cebrian et al. 1999, Milchakova 2000) scales.

Seagrass beds have long been recognised as areas of high faunal diversity and abundance compared with adjacent areas of bare soft sediment (Connolly 1994, Bostrom & Bonsdorff 1997, Sheridan 1997). The increase in diversity has been related to many aspects of the seagrass habitat, such as shoot density (Webster et al. 1998), seagrass biomass (Heck & Orth 1980, Attrill et al. 2000) and the structural complexity of the bed

(Tolan et al. 1997). In these studies numerous physical measurements of the seagrass bed have been taken (e.g. shoot density, leaf length, sediment grain size) and compared with the associated faunal assemblage. Epiphytic algae biomass is often included within these characteristics, although there is generally no further indication of the types of algae and their assemblage composition within this category. The categorisation of epiphytic algae into one single figure, based solely on biomass, is also common in studies of the ecology of seagrass beds in relation to food webs and energy pathways (Penhale 1977, Morgan 1980, Fry 1984, Kitting et al. 1984, Fong et al. 2000, Hily et al. 2000), and studies into primary production and subsequent levels of productivity (Coleman & Burkholder 1994, Lin et al. 1996, Nelson & Waaland 1997).

Categorising epiphytic algae into a single group will disguise the variation that may occur within and amongst seagrass beds, and potentially confound investigations because of sampling artefacts associated with the species-area relationship (Attrill et al. 2000). Patterns of epiphytic algal assemblage composition have, therefore, largely been left unexplored. The lack of knowledge about different types of algae is not surprising, as the work involved in identification and measurement is considerable, and is not usually involved in the primary aims of the generally animal-centric studies. Despite this, a few papers have identified epiphytic algae to species level (e.g. Attrill et al. 2000) or categorised algae into functional groups (e.g. Lavery & Vanderklift 2000a). The use of algal functional groups has been primarily used to examine the feeding behaviour and preferences of herbivorous macrofauna in a seagrass bed (e.g. Morgan & Kitting 1984). However, the method provides a useful, prag-matic approach for the study of patterns in epiphytic algal assemblage composition.

The difference in epiphytic assemblage structure within and amongst beds has received relatively little attention (Kendrick & Burt 1997, Milchakova 2000, Vanderklift & Lavery 2000); in particular, investigations of any changes in assemblage composition that might occur in the vicinity of the seagrass-bed boundary appear to be lacking (but see Bell et al. 2001, Bowden et al. 2001). The influence of edge effects on assemblage structure in terrestrial patchy habitats has a long tradition and has revealed interesting ecological insights (e.g. Soulé 1986, Renhorn et al. 1997, Fagan et al. 1999). The aim of the present study is to test the null hypothesis that epiphyte assemblage structure does not vary with distance from the edge of a seagrass bed.

## MATERIALS AND METHODS

**Field sampling.** Three seagrass beds were selected for sampling around the area of Plymouth Sound, Devon, United Kingdom (Fig. 1). All 3 seagrass beds are broadly comparable in that they are all composed of *Zostera marina* (L.), cover the same depth range (2 to 12 m), are of similar size (30 to 50 m in diameter) and are situated in extreme outer-estuary locations with minimal influence of reduced salinity. The 3 sites were Cawsand Bay on the western side of Plymouth Sound (50° 20.0' N, 4° 11.5' W), Cellars Cove at the mouth of the Yealm estuary (50° 18.5' N, 4° 04.0' W), and Asia Shoal, north of Drakes Island, Plymouth Sound (50° 21.5' N, 4° 09.3' W). Whilst the Yealm site is situated in an estuary mouth, the river flow here is very small and the site is effectively a marine location comparable with the sites in Plymouth Sound.

