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# Changes in habitat complexity negatively affect diverse gastropod assemblages in coralline algal turf

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**Abstract** The physical structure of a habitat generally has a strong influence on the diversity and abundance of associated organisms. I investigated the role of coralline algal turf structure in determining spatial variation of gastropod assemblages at different tidal heights of a rocky shore near Sydney, Australia. The structural characteristics of algal turf tested were frond density (or structural complexity) and frond length (the vertical scale over which structural complexity was measured). This definition of structural complexity assumes that complexity of the habitat increases with increasing frond density. While frond length was unrelated to gastropod community structure, I found significant correlations between density of fronds and multivariate and univariate measures of gastropod assemblages, indicating the importance of structural complexity. In contrast to previous studies, here there were negative relationships between the density of fronds and the richness and abundance of gastropods. Artificial habitat mimics were used to manipulate the density of fronds to test the hypothesis that increasing algal structural complexity decreases the richness and abundance of gastropods. As predicted, there were significantly more species of gastropods in loosely packed than in tightly packed turf at both low- and mid-shore levels. Despite large differences between gastropod assemblages at different tidal heights, the direction and magnitude of these negative effects were similar at low- and mid-shore levels and, therefore, relatively independent of local environmental conditions. These novel results extend our previous understanding of the ecological effects of habitat structure because they demonstrate possible limitations of commonly used definitions of structural complexity, as well as distinct upper thresholds in the relationship between structural complexity and faunal species richness.

**Keywords** Habitat structure · Structural complexity · Species richness · Rocky shore

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## Introduction

It is well known that the physical characteristics of habitats often affect community structure (MacArthur and MacArthur 1961; Lawton 1983; Ellner et al. 2001). Generally, as the physical structure of a habitat increases in complexity, the diversity of associated organisms also increases (Kohn and Leviten 1976; Heck and Wetstone 1977; Downes et al. 1998). One common explanation for this pattern is that greater amounts of structure provide more available surface area and therefore greater resources (for review, see Connor and McCoy 1979). Often tied to this explanation is the idea that an increase in available area and/or diversity of structures increases the number of possible habitats or niches (MacArthur and MacArthur 1961; Schoener 1974). The physical structure of habitats may also affect biological processes and environmental factors. For example, increasing habitat structure may influence competitive interactions (Fletcher and Underwood 1987), the physical harshness of the environment (e.g., increased relative humidity for intertidal animals; Nixon et al. 1971), the impact of disturbances (e.g., effects of wave action; Dommasnes 1968; Whorff et al. 1995), or the relative importance of predation (Orth et al. 1984; Dean and Connell 1987a).

Although most studies find positive associations between habitat structure and faunal diversity, these relationships are not always linear. There are often distinct thresholds, after which the influence of habitat structure on local communities changes in direction and magnitude (for review, see Coull and Wells 1983; Gotceitas and Colgan 1989). Discussions on these thresholds have focused on the minimum amount of structure that is required before positive benefits are realized by associated fauna (e.g., Coull and Wells 1983; Gotceitas and Colgan 1989). Nevertheless, it is also conceivable that there are upper thresholds, beyond which increasing habitat structure has no effect (Fonseca et al. 1996) or possibly even has negative effects on associated organisms. While negative effects of increasing habitat structure have not been demonstrated at the community level to date, it has been shown experimentally that decreasing the amount of structure in extremely complex habitats may have positive effects on abundances of individual species by increasing resource availability (Sullivan and Klenner 2000).

Despite being well studied, habitat structure has received less attention than other factors, such as competition or predation, as a major contributor to local community structure (Dean and Connell 1987b; McCoy and Bell 1991). This lack of recognition has been attributed to the lack of consistency in definitions of habitat structure among studies (McCoy and Bell 1991; Beck 1998). To solve this problem, McCoy and Bell (1991) provided a model of the major components of habitat structure, which are proving exceptionally useful for elucidating differences between the effects of various structural characteristics of habitat (e.g., Downes et al. 1998) and testing the generality of these effects among different habitats (e.g., Beck 1998, 2000). The model has three components: heterogeneity, complexity and scale. Heterogeneity was defined as the relative abundance of different structural components per unit area (e.g., different species or shapes of sea grass shoots). Complexity was defined as the absolute abundance of individual structural components per unit area (e.g., density of sea grass shoots). Scale was defined as the size of the area used to measure heterogeneity or complexity (e.g., size of area sampled). Regardless of how complex or heterogeneous the existing habitat, these definitions assume that any increase in either the number of shapes or the number of structural components per unit area is associated with an increase in habitat heterogeneity or habitat complexity, respectively.

While these definitions allow separation of variation due to different components of habitat structure, it is still possible that the vertical size of the structural unit can change without altering heterogeneity or complexity (e.g., an increase in the average shoot length of sea grass without a change in the density or basic shape of the fronds). Such changes in habitat structure represent a difference in vertical scale and can be incorporated into McCoy and Bell's (1991) general model by expanding the definition of their scale component to include a third dimension.

On rocky intertidal shores, there is generally a positive relationship between the complexity of algal structure and the richness and abundance of the associated fauna (e.g., Hicks 1985; Gibbons 1988; Gee and Warwick 1994a; Davenport et al. 1999). For many other faunal and algal assemblages on rocky shores, differences in the richness, abundance or cover of organisms at different tidal heights are caused by changes in the strength of biological processes (e.g., competition, predation, recruitment or grazing) with environmental conditions (e.g., desiccation stress, impacts of waves, emersion time; Dayton 1971; Paine 1974; Underwood 1994). Because habitat structure can modulate biotic interactions and influence local environmental conditions, its relative effects on associated organisms may vary across environmental gradients, such as tidal height. However, few studies have evaluated the effects of habitat structure under varying environmental conditions (Lohrer et al. 2000).

