Piddocks (Mollusca: Bivalvia: Pholadidae) increase topographical complexity and species diversity in the intertidal

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ABSTRACT: Bioerosion increases the topographic complexity of soft rock habitats, thereby increasing species diversity. This increase in species diversity may either be associated with an increase in complexity or may simply be a consequence of the increase in available surface area for colonisation. The influence of habitat modification by piddocks on intertidal species richness was investigated through field survey using fractal geometry to assess topographical complexity. The relationship between topographical complexity and species diversity was examined using the species spacing technique, which uses fractal dimensions to normalise the species richness data in relation to topographical complexity. Six sites were chosen, comprising either clay or chalk substratum, which had a range of rock hardness. Through their rock-boring activities, piddocks significantly increased the topographical complexity of the shore. Associated with this increase was an increase in species richness at all sites. Using species spacing, at 5 of the 6 sites, the increased species richness was found to be area-independent, with more species being observed than would be expected for a simple increase in surface area alone. However, piddocks are also known to significantly increase the erosion of soft rock habitats, many of which are regarded as being of particular conservation importance because of their rarity within Europe. Piddocks thus increase intertidal biodiversity while at the same time significantly contributing to erosion of the substratum.

KEY WORDS: Biodiversity · Burrow morphology · Ecosystem engineers · Fractal dimensions · Habitat complexity

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INTRODUCTION

The assemblage of organisms that is present at a particular location is the product of physical processes and biological interactions. Acting together, these restrict or enhance the ability of individuals to survive, grow and reproduce. One potentially important interaction is the role of habitat-modification in organising natural communities via ecosystem engineering (Jones et al. 1997). Ecosystem engineers are defined as organisms that modify habitats and the availability of other resources, thereby strongly affecting the pat-

terns of distribution and abundance of other species (Jones et al. 1994). Since its introduction, there has been much debate about the value of the ecosystem engineer concept (e.g. Wilby 2002, Berkenbusch & Rowden 2003). The concept does, however, account for processes occurring between organisms and their environment that are not directly trophic or competitive, and which result in habitat modification, maintenance or creation.

Ecosystem engineers can be broadly divided into 2 types: autogenic and allogenic. Autogenic engineers change the environment via their own physical struc-

tures, i.e. living and dead tissues, whereas allogenic engineers change the environment through their behaviour and activity. However, some species can have both effects. For example, upright bivalve shells projecting from the substratum alter the water flow regime and can provide protection from predation (autogenic engineering), while their feeding activities remove particles from the water, and the production of faeces and pseudofaeces influences the organic matter content of the sediment and, consequently, its associated infauna (allogenic engineering; Commito & Rusignuolo 2000, Norkko et al. 2006, Spooner & Vaughn 2006).

Although often overlooked because of their cryptic lifestyle, piddock bivalves belonging to the family Pholadidae are among the dominant organisms of many intertidal and subtidal soft rock habitats (chalk, limestone, clays, peat and sandstone). Three species of piddock commonly occur on the English south coast: the common piddock *Pholas dactylus* L., the white piddock *Barnea candida* (L.) and the little piddock *B. parva* (Pennant). Piddocks create conical burrows, with a narrow entrance and a larger rounded chamber, by using their shell to mechanically erode the substratum. These rock-boring activities modify soft rock environments by creating crevices and holes, thereby increasing topographical complexity. For the purposes of this study, we considered that piddocks are allogenic ecosystem engineers and that their rock-boring activities result in changes to topographical complexity and, consequently, to species richness.

Increasing topographic complexity generally leads to increased species diversity and abundance (Chapman 2000). However, this may be due to increased area of substratum or as a result of increased habitat diversity (Johnson et al. 2003). The effects of topographical complexity and habitat diversity on biodiversity are difficult to separate. For example, increasing topographical complexity on rocky shores can create mosaics of microclimate (Johnson et al. 1998) and provide refuges from physical and biological disturbances (Menge et al. 1985, Bergeron & Bourget 1986). A few studies have successfully managed to separate the effects of topographical complexity and habitat diversity; examples include Pennycuick (1992), Johnson et al. (2003) and Kostylev et al. (2005).

