

Effects of habitat complexity on the diversity and abundance of macrofauna colonising artificial kelp holdfasts

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ABSTRACT: Habitat complexity plays an important role in the structuring of ecological assemblages in many terrestrial, freshwater and marine habitats. In this study, we investigated the effects of increased habitat complexity on the diversity and abundance of macrofauna colonising artificial kelp holdfasts of 3 varying levels of complexity. The artificial holdfasts were placed within a kelp bed off the coast of Plymouth for 20 d during the summer of 2004. High complexity holdfast mimics were colonised by significantly higher numbers of individuals and species, and had higher species diversity (Shannon-Wiener $H'e$), than either the medium or low complexity holdfasts. The relationship between habitat complexity and species diversity has often been attributed to a surface area effect, as habitats with a greater complexity generally also have a greater surface area to support a larger number of species. Therefore, we compared the observed community metrics with the values expected if indices were increasing in proportion to the surface area. We found that the number of species and individuals colonising both the medium and high complexity artificial kelp holdfasts were significantly greater than can be explained by a simple surface area relationship. Species diversity increased less rapidly than expected from the surface area relationship, largely because of a dominance effect from a few abundant species of amphipods and gastropods in the high complexity holdfasts. This study demonstrates that the relationship between habitat complexity and species diversity cannot be explained by surface area alone.

KEY WORDS: Habitat complexity · Artificial habitats · Kelp holdfasts · Macrofauna · Colonisation

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INTRODUCTION

A fundamental question in ecology is how the abundance and diversity of species are controlled and regulated. In many studies, habitat complexity has been shown to have a positive relationship with species diversity (e.g. Hixon & Menge 1991). For example, in studies of coral reefs (Almany 2004), forest canopies (MacArthur & MacArthur 1961), vegetated freshwater systems (Diehl 1992) and soft bottom marine systems (Talman et al. 2004), habitats of higher structural complexity have been found to support more individuals and have greater species diversity than less complex habitats.

In algal communities in particular, habitat complexity has been identified as the single most powerful

factor influencing meiofaunal communities (Hicks 1985) and a major factor affecting the abundance of organisms in vegetated marine habitats (Choat 1982). A number of different studies have found a correlation between algal complexity and species abundance, with branched, complex algae having a higher amphipod density than structurally more simple algae (Hacker & Steneck 1990, Norderhaug 2004). Epifaunal abundance and size has also been shown to be related to the size and structure of algae, expressed as its fractal dimension, with more epifauna occupying algae with greater complexity (Gee & Warwick 1994a,b).

Several theories have been suggested to explain the pattern of increasing species diversity in structurally more complex algal assemblages. A higher habitat

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complexity is thought to increase the number of niches available for colonisation thus reducing competition (Hicks 1985), provide a larger surface area for interception and colonisation (Conner & McCoy 1979, Gunnill 1982b, Parrish 1989, Attrill et al. 2000), and provide better protection from physical stress (Gibbons 1988). Coupled with this, higher complexity habitats have a high sediment trapping potential, which may increase food availability for invertebrates living on the algae (Hicks 1985). A more complex habitat may also alter the effect that competition and predation have on the invertebrate assemblage (Coull & Wells 1983, Hixon & Menge 1991, Diehl 1992) by providing greater resources and shelter. This would allow the coexistence of potentially competing species through the use of separate microhabitats within a complex system (Beukers & Jones 1997) and increase abundance and species diversity of prey populations by providing refuges from predation (Coull & Wells 1983). Complex habitats may also help to reduce predation by minimising the encounter rate and contact time between predator and prey and by degrading predator foraging efficiency and capture success (Diehl 1992, Beukers & Jones 1997).

Macroalgae, and in particular the kelp *Laminaria hyperborea*, have been shown to house a large and diverse community of invertebrates (Moore 1973a,b). *L. hyperborea* is a brown alga, forming large beds in the NE Atlantic, including the UK (Kain 1967). Kelp can be divided into 3 parts: the frond, the stipe and the holdfast or hapteron. The holdfast is the most structurally complex of the 3 sections as it is made up of a number of root-like sections (haptera) which provide multiple crevices for macro-organisms to inhabit (Norderhaug et al. 2002). As a result, all macrofaunal groups are more abundant (Arroyo et al. 2004) and diverse (Christie et al. 2003) in holdfast samples than in either other parts of the alga or adjacent benthic samples. The complexity of the holdfast increases with age as more haptera are laid down each year (Kain 1963). Space has also been shown to be a limiting factor to colonisation of holdfasts (Christie et al. 2003) and holdfast fauna have been shown to be highly mobile with high colonisation rates (Norderhaug et al. 2002, Christie et al. 2003).