A preliminary survey using a frame-mounted drop-down video camera was undertaken on 13 September 2000 in order to determine the position and extent of the seagrass beds and the location of a suitable bed edge from which transects could be established. At each site, a transect was set perpendicular to the edge at a constant depth of 6 m (mid-tide). Along this transect, 3 replicate samples were taken at 0, 1, 3, and 6 m from the edge of the bed. Samples were collected using SCUBA, and 1 site was sampled per day between 18 and 20 September 2000. Samples of the above-ground seagrass were collected from within plastic rings (diameter
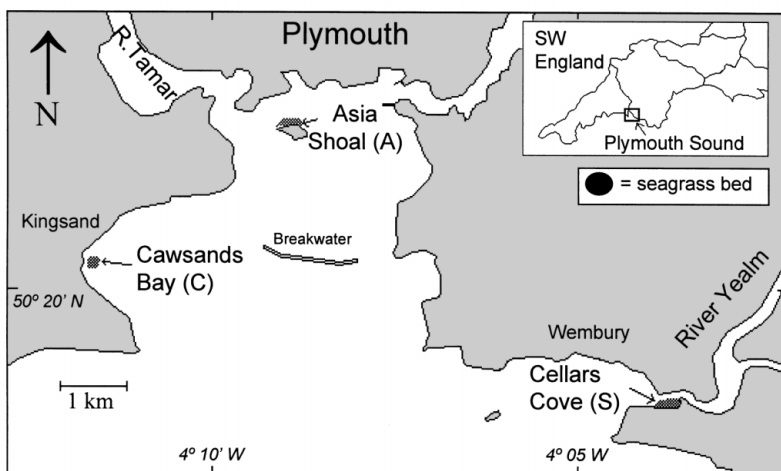


Fig. 1. The locations of the 3 *Zostera marina* sites in relation to Plymouth Sound, UK

24.5 cm, area 0.047 m$^2$) onto which a 500 µm mesh bag was attached. The rings were placed haphazardly over the seagrass, up to 1 m perpendicular to each specific distance on the transect. All leaves within the ring were cut at their base level with the substratum, floated into the mesh bag, the ring removed and the bag shut to contain the sample. On the diving vessel, each sample was transferred to a labelled plastic bag and preserved in 99% alcohol.

**Laboratory analysis.** Plant architecture was quantified by counting the number of seagrass shoots and leaves present in each sample, and measuring the length and width of each seagrass leaf to the nearest mm with a tape measure (allowing total leaf area to be calculated). Epiphytic algae were identified as belonging to the functional groups proposed by Lavery & Vanderklift (2000a). Only 6 of these authors' 8 functional groups were used: filamentous, foliose, corticated filamentous, corticated foliose and saccate; articulated coralline and encrusting coralline were combined into a single coralline group for simplicity. Cyanobacteria were omitted due to enumeration problems that would have been presented due to their size. Counting of individuals was completed under 40× magnification, and epiphytes counted in 10 cm segments from the base. Following algal identification and removal, total above-ground seagrass biomass (fresh weight) was recorded.

Prior to epiphyte identification and enumeration, seagrass samples were washed through a 500 µm sieve, all species of gastropod and amphipod being removed from the residue and their abundance on each seagrass plant counted. Such counts were made to provide an analogue of potential grazing pressure, these groups being the main grazers on seagrass epiphytes present in *Zostera marina* beds (Thom et al. 1995, Kinlan et al. 1997, Nelson 1997, Kharlamenko et al. 2001).

**Data analysis.** To allow analysis of the epiphytic algal abundance and assemblage structure, the number of individuals from each functional group per cm of seagrass leaf was calculated by dividing the total abundance on the leaf sample by its total length. Resulting data were analysed by both univariate and multivariate statistical techniques. ANOVA (GMAV5 package) was performed on total and functional group abundances using a 2-factor orthogonal model, in which within-bed location is a fixed factor and bed is treated as a random factor. All data were tested using Cochran's $C$-test and transformed, $\ln(x + 1)$, where necessary to correct for departures from normality. For all analyses the level of significance was set at $\alpha = 0.05$. For significant results, Student-Newman-Keul's multiple range tests were employed in order to assess the significance of differences between pairs of sites.