Articulated coralline algae often form complex turfs (10–60 mm tall) and are a major component of algal assemblages on many rocky shores (Stewart 1982; Dye 1993; Benedetti-Cecchi and Cinelli 1994). Coralline turf provides a habitat for diverse macrofaunal assemblages (Hicks 1971; Akioka et al. 1999) with very high densities (up to 250,000 individuals per $m^2$; Kelaher et al. 2001). Relative to most algae on rocky shores, coralline turfs have extremely densely packed and highly branched fronds (Coull and Wells 1983; Davenport et al. 1999). Consequently, they have been used in several studies to represent the extreme end of algal structural complexity (e.g., Coull and Wells 1983; Davenport et al. 1999). The physical structure of coralline turf is highly variable, with the density and length of coralline fronds often varying at small spatial scales (Akioka et al. 1999; Kelaher et al. 2001). This variation in physical structure may have a large influence on the spatial patterns of associated fauna.

I investigated the effects of the physical structure of coralline turf on associated gastropod assemblages at different tidal heights of a rocky intertidal shore near Sydney, Australia. I focused on gastropods rather than on the entire macrofaunal assemblage because they are substantially better described taxonomically than other species guilds (see Kelaher 2001). The gastropods in coralline turf encompassed a diverse community (65 species) with complex trophic (e.g., predators, deposit feeders, micro- and macroalgal feeders) and size structure (see Materials and Methods). Using the framework of McCoy and Bell (1991), I defined the density of coralline fronds to represent structural complexity. Using the expanded definition outlined above, the length of fronds represented the vertical scale over which complexity was measured. Field sampling was done to test for relationships between coralline turf structure and the various aspects of gastropod assemblages, including richness and total abundance. Experimental manipulations of frond density using artificial habitat mimics were then done to test the hypothesis that increasing the structural complexity of algal turf negatively affects the diversity and abundance of gastropods.

## Materials and methods

### Study location

The study was done at the Cape Banks Scientific Marine Research Area, on the northern headland of the entrance to Botany Bay, Sydney, Australia (34°00'S, 151°15'E). All the sites used in this study had medium to heavy exposure to waves and gently sloping horizontal rock platforms. On this shore, large patches of coralline algal turf often cover rock platforms between low- and mid-shore areas. These turfs are dominated by *Corallina officinalis* Linneaus, although other algal species have a small contribution to turf structure at different places and times (Kelaher et al. 2001). The coralline turf was also associated with an extremely variable epiphytic assemblage that varied significantly with tidal height but not with the density or length of coralline fronds (Kelaher 2001).

### Variation in gastropod assemblages and relationships with habitat structure

To investigate the spatial and temporal variation of gastropod assemblages and their relationships with the habitat structure, patches of turf were sampled in May 1997, September 1997, and January 1998. At each time, two sites (2×4 m patches of coralline turf) not previously sampled were haphazardly selected in low- and mid-shore areas. These two tidal heights are associated with different environmental conditions (e.g., immersion time) that alter biotic processes and create differences in other macroinvertebrate communities on Australian rocky shores (see Underwood 1994 for review). The heights of mid- and low-shore sites varied between 0.58–0.82 m and 0.21–0.42 m above Indian Low Water Springs (I.L.W.S, tidal datum for Sydney), respectively. At each tidal height, sites were approximately 50 m apart. In each site, four randomly placed replicate cores of coralline turf were collected using a sharpened metal corer, which had an internal diameter of 80 mm (50 $cm^2$). This size of core provides a relatively precise estimate of the richness and abundance of macrofauna in coralline turf (SE/mean <0.07, $n$=5; Kelaher 2001). For each replicate sample, the corer was pushed into the coralline turf and the algae and sediment inside the corer was scraped off at the level of the rock, placed in a plastic bag, and taken to the laboratory. Only areas with 100% primary cover of algae, of which at least 95% was *C. officinalis*, were sampled. All replicates were preserved in a 7% formalin solution.

In the laboratory, each core was washed in a 500 $\mu$m sieve, and the faunal and algal components retained on the sieve were separated. The average length of *C. officinalis* fronds was determined for each core from measurements of four randomly selected fronds. Each frond measured was complete, with an intact holdfast. Because it was difficult to accurately measure the density of fronds directly, it was determined indirectly by dividing the dry weight of coralline fronds per $m^2$ by the average frond length (units = $kg \cdot m^{-3}$). This provided a measure of frond biomass per unit area that was independent of frond length, which varied among replicates. This surrogate measure was shown to be a good representation of the number of fronds per unit area (B.P. Kelaher, unpublished data). To measure the dry weight of coralline fronds, the epibiota on each frond was carefully removed. The cleaned coralline fronds were dried for 48 h at 60 °C, cooled in a desiccator for 4 h, and weighed. All gastropods were sorted and identified to species with a binocular microscope (×16 magnification). In total, 65 species of gastropods were found from 33 different families. The assemblage was comprised of species that were either never more than a few millimeters in size (microgastropods) or juveniles of species of larger gastropods that are usually found in other habitats as adults. Gastropods ranged in size from 0.5 to 30.0 mm. The majority of snails (>90%) were microgastropods between 0.5 and 1.0 mm in width. Gastropods greater than 10 mm in size were extremely rare (<1%).

### Effectiveness of habitat mimic

Because analyses showed that there were strong negative relationships between the density of fronds and the richness and abundance of gastropods, a field experiment was designed using artificial habitat mimics to test the hypothesis that structural complexity of coralline turf negatively affects the richness and abundance of gastropods. Artificial habitat mimics ensure that only structural characteristics of a habitat influence associated organisms rather than biological characteristics (e.g., value of coralline fronds as a food resource). A good structural mimic must have physical characteristics similar to the natural habitat. Artificial turf was a good habitat mimic for coralline turf because it had a similar mat-like structure and frond length, because it trapped sediment, and because it was quickly colonized by epiphytes. The artificial turf (manufactured by the Grass Alternative Pty Ltd, Sydney) was made of bundles of 16 polypropylene strips separated from each other by 6 mm and attached in regular rows (10 mm apart) to a latex back. Each polypropylene strip was 26 mm in length and 1.5 mm wide.