The aim of this study was to develop an understanding of the relationship between habitat complexity and species diversity within kelp holdfasts. We hypothesised that high complexity habitats would support a greater abundance and diversity of macroinvertebrates and epiphytes than a medium complexity structure, which would in turn support a greater abundance and diversity of macroinvertebrates and epiphytes than a low complexity structure. To test this theory, artificial holdfast mimics were left within kelp beds for

a short period of time (20 d) and colonisation studied. The use of artificial holdfast mimics standardises volume and within-treatment architecture (Norderhaug et al. 2002). Artificial holdfast mimics have been shown to house a large number of invertebrates and also tend to be colonised rapidly (Norderhaug et al. 2002), thus providing an excellent model system.

MATERIALS AND METHODS

Study area. We used 2 kelp beds north and south of Renney Rocks, Plymouth, UK (50° 19.182' N, 004° 07.425' W and 50° 18.996' N 004° 07.478' W). Both sites were at similar depths (11.5 and 13 m, respectively) and had the same degree of wave exposure; these factors have been shown to influence the species composition of macroinvertebrates in kelp holdfasts (Moore 1973b).

Artificial substrata. We designed artificial substrata to imitate kelp holdfasts. The mimics were made using 3-strand 18 mm nylon rope set into a cylindrical base. The rope was set directly into plaster of Paris for low complexity mimics (Fig. 1a), split into the 3 main strands for medium complexity mimics (Fig. 1b), and frayed completely for high complexity mimics (Fig. 1c). Based around a frame made of 2 mm galvanised wire, these mimics were then set into 500 g of plaster of Paris which was poured into a 1.92 l container which had been cut to 10 cm height. Each rope was secured at the top with a cable tie, leaving 12 cm of holdfast mimic exposed for colonisation. An additional cable tie secured the rope to the wire to ensure that the holdfast mimics remained upright underwater and did not collapse. The plaster of Paris was then covered with polyurethane varnish to prevent it from breaking up too quickly when submerged. The galvanised wire extended through the base of the container and formed 2 loops so that the holdfasts could be attached with cable ties to a weighted chain placed on the sea bed, ensuring that the holdfast mimics remained in the same location for the duration of the experiment.

Study design. We placed the holdfast mimics in dense kelp at both sites, with 6 replicates of each complexity deployed at each site. The chain was laid in a cross configuration running north to south and east to west. Three replicates were laid in each direction in a predetermined random order spaced 1 m apart. This spacing was chosen as it is a much greater distance than the spacing between natural kelp (between 20 and 30 cm, Norderhaug et al. 2002) and therefore reduces potential competition of colonising organisms between holdfast mimics (Norderhaug et al. 2002). No holdfast mimic was more than 30 cm away from a natural kelp holdfast as both sites were dense kelp beds.

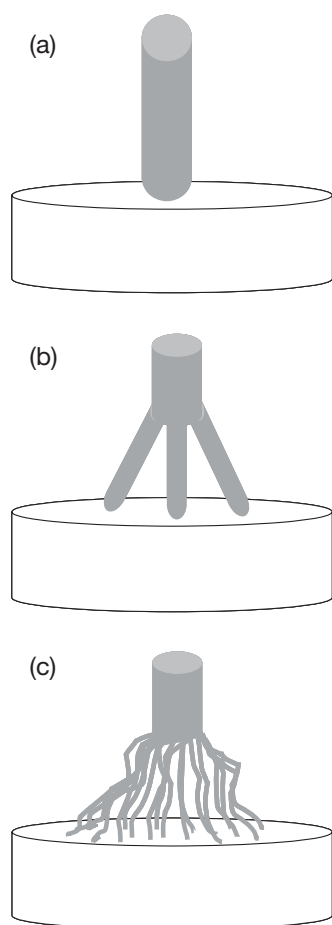


Fig. 1. Artificial kelp holdfasts. Nylon rope was (a) set directly into plaster of Paris for low complexity mimics, (b) split into 3 strands for medium complexity mimics, and (c) frayed completely for high complexity mimics. Log surface area increased by 1.06 from low to medium complexity and by 1.13 from medium to high complexity mimics

At each site SCUBA divers attached the holdfast mimic to the chain whilst underwater. These holdfasts were then left for 20 d from 22 July to 11 August 2004. On recovery, SCUBA divers cut the cable ties and carefully enclosed each holdfast mimic in a separate bag *in situ* and sealed it quickly to ensure all samples were collected without the loss of mobile organisms. In the laboratory, each sample was then washed and sieved through a 0.5 mm mesh. The macrofauna collected were fixed in formalin, counted and identified to the lowest taxonomic level possible. All algae growing on the holdfast mimics were collected, oven dried and the dry weight recorded.