Linear regression was used to investigate the relationship between epiphyte abundance and possible controlling variables such as plant architecture (number of shoots, number of leaves, seagrass area, seagrass biomass) and grazer abundance. All data were tested for normality before analysis (Shapiro-Wilk statistic) and transformed where necessary. The residuals of significant regressions were checked for normality (Shapiro-Wilk) and heteroscedasticity (examination of standardised residual plots).

The PRIMER software package (Clarke & Warwick 2001) was used for multivariate analysis of the assemblage structure of the epiphytic algae. Data were double square-root-transformed (to reduce the influence of dominant taxa) and the Bray-Curtis index used to construct the similarity matrix. Similarities in epiphyte assemblage composition were displayed by constructing a dendrogram and ordination from the similarity matrix. The dendrogram was constructed using agglomerative, hierarchical clustering with group-averaging, whilst ordination used non-metric multidimensional scaling (n-MDS). Significant differences in assemblage composition between the *a priori* groupings of samples were investigated using a 2-way analysis of similarity (ANOSIM, Clarke & Green 1988), the main species contributing to any dissimilarity between groupings being assessed using SIMPER (similarity percentages, Clarke 1993). To investigate which measured environmental variables (including grazer abundances) best explained the observed assemblage composition, the BIOENV procedure was utilised (Clarke & Ainsworth 1993).

## RESULTS

Average epiphytic abundance over all seagrass samples was 4.19 ind. cm$^{-1}$. However, there was a large variation in the abundance of each functional group (Fig. 2). Filamentous algae were, on average, the most abundant with 2.03 ind. cm$^{-1}$, followed by encrusting coralline algae with 1.44 ind. cm$^{-1}$. Cawsand Bay had the lowest overall abundance of algae (1.21 ind. cm$^{-1}$), and Cellars Cove had the highest (7.96 ind. cm$^{-1}$).