While in many respects the physical structure of the artificial turf closely resembled loosely packed coralline turf, there were differences in physical structure (e.g., natural coralline fronds were branched and slightly thicker than artificial fronds) and construction materials. To evaluate whether these differences significantly affected the associated gastropod assemblages, 12 patches (100 mm in diameter, 78.5 $cm^2$) were placed in a 20×5 m area of the rock platform that had an extensive cover of loosely packed coralline turf (mean±SD frond density=49.04±9.05 $kg \cdot m^{-3}$, $n$=4) in December 1997. Each patch of artificial turf was glued to an aluminum sheet (0.6 mm thick) for rigidity. For each patch, a circular clearing of 100 mm in diameter was made in natural coralline turf between 0.45 and 0.55 m above I.L.W.S. Rather than high- and low-shore levels, an intermediate height was used to minimize the number of replicates required to test the hypothesis. Patches of artificial turf were attached to these cleared areas by three stainless steel screws. Clearings were carefully made to minimize the gap between the edge of the artificial turf and the surrounding coralline algae. Four patches of artificial turf and similar-sized cores of natural coralline turf were collected 2, 4, and 12 months after the experiment began. The experiment was sampled at multiple times to determine how long gastropods take to colonize artificial turf in densities similar to natural coralline turf. Each replicate of natural and artificial turf was thoroughly washed in a 500 $\mu$m sieve, and the remaining gastropods were sorted and identified.

### Experimental manipulations of habitat structure

Because artificial turf is an excellent surrogate for natural turf (see Results), a field experiment was set up in May 1999 using patches of artificial turf (80 mm in diameter, 50 $cm^2$) with tightly packed fronds and with loosely packed fronds to test the hypotheses that increasing structural complexity of loosely packed coralline turf decreases the richness and abundance of gastropods. Loosely packed turf was similar in construction to the artificial turf described above. Tightly packed turf was virtually identical in construction except that the rows of fronds were separated by 5 mm (rather than 10 mm) and the bundles of fronds in each row were 3 mm (rather than 6 mm) apart. The density of fronds in tightly packed turf was, therefore, four times greater than in loosely packed turf, which is approximately the difference between loosely and tightly packed natural coralline turf.

Six sites (2×2 m areas of coralline turf) were haphazardly selected in both low- (0.35–0.44 m above I.L.W.S) and mid-shore (046–0.81 m above I.L.W.S) areas. Each site was approximately 10–20 m from its nearest neighbor. At each height on the shore, three sites were randomly allocated to a treatment with tightly packed turf, and the remaining three sites were allocated to a treatment with loosely packed turf. This random allocation ensured that any differences in frond density of natural turf could not systematically affect the results. In each site, four patches of artificial turf of the particular treatment were attached to the rock platform using the methods described above. After 6 months, all patches were collected and preserved in 7% formalin. Six months was considered an appropriate amount of time to ensure that densities of gastropods in artificial turf were similar to those in natural coralline turf (see Results). In the laboratory, each replicate patch was washed thoroughly in a 500 $\mu$m sieve, and all gastropods retained were counted and identified.

Many common gastropod species in coralline turf are strongly associated with the sediment at bottom of the turf, while others are mostly found foraging on the fronds (Olabarria and Chapman 2001a, 2001b). Previous work has shown a strong negative relationship between the amount of sediment in coralline turf and the density of fronds (Pearson's $r$=–0.41, $n$=40, $P$<0.01; Kelaher 2001). In addition, changes in the density of fronds alter the amount of frond surface area available and influence the spacing between fronds. To evaluate the importance of these factors, analyses were done on the abundance of six of the most common gastropods in coralline turf. Three of these species, the small snails *Amphithalamus incidata*, *Eatonina rubrilabiata* and *Rissoella micra*, are associated with the sediment at the base of the fronds. The other three, the small snail *Eatoniella atropurpurea* and the juvenile limpets *Patelliodа mufria* and *Montfortula rugosa*, are generally found grazing on the fronds.

### Statistical analyses

Non-parametric multivariate analyses of variance (np-MANOVA) were used to test hypotheses about differences in gastropod assemblages (Anderson 2001a; McArdle and Anderson 2001). The input for each of these analyses was a species-by-samples matrix of abundances of each gastropod species found. Analyses tested for overall multivariate changes in gastropod assemblage structure, which may include differences in composition, richness, and/or individual species abundances. This relatively new statistical method was used because the designs of experiments were relatively complex (usually involving three factors) and because, similar to most other studies on diverse communities, the data did not meet the assumptions of traditional multivariate statistical analyses (e.g., MANOVA). Like other non-parametric multivariate methods (e.g., ANOSIM; Clarke 1993), np-MANOVA has less stringent assumptions than traditional multivariate tests. It improves on previous methods because it allows the direct additive partitioning of variation, which enables tests of multivariate interactions in complex experimental designs. The test statistic (*pseudo-F*) is a multivariate analogue of Fisher's $F$ ratio and is calculated from a symmetric dissimilarity matrix. $P$-values are then obtained by permutation tests (see Anderson 2001a, 2001b). The construction of these tests is dependent on the availability of permutable units in the denominator of each *pseudo-F* ratio and therefore varies among terms in the model (Anderson 2001b). Here, the $P$-values for each term in the model were generated using 5,000 permutations. To graphically visualize multivariate patterns in gastropod assemblages, non-metric multidimensional scaling (nMDS; Field et al. 1982) was used to produce two-dimensional ordination plots. All multivariate analyses were done using the Bray-Curtis similarity coefficient (Bray and Curtis 1957).

Hypotheses about the richness and abundance of gastropods and habitat variables were tested with univariate analyses of variance (ANOVA). ANOVAs were preceded with Cochran's test for homogeneity of variances and data were transformed to $x'$=ln ($x$+1) where necessary (Underwood 1997). ANOVAs were followed by Student-Newman-Keul (SNK) tests to identify significant differences among means.

Mantel's test was used to test for significant multivariate associations between gastropod assemblages and habitat variables (Mantel 1967). The Mantel test calculates the correlation between dissimilarities among objects based on one set of variables (e.g., assemblage data) and the distance among objects based on another set (e.g., one or more habitat variables), while holding the other set fixed. For each Mantel test, $P$-values were calculated using 5,000 permutations. Univariate patterns of association were tested using Pearson's correlation coefficient $r$ (Winer et al. 1991). Because univariate correlation data were used for multiple comparisons, significance levels were corrected using the sequential Bonferroni technique (Rice 1989). This method is less conservative than the standard Bonferroni technique but ensures that an appropriate type-I error rate is maintained.