Statistical methods. We used ANOVA to test for differences in the algal dry weight, macrofauna abundance (total number of individuals per holdfast), species number (total number of species per holdfast) and Shannon-Wiener diversity ($H'e$) between the 3

levels of holdfast complexity. All univariate statistics were calculated using SPSS 11.5 for Windows. Due to significant heterogeneity of variances, species number and abundance data were \log_{10} transformed prior to analysis. If surface area was the only mechanism driving the relationship between univariate community metrics and habitat complexity, then these variables would be expected to increase in proportion to surface area. We used the calculated surface areas of the low, medium and high complexity holdfasts (6786, 11 311 and 37 257 mm², respectively) to calculate the expected species number, abundance and diversity for medium and high complexity holdfasts relative to low complexity ones. Differences between observed and expected values were then analysed using 1-sample *t*-tests. Algal colonisation was almost absent on low and medium complexity holdfasts, but occurred to some extent on all high complexity mimics. We used a linear regression to test for a relationship between diversity indices of the high complexity holdfast mimic and the wet algal weight. Only high complexity diversity and algal weight was used as this was the only level of complexity with large quantities of algae present.

Multivariate analyses of the data were carried out to determine if there were differences in the community composition found on artificial holdfasts of differing complexity. No site effects were found in the multivariate analysis and so the data were pooled (Underwood 1997). All multivariate analyses were carried out using the PRIMER 5 (Plymouth Routines in Multivariate Ecological Research) package. To examine the overall similarity of the holdfast mimic communities, cluster analysis and a multidimensional scaling (MDS) were undertaken. Both methods used the Bray-Curtis index of similarity on 4th-root transformed data to down-weight the influence of abundant taxa (Clarke 1993). Dendrograms were constructed to display the results of cluster analysis, using hierarchical agglomerative clustering with group averaging. MDS analysis was displayed using 2-dimensional ordination. To formally test for differences in the similarity of the holdfast mimics, analysis of similarities (ANOSIM) was performed. Similarity percentages (SIMPER) analysis was conducted to determine the species that contributed most to the similarities within, and dissimilarities between, holdfast complexity groupings (Clarke & Warwick 2001).

RESULTS

In total, 968 individuals from 29 species were recorded (Table 1). Amphipods and gastropods were the 2 most dominant groups each representing 42% of the abundance (number of individuals) and 14 and 28% of the numbers of species, respectively. These

Table 1. Total number of each invertebrate species found in high, medium and low complexity holdfast mimics

Major group	Species	Complexity level		
		High	Medium	Low
Polychaetes	<i>Nereis zonata</i>	2	1	0
	<i>Spirorbis</i> spp.	22	0	0
	<i>Platyneries dumerilii</i>	0	1	0
Mysids	<i>Siriella armata</i>	1	0	0
Isopods	<i>Cymodoce truncata</i>	1	0	0
	<i>Lekanesphaera rugicauda</i>	32	1	0
	<i>Idotea baltica</i>	1	0	0
	<i>Synisoma lancifer</i>	10	0	0
Amphipods	<i>Gammarella fucicola</i>	1	0	0
	<i>Dexamine spinosa</i>	176	3	3
	<i>Aora gracilis</i>	156	1	0
	<i>Ampithoe rubricata</i>	3	54	6
Decapods	<i>Eualus occultus</i>	15	1	6
	<i>Macropodia tenuirostris</i>	1	0	0
	<i>Carcinus maenas</i>	2	0	0
	<i>Gastropods</i>	<i>Gibbula cineraria</i>	11	2
	<i>Tricolia pullus</i>	1	0	0
	<i>Lacuna parva</i>	10	0	0
	<i>Lacuna vincta</i>	99	2	5
	<i>Littorina obtusata</i>	3	0	1
	<i>Rissoa parva</i>	180	16	13
	<i>Cerithiopsis tubercularis</i>	59	0	2
	<i>Aplysia punctata</i>	1	0	0
Bivalves	<i>Mytilus edulis</i>	19	0	0
Echinoderms	<i>Asterina gibbosa</i>	9	0	0
	<i>Asterias rubens</i>	5	0	0
	<i>Amphipholis squamata</i>	5	12	4
	<i>Ophiothrix fragilis</i>	1	1	3
Fish	Juvenile fish	2	2	0