For both total abundance and abundance of each functional group, there was no significant difference in abundance with distance into the bed (Table 1). Amongst-bed variation, however, was significant for 3 functional groups: corticated filamentous, filamentous and coralline algae (Table 1). As these 3 groups made up 99% of all epiphytes, the total abundance of algal epiphytes amongst beds is also significantly different (all $p < 0.01$). There were no significant differences in seagrass architectural parameters or gastropod abun-
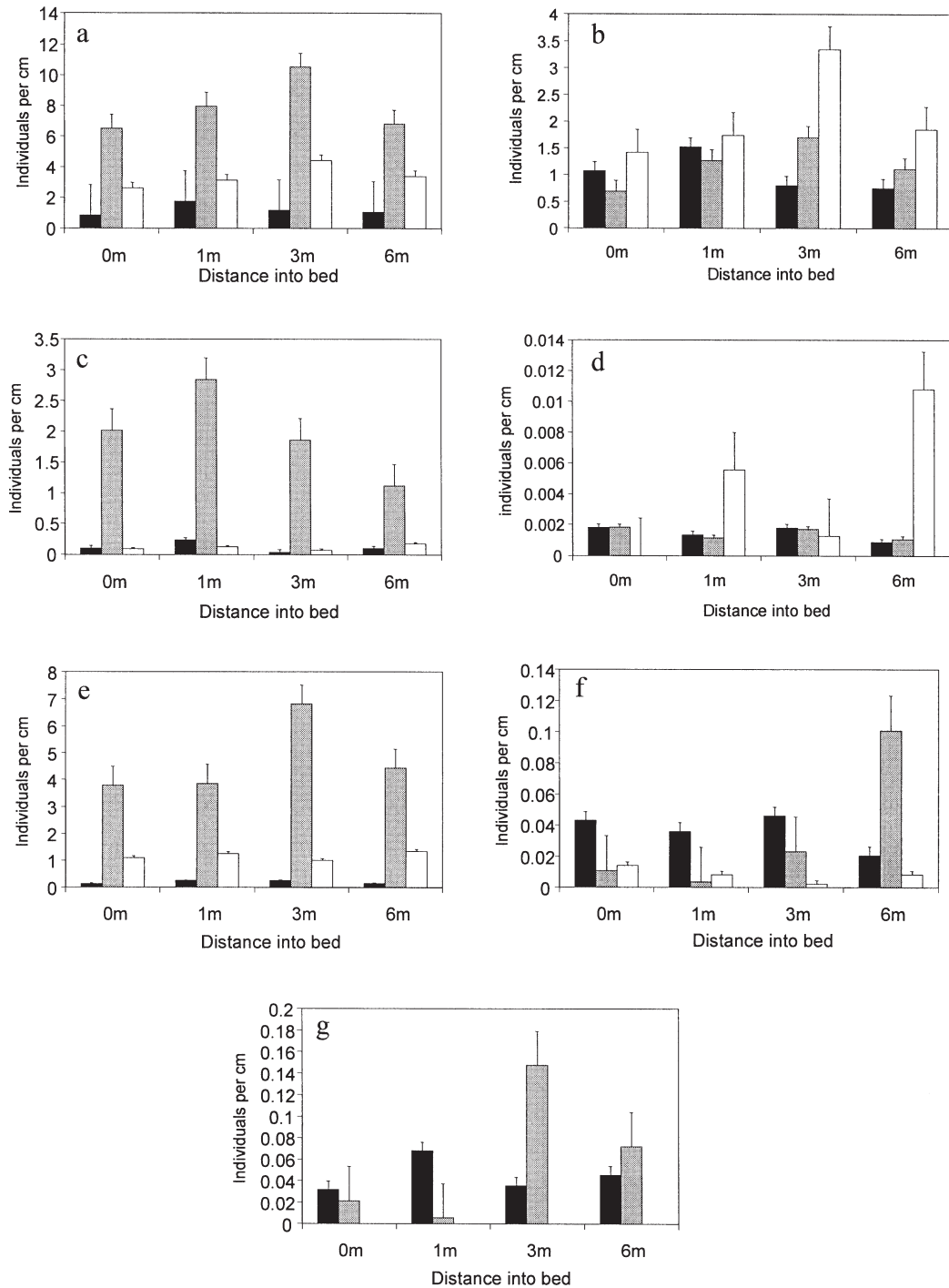
Fig. 2. *Zostera marina*. Abundance of each functional group at distance within and amongst *Zostera marina* beds. Total number of (a) epiphytes, (b) coralline algae, (c) corticated filaments, (d) corticated foliose, (e) filaments, (f) foliose, and (g) saccate. Cawsand Bay = dark shading, Cellars Cove = light shading and Asia Shoal = clear

dance within or amongst beds (all p > 0.10, Table 2). Cawsand Bay, however, had a significantly lower abundance of amphipods than the other 2 sites (Table 2). No significant relationships were apparent between any aspect of epiphyte abundance and either seagrass architectural measures (linear regressions: all p > 0.20) or gastropod abundance (p = 0.511), but a positive relationship with amphipod abundance was apparent (both variables transformed $\ln(x + 1)$, $r^2 = 0.338$, p < 0.001, all residuals normal and homoscedastic).

Table 1. Results of ANOVA on abundance of epiphyte functional groups within and amongst seagrass *Zostera marina* beds. *Ln* after functional type indicates (ln + 1) transformation required. Corticated foliose algae were in low abundance, with all MS < 0.0001, therefore not reported. Amphipod abundance was the only complementary variable varying significantly either within or amongst beds, therefore is reported