## Results

### Variation in gastropod assemblages and relationships with habitat structure

At all times of sampling, there were significant differences between gastropod assemblages in low- and mid-shore areas (*pseudo-*$F_{(1,6)}$=2.43, $P$=0.038; Fig. 1). Despite significant temporal variation (*pseudo-*$F_{(2,6)}$=1.83, $P$=0.044), the direction and magnitude of these differences were relatively consistent among times of sampling (height × time interaction, *pseudo-*$F_{(2,6)}$=1.67, $P$=0.090). There were also significant differences between sites in both low- and mid-shore areas (*pseudo-*$F_{(6,36)}$=2.93, $P$<0.001, Fig. 1).

At the first two times of sampling the richness of gastropods did not differ significantly between low- and mid-shore areas (Table 1, Fig. 2a). There were, however, significantly more species of gastropods in coralline turf in low- than in mid-shore areas in January 1998 (SNK, $P$<0.05). At this time of sampling, there was also a significantly greater abundance and greater richness of

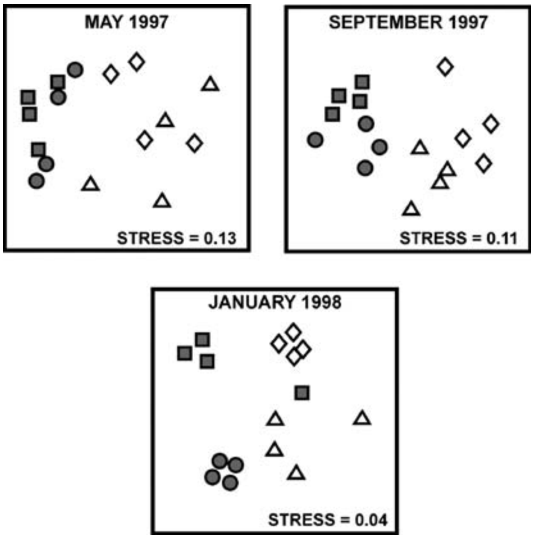

**Fig. 1** Two-dimensional nMDS ordination plots ($n$=4) comparing gastropod assemblages in low-shore (*gray symbols*) and mid-shore (*clear symbols*) areas at each time of sampling. Different shaped symbols indicate sites nested in tidal height and time of sampling. Each individual symbol represents the gastropod assemblage in a replicate sample, and the relative distance between symbols indicates the dissimilarity between samples. Stress values are an indication of how effectively the multidimensional information is represented by the two-dimensional plot. Stress values <0.15 indicate that reliable interpretations can be made from the two-dimensional plot (Clarke 1993)

**Table 1** ANOVAs of assemblage measures and habitat variables ($n$=4). *ti* is the comparison among three randomly chosen times of sampling, and *he* is the fixed comparison between low- and mid-shore areas. “Site” is the comparison of sites nested in the interaction term

| | Species richness | | | Total abundance[a] | | | |
|---|---|---|---|---|---|---|---|
| | *df* | MS | *F* | *P* | MS | *F* | *P* |
| Time of sampling (*ti*) | 2 | 103.15 | 9.24 | 0.015 | 9.20 | 21.60 | 0.002 |
| Height on shore (*he*) | 1 | 161.33 | 2.02 | 0.291 | 6.08 | 8.50 | 0.100 |
| *ti* × *he* | 2 | 79.77 | 7.14 | 0.026 | 0.72 | 1.68 | 0.264 |
| Site (*ti* × *he*) | 6 | 11.17 | 1.34 | 0.264 | 0.43 | 0.89 | 0.512 |
| Residual | 36 | 8.32 | | | 0.48 | | |
| | Length of fronds | | | Density of fronds[a] | | | |
| | *df* | MS | *F* | *P* | MS | *F* | *P* |
| Time of sampling (*ti*) | 2 | 34.99 | 0.29 | 0.758 | 0.71 | 2.16 | 0.197 |
| Height on shore (*he*) | 1 | 1318.96 | 20.15 | 0.046 | 4.55 | 35.52 | 0.027 |
| *ti* × *he* | 2 | 65.45 | 0.54 | 0.607 | 0.13 | 0.39 | 0.693 |
| Site (*ti* × *he*) | 6 | 120.54 | 11.99 | <0.001 | 0.33 | 3.45 | 0.009 |
| Residual | 36 | 8.32 | | | 0.10 | | |

[a] Data were transformed by $x' = \ln(x+1)$

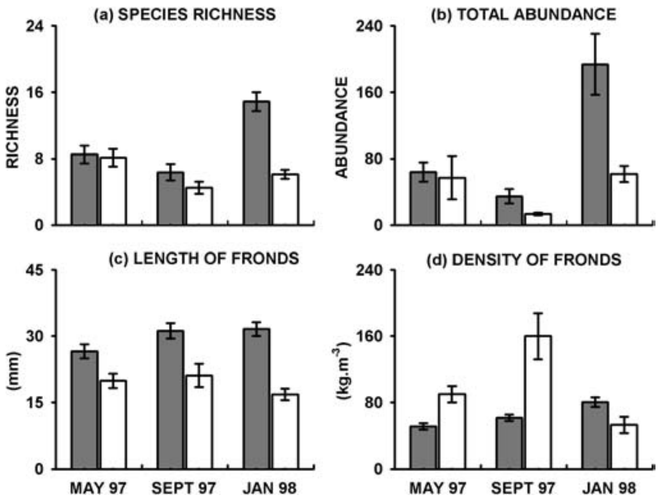

**Fig. 2a–d** Comparisons of mean (SE, $n$=4) univariate measures of gastropod assemblages and habitat structure variables in each core (50 cm$^2$) in low-shore (*gray symbols*) and mid-shore (*clear symbols*) areas at the three times of sampling