findings are consistent with a number of other studies (Norderhaug et al. 2002, Christie et al. 2003). Other well represented groups included the isopods (5%) and the echinoderms (4%), which were found to be in abundance only on the most complex holdfast mimics. Mimics of medium complexity were dominated by 1 or 2 gastropod and amphipod species (Table 1). All species found were most abundant in high complexity holdfasts, with the exception of the polychaete *Platyneries dumerilii*, the echinoderm *Amphipholis squamata* and, in particular, the amphipod *Ampithoe rubricata* which were found in highest abundances in the medium complexity holdfasts.

We found a significant treatment effect on algal dry weight (ANOVA: $F_{2,33} = 92.88$, $p < 0.001$), with virtually no algae colonising low and medium complexity holdfasts. For high complexity holdfasts, we found no significant relationship between algal dry weight and invertebrate species number (regression: $r^2 = 0.148$, $n = 12$, $p > 0.05$), invertebrate abundance ($r^2 = 0.219$, $n = 12$, $p > 0.05$), or the diversity of macrofauna ($r^2 = 0.179$, $n = 12$, $p > 0.05$).

The number of species, abundance and species diversity all increased with increasing complexity. We found significant treatment effects for abundance (ANOVA: $F_{2,33} = 53.05$, $p < 0.0001$; Fig. 2a), number of species (ANOVA: $F_{2,33} = 33.24$, $p < 0.0001$; Fig. 2b), and species diversity (ANOVA: $F_{2,33} = 25.26$, $p < 0.0001$; Fig. 2c). For all 3 variables, post-hoc SNK tests showed significant differences between high complexity habitats and medium and low complexity mimics. In the case of number of species and number of individuals, post-hoc SNK tests also showed significant differences between medium and low complexity mimics.

The number of species, individual abundance and diversity did not increase in proportion to surface area alone. Medium and high complexity habitats supported significantly more individuals (t -test: $t = 3.02$, $df = 11$, $p = 0.012$ and $t = 19.31$, $df = 11$, $p < 0.001$, respectively; Fig. 2a) and more species (t -test: $t = 4.55$, $df = 11$, $p = 0.01$ and $t = 12.48$, $df = 11$, $p < 0.001$, respectively; Fig. 2b) than expected. Species diversity increased less rapidly than expected in high complexity holdfasts (t -test: $t = 13.92$, $df = 11$, $p < 0.001$; Fig. 2c), largely because of the dominance of a few amphipod and gastropod species (Table 1).

Multivariate analysis revealed clear differences in community composition between the high complexity mimics and medium and low complexity mimics (Fig. 3), with high complexity mimics grouping discretely whereas the groupings of the medium and low complexity mimics were less well defined. ANOSIM confirmed that assemblages in high complexity mimics were significantly different from both the medium and low complexity mimics ($r = 0.73$, $p < 0.001$ and $r = 0.628$, $p < 0.001$, respectively), but those in medium and low complexity mimics were not significantly different from each other. SIMPER analysis revealed that the species composition of high complexity holdfasts was 89.16% different from that of medium complexity holdfasts, with *Dexamine spinosa* and *Rissoa parva* contributing greatly to the dissimilarities between the two (Table 2a). The species composition of high complexity holdfasts was 83.74% different from that of low complexity holdfasts, with *D. spinosa* and *Aora gracilis* contributing the most to the dissimilarity (Table 2b). Although medium and low complexity holdfasts were not found to be significantly different from each other, SIMPER analysis determined that their species compositions were 78.39% different from