| Source | df | MS | *F* | p |
|---|---|---|---|---|
| Saccate | | | | |
| Site | 2 | 0.0122 | 2.08 | 0.147 |
| Distance | 3 | 0.0033 | 0.68 | 0.594 |
| Site × Distance | 6 | 0.0048 | 0.82 | 0.562 |
| Residual | 24 | 0.0059 | | |
| Foliose | | | | |
| Site | 2 | 0.0030 | 1.13 | 0.340 |
| Distance | 3 | 0.0012 | 0.47 | 0.713 |
| Site × Distance | 6 | 0.0026 | 1.00 | 0.451 |
| Residual | 24 | 0.0026 | | |
| Filamentous | | | | |
| Site | 2 | 67.98 | 48.73 | <0.001 |
| Distance | 3 | 1.872 | 0.88 | 0.503 |
| Site × Distance | 6 | 2.131 | 1.53 | 0.212 |
| Residual | 24 | 1.395 | | |
| Coralline (*Ln*) | | | | |
| Site | 2 | 0.6742 | 7.64 | 0.003 |
| Distance | 3 | 0.1262 | 1.87 | 0.236 |
| Site × Distance | 6 | 0.0675 | 0.77 | 0.604 |
| Residual | 24 | 0.0883 | | |
| Corticated filamentous | | | | |
| Site | 2 | 13.58 | 17.19 | <0.001 |
| Distance | 3 | 0.5728 | 1.19 | 0.390 |
| Site × Distance | 6 | 0.4810 | 0.61 | 0.721 |
| Residual | 24 | 0.7900 | | |
| Total abundance | | | | |
| Site | 2 | 5.294 | 77.87 | <0.001 |
| Distance | 3 | 0.0994 | 1.92 | 0.227 |
| Site × Distance | 6 | 0.0517 | 0.76 | 0.608 |
| Residual | 24 | 0.0680 | | |
| Amphipod abundance | | | | |
| Site | 2 | 14.39 | 15.68 | <0.001 |
| Distance | 3 | 0.8234 | 2.59 | 0.148 |
| Site × Distance | 6 | 0.3182 | 0.35 | 0.905 |
| Residual | 24 | 0.9183 | | |

Table 2. Mean values (±SE) for seagrass *Zostera marina* architectural parameters and potential grazer abundance for each site (per sample, 0.047 m²). Differences within and amongst beds were insignificant for all parameters except amphipod abundance (2-way ANOVA, all p > 0.10). n = 12 for all parameters. *Significantly different from other sites (SNK test)

| Parameter | Cawsand Bay | Cellars Cove | Asia Shoal |
|---|---|---|---|
| Number of shoots | 4.58 ± 1.11 | 3.25 ± 0.71 | 4.00 ± 0.72 |
| Leaves per shoot | 3.63 ± 0.15 | 4.03 ± 0.23 | 3.82 ± 0.15 |
| Total leaf area (cm²) | 313.33 ± 87.91 | 193.41 ± 36.23 | 399.32 ± 80.59 |
| Total plant biomass (g) | 8.32 ± 2.59 | 7.70 ± 2.67 | 15.68 ± 3.23 |
| Gastropod abundance | 3.00 ± 0.68 | 5.50 ± 1.40 | 5.33 ± 1.81 |
| Amphipod abundance | 1.08 ± 0.34* | 16.42 ± 4.75 | 17.08 ± 3.53 |

Multivariate analysis of the assemblage composition supported the results of the ANOVA. ANOSIM results indicated that there was no significant difference in composition between within-bed locations (r = −0.031, p = 0.655), whilst differences in epiphyte assemblage composition between each seagrass bed were significant (r = 0.943, p < 0.001). The dendrogram and n-MDS ordination of the data clearly illustrate the patterns in assemblage composition, with samples from the sites forming 3 separate groupings in which no sub-grouping by distance from bed edge is apparent (Fig. 3). The Cellars Cove site (Yealm estuary) is clustered with one of the Plymouth Sound sites, the other site being in a separate cluster, suggesting that environmental conditions in the mouth of the Yealm do not result in a vastly different assemblage from those in Plymouth Sound. SIMPER analysis indicated that different functional groups contributed most to dissimilarity between each pair of beds (Table 3), reflecting the overall differences in assemblage composition amongst beds. None of the measured environmental parameters explained the assemblage patterns, the only measured variable that demonstrated a weak correlation being amphipod abundance (BIOENV analysis, r = 0.142), reflecting the lower numbers recorded at Cawsand Bay (all other variables, r < 0.06).