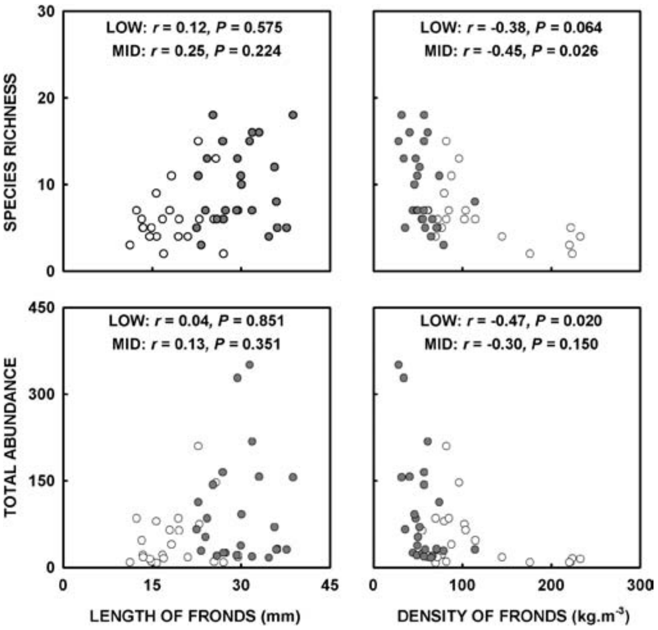

**Fig. 3** Plots showing the relationship between univariate measures of gastropod assemblages and habitat structure variables in low-shore (*gray symbols*) and mid-shore (*clear symbols*) areas. Data are pooled across times of sampling ($n$=24). Plots also show Pearson’s $r$ correlation coefficient and $P$-value for each relationship

gastropods in low-shore areas (Table 1a, b) relative to other times of sampling (SNK, $P$<0.05, Fig. 2a, b). The differences in richness and abundance are likely to have had major contributions to the large differences in the multivariate measures of assemblages between January 1998 and the other times of sampling. In contrast to the multivariate results, the richness and abundance of gastropods did not significantly vary among sites (Table 1a). Coralline fronds were longer and more loosely packed (less dense) in mid- than in low-shore areas (Table 1c, d, Fig. 2c, d) and the length and density of fronds significantly varied among sites (Table 1c, d, Fig. 2a, b).

There were significant associations between the density of fronds and gastropod assemblages in low-shore (Mantel test, $r$=0.51, $P$=0.010) and mid-shore (Mantel test, $r$=0.38, $P$=0.037) areas. There was also a significant association between the length of fronds and gastropod assemblages in mid-shore areas (Mantel test, $r$=0.49, $P$=0.002), but not in low-shore areas (Mantel test, $r$=-0.04, $P$=0.463). After being corrected for multiple comparisons, there were no significant correlations between the length and density of fronds and richness and abundance of gastropods in either low- or mid-shore areas ($P$>0.0125; Fig. 3). Nevertheless, the directions of the relationships between density of fronds and gastropod diversity and abundance were all strongly negative ($P \leq 0.15$), with two of four comparisons having $P$-values less than 0.05 (Fig. 3). In contrast to the density of fronds, there were no consistent relationships between the length of fronds and the richness or abundance of gastropods.

**Table 2** np-MANOVA (entire assemblage) and ANOVAs (species richness, total abundance) of measures of gastropod assemblages ($n$=4). *ti* is the fixed comparison among assemblages at 2, 4, and 12 months; *tu* is the fixed comparison between assemblages in natural and artificial turf

| | *df* | Entire assemblage | | Species richness | | | Total abundance[a] | | |
|---|---|---|---|---|---|---|---|---|---|
| | | *Pseudo-F* | *P* | MS | *F* | *P* | MS | *F* | *P* |
| Time of sampling (*ti*) | 2 | 2.10 | 0.065 | 18.29 | 4.10 | 0.034 | 0.94 | 3.20 | 0.064 |
| Type of turf (*tu*) | 1 | 1.43 | 0.216 | 0.04 | 0.01 | 0.092 | 0.01 | 0.02 | 0.878 |
| *ti* × *tu* | 2 | 0.88 | 0.506 | 2.04 | 0.46 | 0.640 | 0.16 | 0.53 | 0.596 |
| Residual | | 18 | | 4.46 | | | 0.29 | | |

[a] Data were transformed by $x'=\ln(x+1)$

**Table 3** np-MANOVA (entire assemblage) and ANOVAs (species richness, total abundance) ($n$=4). *he* is the fixed comparison between low- and mid-shore areas; *de* is the fixed comparison between loosely and tightly packed turf; "Site" is the comparison of sites nested in the interaction term

| | *df* | Entire assemblage | | Species richness | | | Total abundance[a] | | |
|---|---|---|---|---|---|---|---|---|---|
| | | *Pseudo-F* | *P* | MS | *F* | *P* | MS | *F* | *P* |
| Height on shore (*he*) | 1 | 6.18 | 0.001 | 31.68 | 2.69 | 0.140 | 10.00 | 5.80 | 0.043 |
| Density of fronds (*de*) | 1 | 2.40 | 0.031 | 123.52 | 10.49 | 0.012 | 6.04 | 3.51 | 0.098 |
| *he* × *de* | 1 | 1.68 | 0.130 | 4.69 | 0.40 | 0.546 | 0.13 | 0.08 | 0.791 |
| Site (*he* × *de*) | 8 | 3.25 | 0.001 | 11.77 | 3.37 | 0.006 | 1.72 | 6.67 | <0.001 |
| Residual | 36 | | | 3.49 | | | 0.26 | | |

[a] Data were transformed by $x'=\ln(x+1)$

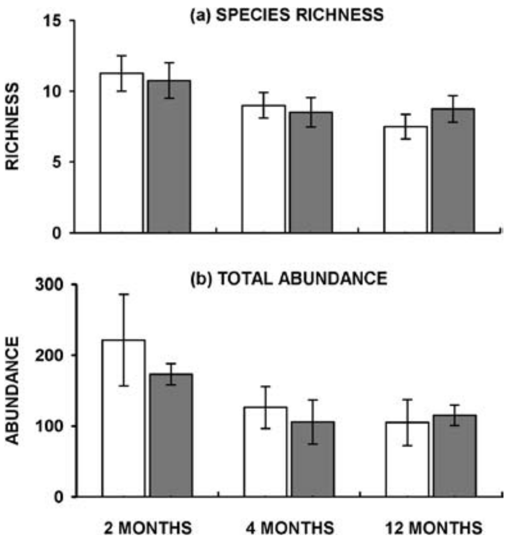

**Fig. 4a, b** Comparisons of mean (SE, $n$=4) univariate measures of gastropod assemblages in each sample (78.5 $cm^2$) of natural coralline turf (*clear bars*) and in artificial turf (*gray bars*) at the three times of sampling

## Effectiveness of habitat mimic

Two months after the deployment, there were no significant differences between gastropod assemblages in natural coralline turf and in artificial turf using either multivariate or univariate measures (Table 2, Fig. 4). Similar results were also found at 4 and 12 months. Therefore, artificial turf made an excellent surrogate for natural coralline turf.