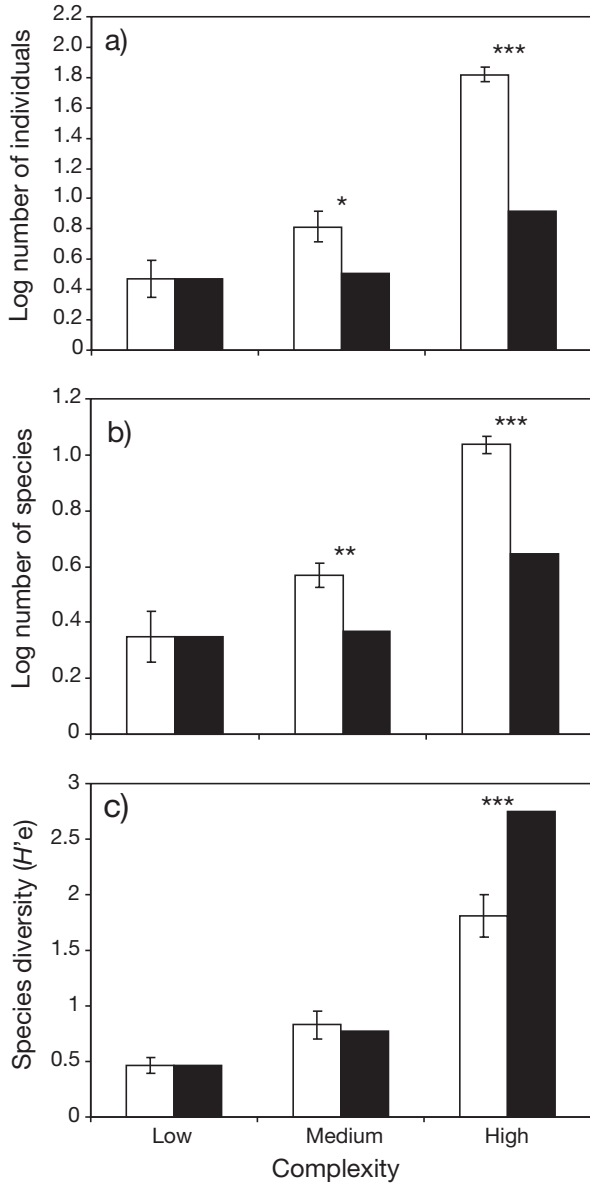


Fig. 2. Univariate assemblage indices from artificial kelp holdfasts of differing levels of complexity. White bars display the mean (\pm SE) for (a) log number of individuals ($F_{2,33} = 53.05$, $p < 0.0001$), and (b) log number of species ($F_{2,33} = 33.24$, $p < 0.0001$), and (c) Shannon-Wiener species diversity index ($H'e$) ($F_{2,33} = 53.05$, $p < 0.0001$). Black bars illustrate the predicted values based on the assumption that all indices would increase in proportion to surface area, the difference between observed and predicted values being assessed using a 1-sample t -test. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

each other, with *Ampithoe rubricata* and *R. parva* causing the main differences (Table 2c). The lack of significance between medium and low complexity holdfast composition is probably explained by the large variance in the data, especially in the low complexity mimics, as the SIMPER analysis determined that the overall similarities within low complexity mim-

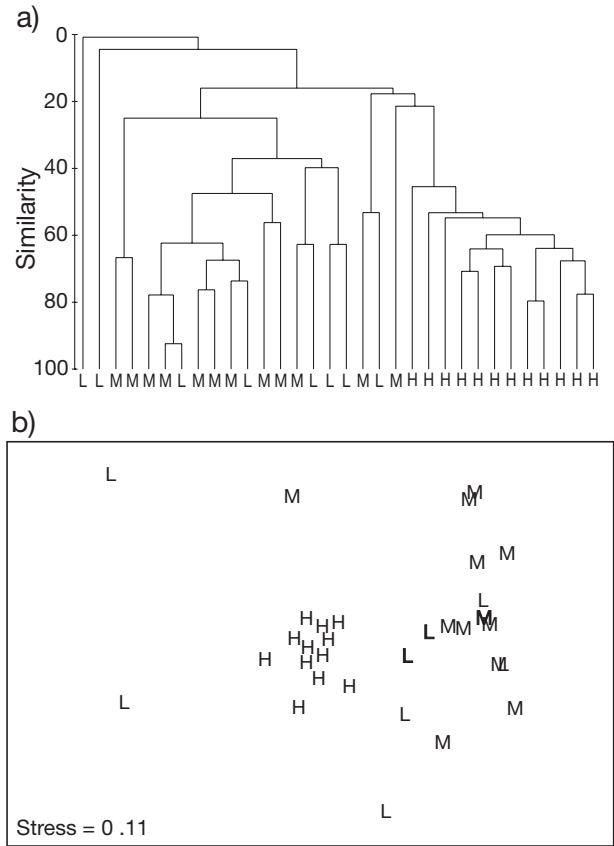


Fig. 3. (a) Results of cluster analysis (Bray-Curtis similarity index) on holdfast assemblage abundance data from high (H), medium (M) and low (L) complexity units. (b) MDS ordination of same data

ics was only 17.19%. The species compositions of high complexity and medium complexity mimics were found to be 56.74 and 30.72% similar, respectively; community similarity was therefore increasing with habitat complexity.