## DISCUSSION

The abundance and composition of the sampled epiphytic algal assemblages showed no pattern of distribution or gradient of change relating to increasing distance from the edge of the seagrass bed and, additionally, no relationship with either measure of plant architecture or gastropod abundance. Amongst-bed variation of epiphytic algae was considerable, despite the fact that the sites sampled were chosen for their apparent comparability. Clearly, failing to obtain a significant within-bed effect may be due to insufficient levels of replication at this scale, in what is potentially a highly variable system. Therefore, whilst it can be positively stated that amongst-bed variations were more pronounced than within-bed variations (which were not significant), the existence of within-bed patterns cannot be completely ruled out in the present study due to comparatively low power of the analysis. Nevertheless, the magnitude of the amongst-bed differences, when compared with within-bed differences, was unexpected, as the abun-

dance and composition of epiphytic algae can potentially be influenced by a number of factors that have been shown to vary depending upon location within a seagrass bed.

Within a seagrass bed, biological factors such as herbivory are potentially the most important in structuring



Fig. 3. *Zostera marina.* (a) Dendrogram of epiphyte assemblage data based on the Bray Curtis similarity index. Sample codes: C = Cawsand Bay, S = Cellars Cove and A = Asia Shoal. 0, 1, 3 and 6 correspond to distances (m) into bed. A, B and C represent the 3 replicates at each distance. (b) MDS ordination of the same data, see dendrogram for codes

algal epiphyte assemblages. Many species of herbivore feed directly on the epiphytic algae as opposed to the seagrass (Thayer et al. 1978, Zimmerman et al. 1979, Morgan 1980, Fry 1984, Kitting et al. 1984, Morgan & Kitting 1984, Jernakoff & Nielson 1997, Hily et al. 2000), and the concentration of this herbivory has been shown to alter the abundance and community structure of the epiphytic algae (Alcoverro et al. 1997, Jernakoff & Nielsen 1997, Fong et el. 2000). In an analogue of predation impact (Irlandi 1997, Bologna & Heck 1999) it could be hypothesised that grazing pressure, and thus epiphyte algal assemblage composition, at the edge of beds may be different to that at further distances into the bed. In the present study, we attempted to give a measure of potential herbivory by enumerating the group of main algal grazers within these *Zostera* beds, namely the gastropods and amphipods. From our results, there were no significant differences in gastropod abundance within, or amongst, beds, the latter in contrast to the epiphyte results. However, gastropod grazing may potentially be affecting epiphyte abundance at a smaller scale (i.e. plant, Fong et al. 2000), but there was no significant linear relationship between epiphyte and gastropod abundance. Conversely, there was a significant positive relationship between amphipod abundance and total epiphyte density, the low levels of epiphytes in Cawsand reflected in significantly low amphipod abundance at this site. The positive nature of this relationship suggests that the amphipods are responding to the additional available habitat (Attrill et al. 2000) rather than exerting a grazing effect on the epiphyte assemblage, the density of amphipods being relative to the amount of algae present. Certainly, from our
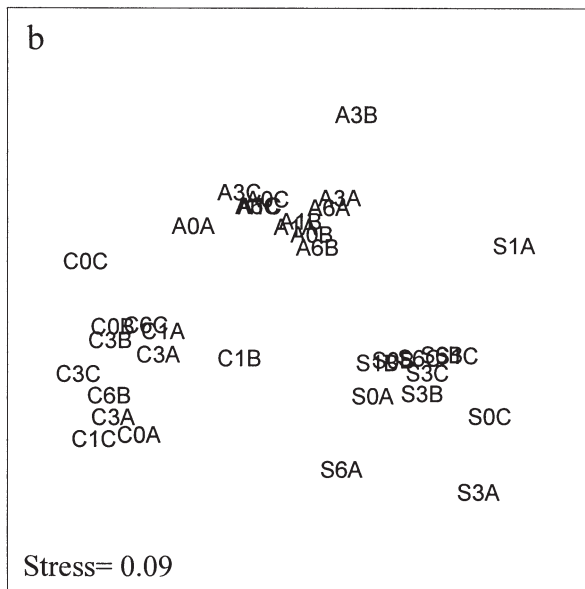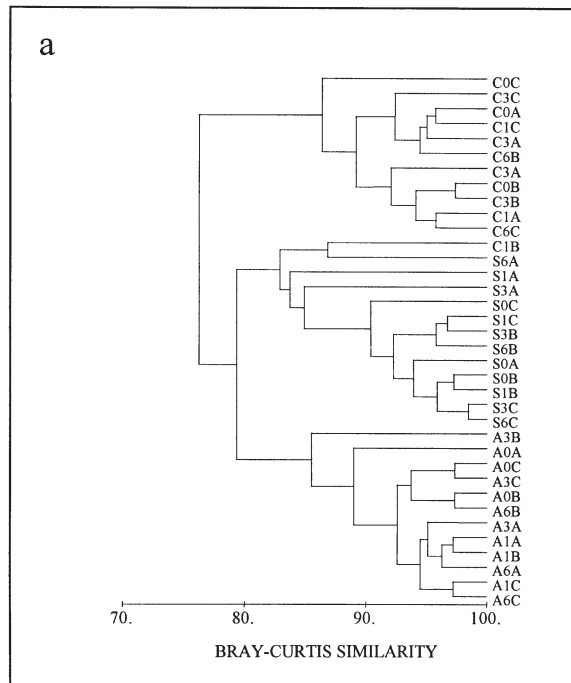
Table 3. Results of SIMPER analysis, highlighting the 3 epiphyte algal functional groups contributing most to dissimilarity between assemblage composition in each pair of seagrass *Zostera marina* beds. Data were 4th-root-transformed prior to analysis