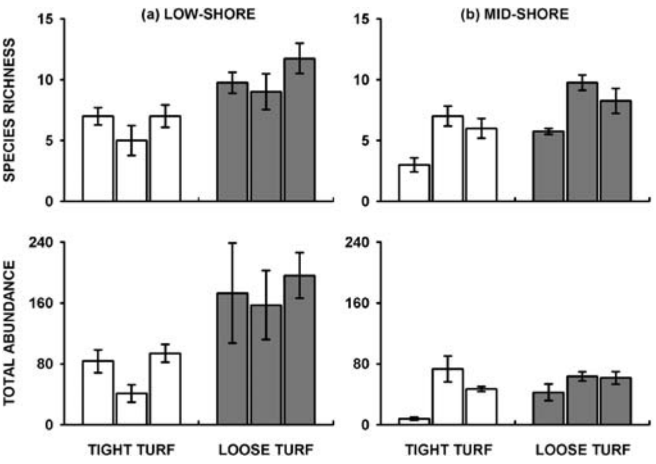

**Fig. 5a, b** Comparisons of mean (SE, $n$=4) univariate measures of gastropod assemblages in each patch (50 $cm^2$) of tightly packed (*clear bars*) and loosely packed (*gray bars*) turf in low- and mid-shore areas. Each bar represents a different site

## Experimental manipulations of habitat structure

There were significant differences between gastropod assemblages in tightly and loosely packed artificial turf (Table 3a). Despite highly significant differences in gastropod assemblages in artificial turf at different tidal heights, the direction and magnitude of changes in gastropod assemblages were relatively consistent between low- and mid-shore areas (see non-significant interactions in Table 3a). There were significantly fewer species of gastropods in tightly packed turf than in loosely packed turf (Table 3b, Fig. 5a). A similar trend was also shown

**Table 4** ANOVAs of abundances of common sediment-dwelling (*Amphithalamus incidata*, *Eatonina rubrilabiata*, *Rissoella micra*) and frond-dwelling (*Eatoniella atropurpurea, Patelloida mufria*, *Montfortula rugosa*) gastropod species ($n$=4). *he* is the fixed comparison between low- and mid-shore areas; *de* is the fixed comparison between loosely and tightly packed turf; “Site” is the comparison of sites nested in the interaction term. For all analyses, data were transformed by $x'$=ln ($x$+1)

| | *df* | *Amphithalamus incidata* | | | *Eatonina rubrilabiata* | | | *Rissoella micra* | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | MS | *F* | *P* | MS | *F* | *P* | MS | *F* | *P* |
| Height on shore (*he*) | 1 | 20.28 | 11.32 | 0.010 | 33.57 | 13.83 | 0.006 | 10.66 | 10.31 | 0.012 |
| Density of fronds (*de*) | 1 | 19.19 | 10.71 | 0.011 | 17.35 | 7.15 | 0.028 | 10.36 | 10.03 | 0.013 |
| *he* × *de* | 1 | 8.99 | 5.02 | 0.055 | 7.96 | 3.28 | 0.108 | 1.21 | 1.17 | 0.311 |
| Site (*he* × *de*) | 8 | 1.79 | 2.51 | 0.028 | 2.43 | 6.18 | < 0.001 | 1.03 | 2.30 | 0.042 |
| Residual | 36 | 0.71 | | | 0.39 | | | 0.45 | | |

| | *df* | *Eatoniella atropurpurea* | | | *Patelloida mufria* | | | *Montfortula rugosa* | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | MS | *F* | *P* | MS | *F* | *P* | MS | *F* | *P* |
| Height on shore (*he*) | 1 | 27.09 | 8.02 | 0.022 | 2.49 | 1.28 | 0.291 | 0.65 | 0.77 | 0.404 |
| Density of fronds (*de*) | 1 | 0.45 | 0.13 | 0.725 | 7.53 | 3.86 | 0.085 | 3.26 | 3.89 | 0.084 |
| *he* × *de* | 1 | 0.34 | 0.10 | 0.759 | 1.98 | 1.01 | 0.343 | 1.19 | 1.41 | 0.268 |
| Site (*he* × *de*) | 8 | 3.38 | 6.32 | < 0.001 | 1.95 | 3.71 | 0.003 | 0.84 | 2.47 | 0.030 |
| Residual | 36 | 0.53 | | | 0.53 | | | 0.34 | | |

**Table 5** List of species that were found only in samples of loosely packed or tightly packed turf. *P*, *S*, and *L* indicate species that are predatory whelks, are associated with sediment, or are juveniles that are often found adults in other habitats, respectively

| Found only in loosely packed turf |
|---|
| *Dicathias orbita* (P, L), *Agnewia tritoniformis* (P, L), *Mitrella semiconvexa* (P, L), *Morula marginalba* (P, L), *Zafra atkinsoni* (P), *Bembicium nanum* (L), *Turbo undulatus* (L), *Lodderina minima* (S), *Scrobs luteofuscus* (S), *Crassitoniella flammea* (S), *Oscilla tasmanica* (S), *Cinctiuga diaphana* (S), *Puncturella* sp. |
| Found only in tightly packed turf |
| *Patellioda latistrigata*, *Diaphana* sp. |

for the abundance of gastropods in low-shore areas (Fig. 5a), but these differences were not statistically significant. Multivariate measures of assemblages, species richness, and total abundance of gastropods all varied significantly among sites (Table 3).

To get insights into the mechanisms responsible for differences between gastropod assemblages in loosely and tightly packed turf, the species that were found in either one treatment or the other are presented in Table 4. Although the abundances of these species were generally too low for statistical analysis, there seems to be some trends in the biological characteristics of the 13 gastropod species that were found only in loosely packed turf. Five of these species were predatory whelks, which constitutes about 50% of the total predatory snails found in the study. Six of the species were gastropods that are usually at the upper end of the size distribution of snails in coralline turf and are generally found as adults in other habitats. Finally, five of the gastropod species were snails that are closely associated with the sediment at the base of the fronds (see Table 4 for details).