DISCUSSION

Our study demonstrates that high complexity habitats support a larger diversity of species, a greater abundance of individuals and a greater mass of epiphytes than medium or low diversity habitats. Increased algal complexity has been found in a number of other studies to have a significant effect on the abundance of macroinvertebrates (e.g. Hull 1997, Chemello & Milazzo 2002) as increasing the structural complexity of habitats influences a variety of biological processes. An accepted view is that the more complex the habitat, the larger the surface area available for colonisation by meiofauna, macrofauna and epiphytic algae, with high diversity being a simple species-area

Table 2. Results of SIMPER analysis displaying the average dissimilarity between macrofaunal assemblages within holdfasts of high, medium and low complexity, together with the species contributing the most to the dissimilarity between each complexity pair (cut off point 70%)

Species	Contribution (%)	Cumulative (%)	Avg. abundance		Avg. dissimilarity
			High	Medium	
(a) Avg. dissimilarity = 89.16			High	Medium	
<i>Dexamine spinosa</i>	15.40	15.40	14.67	0.25	13.73
<i>Rissoa parva</i>	11.68	27.08	15.00	1.33	10.42
<i>Aora gracilis</i>	11.51	38.60	13.00	0.08	10.27
<i>Lacuna vincta</i>	11.03	49.63	8.25	0.17	9.83
<i>Cerithiopsis tubercularis</i>	7.41	57.04	4.92	0.00	6.61
<i>Ampithoe rubricata</i>	6.20	63.25	0.25	4.50	5.53
(b) Avg. dissimilarity = 83.74			High	Low	
<i>Dexamine spinosa</i>	15.06	15.06	14.67	0.75	12.61
<i>Aora gracilis</i>	12.68	27.74	13.00	0.00	10.62
<i>Rissoa parva</i>	12.22	39.96	15.00	1.63	10.23
<i>Lacuna vincta</i>	11.03	50.98	8.25	0.63	9.23
<i>Cerithiopsis tubercularis</i>	7.70	58.68	4.92	0.25	6.45
<i>Lekanaesphaera rugicauda</i>	6.43	65.11	2.67	0.00	5.38
(c) Avg. dissimilarity = 78.39			Medium	Low	
<i>Ampithoe rubricata</i>	22.56	22.56	4.50	0.75	17.69
<i>Rissoa parva</i>	15.90	38.47	1.33	1.63	12.47
<i>Amphipholis squamata</i>	13.50	51.97	1.00	0.50	10.59
<i>Dexamine spinosa</i>	10.86	62.83	0.25	0.75	8.52

effect (Gunnill 1982b, Gee & Warwick 1994a,b). This spatial component of algal complexity has been shown to be the most important factor in determining amphipod patterns (Hacker & Steneck 1990), algae with a higher degree of branching, algal width and stem width resulting in higher abundance, greater species richness and greater diversity of many species than algae with a less complex structure (Hull 1997, Chemello & Milazzo 2002). Additionally, surface area has also been shown to be the most important factor in determining size and composition of macroinvertebrate communities in seagrass beds (Attrill et al 2000), with no clear additional effect of complexity per se. The results of this study have demonstrated that this may not be the case for kelp holdfasts. We found significant differences between the observed number of individuals and species and the number expected just from increasing available area, demonstrating that surface area alone cannot account for the increasing numbers. However, as the results show, the diversity of species (in terms of the Shannon-Wiener index) was actually lower than predicted if surface area was solely responsible for the relationship between habitat complexity and species diversity. This would suggest that diversity reaches a maximum threshold as well, after which an increase in surface area, although allowing more individuals and species to colonise, does not create an increase in diversity as measured by this particular index.