| Bed pair<br>Algal functional group | Average<br>term | %<br>contribution |
|---|---|---|
| **Cawsand vs Cellars Cove** | | |
| Filamentous | 10.84 | 38.71 |
| Corticated filamentous | 8.21 | 29.35 |
| Foliose | 2.76 | 9.87 |
| **Cawsand vs Asia Shoal** | | |
| Saccate | 7.07 | 29.40 |
| Filamentous | 6.17 | 25.66 |
| Encrusting | 3.75 | 15.59 |
| **Cellars Cove vs Asia Shoal** | | |
| Corticated filamentous | 7.85 | 31.12 |
| Filamentous | 5.56 | 22.04 |
| Saccate | 4.78 | 18.96 |

results there is no evidence that herbivore pressure was affecting the epiphyte assemblage over the spatial scale examined, although potential grazing pressure by alternative herbivores which were not enumerated (e.g. fish) remains a possibility.

Environmental factors in the seagrass bed can also influence the epiphytic assemblage, such as light levels (Ruiz & Romero 2001) and small-scale hydrodynamics (Kendrick & Burt 1997). Light levels and water current characteristics were not directly assessed in the present study for they are difficult and costly to effect in practice; however, the measures made of plant architecture can be used as proxy indicators in order to interpret the results. It is feasible that epiphytes at the edge of beds may experience less shading than those in the middle, particularly if there are changes in self-shading concomitant with variations in seagrass physical architecture with distance from the bed edge (Cebrian et al. 1999). At the study sites, however, neither shoot density nor number of leaves exhibited any significant increase or variation along the sample transect. Thus, any associated light variability does not appear to be influencing the amount, or composition, of the epiphyte assemblage within the seagrass beds. Similarly, any reductions in water flow that occur with increasing distance into a seagrass bed (Fonseca & Bell 1998), and with changes in shoot/leaf density (Eckman 1987), are not reflected in any observable differences in the epiphytic algae assemblage. Clearly, further studies using direct measures of light and current are required before any firm conclusions can be drawn about the apparent lack of influence of these variables on assemblage composition within a seagrass bed.