The six common gastropod species selected for analyses accounted for 89% and 77% of the total dissimilarity between gastropod assemblages in loosely and tightly packed turf in low- and mid-shore areas, respectively. The three species associated with sediment at the bottom of the turf (*Amphithalamus incidata*, *Eatonina rubrilabiata*, and *Rissoella micra*) were all

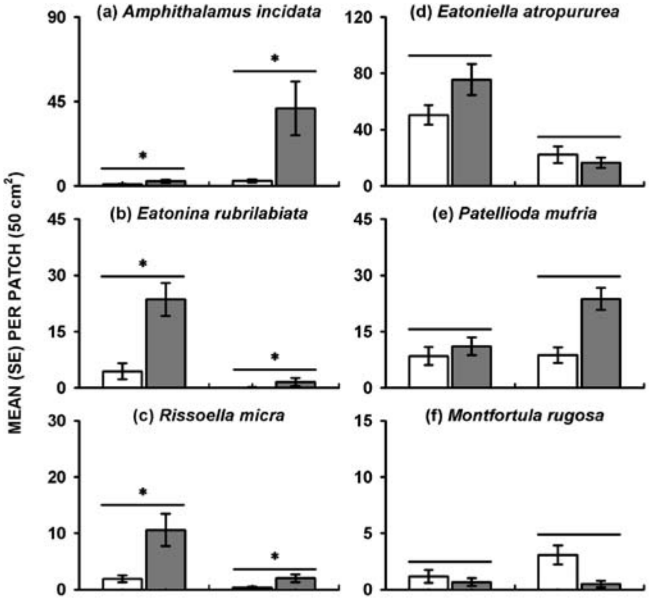

**Fig. 6a–f** Comparisons of mean (SE, $n$=4) abundances of common gastropod species in tightly packed (*clear bars*) and loosely packed (*gray bars*) turf in low- and mid-shore areas. Data are presented for sediment-dwelling (**a–c**) and frond-dwelling (**d–f**) species. *Asterisk* indicates significant difference (ANOVA, $P$<0.05)

significantly negatively affected by greater frond density (Table 5, Fig. 6a–c). In contrast, there were no significant differences between frond-dwelling species (*Eatoniella atropurpurea*, *Patellioda mufria*, and *Montfortula rugosa*) in loosely and tightly packed turf (Table 5, Fig. 6d–f). Despite significant differences in abundance between low- and mid-shore levels for four out of six species, the direction and magnitude of each species' response to frond density was relatively consistent at the different tidal heights (no significant height × frond density interactions; Table 5), which was certainly a major influence in the non-significant multivariate interaction between tidal height and frond density (Table 3a). The one exception was *A. incidata*, whose response to frond density appeared to be much greater in low- than in mid-shore areas.

## Discussion

The physical architecture of coralline turf influenced the structure of associated gastropod communities. Despite the fact that gastropod assemblages and the length and density of fronds all varied at similar spatial scales (among replicates and sites), only the density of fronds showed consistent and strong relationships with gastropod diversity. The density of fronds explained much more variation in gastropod assemblages than variations in vertical scale due to frond length. Similar to other studies, the results demonstrate that different aspects of habitat structure generally have different effects on local community structure (Downes et al. 1998; Beck 2000).

Because the shape of coralline fronds changes with length and density of fronds and with local environmental conditions (Akioka et al. 1999; Kelaher 2001), the manipulation of structural complexity using artificial turf ensured that heterogeneity of coralline fronds did not confound interpretations of effects attributable to structural complexity. The use of artificial turf also meant that biological characteristics of coralline fronds, such as nutritional value (Worthington and Fairweather 1989) or exuded chemicals that attract or repel molluscan larvae (Underwood 1979), did not influence interpretations. Biological characteristics of many biogenic habitats have the potential to have major effects on associated organisms (e.g., soft corals; Syms and Jones 2000). Therefore, experiments examining natural components of habitat structure may be difficult to interpret. For coralline turf, however, the effects attributable to physical characteristics are clearly much greater than those associated with biological characteristics (Kelaher 2002), making it an ideal habitat to investigate the effects of habitat structure.

Increasing the structural complexity of habitats has been shown to influence a variety of biological processes. Algal turf on rocky intertidal shores often provides a refuge from predation (Coull and Wells 1983; Dean and Connell 1987a) and from the physical harshness of the environment (Gibbons 1988). For many other faunal and algal assemblages, the influence of biological processes generally varies with tidal height (e.g., Dayton 1971; Paine 1974). Despite large differences in gastropod assemblages between low- and mid-shore areas, however, multivariate and univariate analyses showed that the direction and magnitude of effects attributable to structural complexity did not significantly differ between tidal heights. Overall, the non-significant multivariate interaction between height on the shore and structural complexity probably indicated that the major biological processes that are influenced by the structural complexity of coralline turf are relatively independent of local environmental conditions at different tidal heights. Alternatively, but less likely, it is possible that different biological processes have very similar effects on gastropod assemblages at different tidal heights.

Both correlative and experimental evidence showed that increased density of fronds negatively affected richness of gastropods in low- and mid-shore areas. In addition, the total abundance of gastropods showed similar negative trends in low-shore areas, but variation among replicates was extremely large and no statistically significant difference was detected. Most of the common species showed similar negative effects, or at least negative trends, except for two notable exceptions: *Eatoniella atropurpurea* and *Montfortula rugosa*. Negative effects of structural complexity on the abundances of individual species have rarely been reported in the literature (e.g., Sullivan and Klenner 2000). Following the definition of structural complexity proposed by McCoy and Bell (1991) (i.e., the number of structural components per unit area), this is perhaps the first experimental evidence for a negative relationship between habitat complexity and an associated faunal community. Kelaher et al. (2001) reported similar negative correlations between the density of coralline fronds and gastropod diversity at a number of different shores spanning 120 km of coast. It is therefore unlikely that these results are simply a local phenomenon.