Coupled with the idea that a higher complexity can provide a greater surface area for organisms is the idea that such habitats provide a greater target for the accumulation of individuals and species transported passively by wave action. It has been shown that many organisms transport themselves through the water column by floating or rafting. This is particularly common in gastropods and bivalves such as *Mytilus edulis* (Martel & Diefenbach 1993). If a higher complexity habitat offers a greater surface area for attachment, it can also be argued that it will provide a larger surface area to catch organisms floating in the water column. Furthermore, as a higher complexity habitat may provide more resistance to water (Gibbons 1988), and consequently micro-turbulence, an organism may have a better chance of settling onto a high complexity habitat. In this study, the high complexity holdfasts contained both the highest species number and also highest abundance of all but 3 species (Table 1). It would appear, therefore, that this was an easier habitat to colonise. Only *Playneries dumerilii*, *Amphipholis squamata* and *Ampithoe rubricata* were found in higher numbers on the medium complexity habitat, and only *A. rubricata* in substantially higher numbers. It would appear therefore that *A. rubricata* is either a poor competitor or a better coloniser, thus readily able to colonise less complex habitats.

As our study demonstrated higher abundance and number of species in complex habitats than can be

explained by a simple area effect, other factors associated with complexity must also be important. Habitat complexity can affect the role that predation has to play on an assemblage. Kelp invertebrates are exposed to fish predation (Nelson 1979, Kennelly 1983, 1991, Holmlund et al. 1990, Fjøsne & Gjørseter 1996) and epifauna abundance increases when predators are removed (Kennelly 1983). A high complexity habitat can reduce predation pressures for 2 reasons. Firstly, a more complex habitat can provide more refuges for the prey by increasing the proportion of a habitat that is safe from predation (Hixon & Menge 1991); e.g. high complexity algae provide the best refuge for total meiofauna from predation (Coull & Wells 1983). Secondly, high complexity habitats can alter the foraging efficiency and encounter rates of the predator with the prey (Diehl 1992). It has been demonstrated that predators are less efficient in more dense (and thus more complex) eelgrass beds as such habitats make manoeuvring difficult and decrease the visibility of the predator (Nelson 1979). In this case, high complexity habitats certainly provided more refugia for macrofauna from predators, whereas medium and low complexity habitats offered comparatively few refugia and permitted a predator to manoeuvre easily through them. The presence of juvenile fishes in the high complexity habitats is consistent with the idea that these habitats offer good protection. These may well have been using the high complexity habitat as a nursery habitat where they could find suitable refuge from predators, although juvenile fishes occurred too infrequently to draw robust conclusions.

High complexity habitats also offer greater protection to organisms from wave abrasion. Highly complex fronds or epifauna have been shown to provide good protection from physical stress, especially from wave shock (Gibbons 1988), large flat fronds offering little resistance to water movement and thus small animals are likely to be flushed from the algae when faced with strong water movement (Gibbons 1988). A more complex habitat will offer more resistance to the water, slowing it down and thus reducing the risk of an organism being washed away, as well as potentially boosting settlement. In this case, the high complexity mimics offered a greater number of crevices in which organisms could avoid wave stresses. However, the medium and particularly the low complexity habitats offered little refuge other than on the outside of the mimic. Thus, in times of high wave pressure and water movement, it is likely that organisms would be much more likely to be flushed from the surface.

In this study, the higher complexity habitats had a larger amount of epiphytic algae growing on them. Epiphytic algae have a significant effect on faunal abundance as they increase habitat and food sources

(Martin-Smith 1993, Pavia et al. 1999). In fact it has been argued that the presence of colonising epifauna will add further intricacy to the microhabitat structure, facilitating the development of meiofaunal communities (Gunnill 1982a,b, Johnson & Scheibling 1987). Coupled with this, it is thought that increases in algal matter decrease predation by providing refuges and decreasing the efficiency of a predator, thereby increasing the number of species found on high complexity habitats (Talman et al. 2004). It might be that the increase of epiphytes on the high complexity habitats lead to a greater abundance of macrofauna by providing food and further structural complexity. However, we found that epiphyte biomass was unrelated to macrofaunal numbers or diversity within the complex holdfasts. The increase in habitat complexity clearly led to an increase in both macrofauna and epiphytic algae, but we were unable to demonstrate that they affected each other. This agrees with a number of studies which found that the presence of epiphytes has a negligible effect on the presence of epifauna and that physical aspects of the algal structure were more important than biological ones (Dean & Connell 1987, Norderhaug 2004).

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