However, the similarity of the epiphytic assemblage observed within the seagrass beds of Plymouth Sound is consistent with some results from the few relevant recent studies. Vanderklift & Lavery (2000), using data that held shoot density constant, found that within-bed samples separated by 10s of cm displayed a homogenous algal epiphyte assemblage structure. Nonetheless, differences between assemblages 1 to 10 m apart were observed in the majority of samples analysed from within the 2 beds studied (Vanderklift & Lavery 2000). Attrill et al. (2000) found that epiphytic algal assemblage composition within a single seagrass bed was not significantly different, despite sample groups being taken from areas of differing shoot density (10s of m apart).

Amongst-bed differences in epiphytic algae of seagrass, as observed in the present study, have been found in previous studies on *Posidonia* species. Two seagrass beds, 8 km apart, were examined by Kendrick & Burt (1997), who found distinct epiphytic assemblages at each site. However, the 2 sites studied

contrasted in environmental setting, one being offshore-exposed and the other inshore-protected (Kendrick & Burt 1997). In a study on a similar scale to the present one, but which concerned a more morphologically complex seagrass species in oligotrophic waters, Vanderklift & Lavery (2000) found differences in epiphyte assemblage structure between 2 areas of seagrass on the same sand bank that were only 2 km apart. Despite selecting for seagrass beds of a similar physical arrangement in relatively close proximity (4 to 9 km apart) for the present study, it appears that environmental conditions at each site were probably dissimilar enough to result in marked amongst-bed differences in epiphytic algal assemblage composition. Potential controlling factors include nutrient levels, light levels (through variations in turbidity) and particularly local hydrodynamics influencing the settlement and dispersal of algae (Coleman & Burkholder 1994, Harwell & Orth 1999, Moore & Wetzel 2000). If the amongst-site variation in epiphytic algae is due to a single factor, or more likely a combination of many, it is impossible from this study to state categorically what these factors are. Similarly, studies which have examined spatial patterns of macroinvertebrate assemblages associated with seagrass beds have found that within-bed differences in composition are minor compared to those observable amongst beds. Even when beds are separated by only kilometres in areas of apparently similar environmental conditions, the factors responsible for the distinctions remain largely unidentified (Turner et al. 1999, Bowden et al. 2001). Therefore, the amongst-bed factors appear to have a far greater influence on assemblage composition than variation in location from the edge of a bed, and further research addressing variability at this scale should be a priority in seagrass research.

## CONCLUSIONS

The findings of the present study support the few previous investigations in this area, which have concluded that epiphytic algal abundance and distribution is not a constant factor amongst seagrass beds. More importantly, however, the results indicate that the within-bed algal epiphyte assemblage may potentially be considered uniform, with no edge effects being detectable for epiphyte assemblages at the scale of metres, though further studies incorporating seasonal fluctuations and increased replication at the lowest scale would be needed to confirm this. The causes of the larger-scale variation are likely to be related to a number of environmental factors, which to varying degrees will influence the success of epiphytic species in colonising (e.g. hydrography) and persisting (e.g.

grazing pressure) on seagrass blades. The scale of this environmental variation would appear to be the factor best explaining the consistency in abundance and composition of epiphytic algae within a seagrass bed. Over the distance of a single bed, any variation or gradient in these conditions will be very small or negligible, and does not produce changes in the epiphytic assemblage, resulting in the homogenous assemblage found within each of the 3 beds examined, although again this requires further work to confirm the lack of within-bed patterns. Seagrass beds separated by several kilometres, as in this study, will apparently be subjected to unique environmental conditions resulting in an equally distinct epiphytic algae assemblage. Thus, the results of this study provide further evidence for the importance of scale when devising and analysing experiments on seagrass beds. This consistency across independent studies is an important result for future examinations of spatial pattern in epiphytic algal assemblages. The results of this study preliminarily suggest that epiphytes of a single seagrass bed can be treated justifiably as a homogenous assemblage, whilst the assemblages of separate beds should be considered *a priori* as being discrete.

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