Although many possible factors may contribute to these negative relationships, there are several that probably have a large influence. One in particular is the amount of sediment at the base of the fronds, which is negatively correlated with density of fronds (Kelaher 2001). In other studies, the amount of sediment in algal turf has been positively associated with greater richness and abundance of gastropods (Wigham 1975; Kelaher et al. 2001) and with larger amounts of detritus (Hicks 1980). Sediment trapped by algal turf provides habitat for many species of gastropods (Olabarria and Chapman 2001a, 2001b), and detritus is an important source of food (Edgar et al. 1994). Here, increases in frond density were associated with decreases in the abundances of common gastropods that are usually found associated with the sediment. In addition, 5 of 13 species that were found only in loosely packed coralline turf were snails that are also usually found in association with sediment. Unfortunately, the amount of sediment in experimental treatments was not quantified in this study. The indirect evidence suggests, however, that investigating the relationship among frond density, sediment, and gastropods would be an excellent research direction to unravel the negative effects of frond density on gastropod diversity.

Another possible important factor is the reduction in interstitial space associated with the increase in structural complexity. When coralline fronds are packed tightly against their neighbors, the amount of light available for growth of microalgal films and macroalgal epiphytes is less than when the fronds are loosely packed, which may reduce the amount of food available for gastropods. Because coralline fronds are relatively rigid, the limited interstitial space associated with densely packed coralline turf may also restrict the movement and foraging of gastropods. Several studies have demonstrated that decreasing interstitial space in a complex habitat substantially reduces the foraging efficiency of predators (Coull and Wells 1983; Bartholomew et al. 2000). Here the diversity of predatory whelks and possibly larger gastropods was negatively affected by the increase in frond density. In contrast, it appeared that the increase in frond density did not particularly influence the abundance of the small gastropod *Eatoniella atropurpurea.* It is therefore possible that increasing frond density and reducing interstitial space also changes the size and trophic structure of the gastropod community.

The fact that the large-bodied gastropods were more likely to be excluded from the tightly packed turf than smaller frond-dwelling gastropods raises the interesting issue of whether increasing frond density actually created more or less complex habitat for the larger-bodied organisms. Previous studies have shown that snails greater than 5 mm in size respond to habitat structure at the scale of centimeters (e.g., pits and depressions; Beck 1998, 2000). Increasing the density of rigid fronds from loosely to tightly packed turf may decrease rather than increase structural complexity at this scale. In contrast, for organisms at the scale of the more abundant microgastropods (0.5–1.0 mm in width), increasing the density of fronds from loosely to tightly packed turf probably still represented an increase in structural complexity. If, however, the density of fronds continued to be increased artificially beyond tightly packed turf, the habitat would eventually become an almost laminar structure with little complexity for even the smallest gastropod. Consequently, the positive relationship between the number of structural components per unit area (e.g., density of fronds) and the structural complexity of the habitat cannot exist indefinitely. Eventually, adding more structural components must cause this relationship to peak and then become negative, with the location of the peak dependent on the body-size of the organism in question.

In contrast to microgastropods, the negative response of large-bodied gastropods may be attributed to a decrease in structural complexity associated with an increase in frond density. These results, therefore, further emphasize the need to consider body size when evaluating the relationship between faunal assemblages and habitat complexity (see also Gee and Warwick 1994b; Robbins and Bell 1994; Atrill et al. 2000). More importantly, they also imply that for a particular body size there is unique nonlinear (possibly quadratic) relationship between the number of structural components per unit area and the structural complexity of the habitat as perceived by the organisms. Consequently, some caution is needed when applying McCoy and Bell's (1991) definition of structural complexity, because it is useful only if the natural range of habitat complexity falls on the positive side of the relationship between the density of structural components and structural complexity. While this appears to be the case for most studies of natural habitats (e.g., Downes et al. 1998; Beck 2000), careful consideration should be given to investigations of relatively large organisms in extremely complex habitats.

The influence of algal structural complexity on the richness of associated fauna on rocky shores has been investigated by a number of studies (Hicks 1980; Dean and Connell 1987b; Gee and Warwick 1994a). Although definitions of complexity often vary between studies (see discussions in McCoy and Bell 1991 and Beck 1998), a general relationship has been established. First, there is a minimum threshold of algal structural complexity that is necessary before any positive effects of habitat structure are realized (Coull and Wells 1983). After this threshold is crossed, the number of associated faunal species increases as the structural complexity of algae increases and loose turfs are formed (Hicks 1980; Coull and Wells 1983; Dean and Connell 1987b; Davenport et al. 1999). The most diverse and abundant faunal assemblages are always associated with dense algal turfs, which have the highest structural complexity (Hicks 1980; Coull and Wells 1983; Dean and Connell 1987b; Davenport et al. 1999). This nonlinear relationship incorporates a range of algal species with differing structural complexity and is clearly strongly dependant on the body size of organisms relative to the habitat being investigated (Gee and Warwick 1994b; Robbins and Bell 1994; Atrill et al. 2000). Because the structural complexity of most algal species is above the lower threshold, a positive linear relationship between complexity and diversity is generally observed (e.g., Hicks 1980; Dean and Connell 1987b).

Coralline algal turf is one of the most complex algal structures on rocky shores (Hicks 1980; Coull and Wells 1983; Davenport et al. 1999). Compared to other algal turfs, coralline turf is associated with a more diverse and abundant fauna (e.g., Hicks 1980; Coull and Wells 1983; Davenport et al. 1999). This study has shown that loosely packed turf has a greater number of species than does tightly packed turf. These results therefore imply that loosely packed coralline turf represents an upper threshold of algal habitat structure, after which increasing frond density has negative effects on species richness. Combined with previous studies on rocky shores, these results demonstrate that there may be an optimal level of algal structural complexity (e.g., loosely packed coralline turf) where species diversity is maximized.

Many studies in both terrestrial and aquatic systems have found that habitat structure has a positive, but often nonlinear, influence on the diversity of species at local scales. This study has shown that for extremely complex habitats on rocky shores these relationships may not always be positive and that there may be an upper threshold in the relationship between structural complexity and local species richness. It remains to be tested whether similar patterns exist in other habitats with extreme structural complexity and, if so, whether there is generality in the ecological processes that cause them.

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