The overall aim of this study was to assess whether ecosystem engineering by piddocks has an affect on intertidal species richness. We hypothesised that their rock-boring activities would significantly increase topographical complexity, in turn influencing species richness. The extent of this influence may vary depending on rock type and hardness. We also attempted to distinguish between the area-dependent effects of topographical complexity (i.e. an increase in biodiver-

sity due to a simple increase in surface area) and area-independent effects (i.e. the increase in biodiversity is greater than expected due to associated changes in habitat diversity).

MATERIALS AND METHODS

Site description. Six sites were chosen for this work, encompassing a variety of soft rock habitat types: Lyme Regis (clay); Bembridge Ledges, Isle of Wight (clay); Compton, Isle of Wight (clay); Newhaven (chalk); and 2 locations at Eastbourne (location 1: the Pound, chalk, hereafter referred to as Eastbourne chalk; location 2: south-east of the Pound, clay, hereafter referred to as Eastbourne clay; Fig. 1). All sampling was undertaken at low water during spring tides, the only time the piddock beds were exposed for short periods. The hardness of the substratum at each location was assessed as the reciprocal of the mean depth of 10 replicate holes of 6 mm diameter drilled for 10 s (Evans 1968). This method served as a good proxy for the relative difficulty that a piddock might experience in creating its burrow. The positions chosen at each site to assess substratum hardness were selected randomly, although positions were constrained by the presence of piddock burrows.

Topographical complexity. Due to the friable nature of the rock substratum and the limited sampling time available at mean low water spring (MLWS), it was not possible to use casting methods such as that described by Commito & Rusignuolo (2000) to assess topographical complexity. Instead, profiles of the substratum were drawn at each site using a profile gauge made up of 300 1 mm plastic sliders held perpendicular to the rock surface. Ten profiles were taken on substratum inhabited by piddocks and 10 without piddocks at each site. The positions chosen at each site to assess topographical complexity were selected randomly. However, for the non-piddock influenced habitat of the same substratum at the same height on the shore, the positions used were constrained by the presence of piddock burrows.
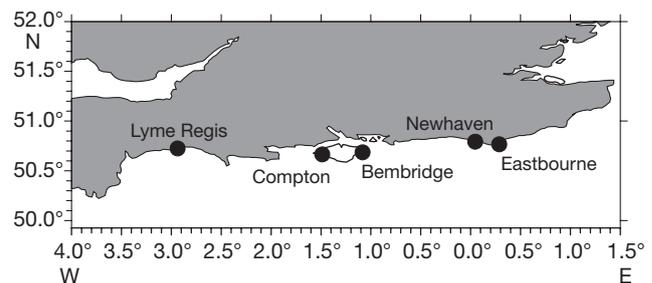

Fig. 1. Sampling sites on the south coast of England

The influence of piddock borings on topographical complexity was analysed using fractal geometry. Fractals have regularly been used as a means of descriptive parameterisation of patterns of tortuosity and topographical complexity (Nams 1996, Frost et al. 2005). The fractal dimension characterises the extent to which the fractal fills up the embedding space. In our study, this could vary between 1 for a completely straight line and 2 for a line that completely fills the plane on which it occurs. We recognised that the fractal dimension of each profile from the piddock-influenced habitat would be underestimated, as a profile gauge cannot measure a surface with an overhang, such as that presented by the rounded chamber of a piddock burrow. However, the risk of a type 2 error in the statistical analysis due to the underestimate was considered acceptable.

The profiles were digitised using TechDig 2.0 (R.B. Jones[©]). The fractal dimension (D) of each digitised profile was evaluated using the Fractal programme (Nams 1996). The mean fractal was calculated, which estimates the fractal D using a re-sampling version of the divider method. The fractal Ds of areas with and without piddocks were compared using 2-way analysis of variance (ANOVA) for the factors site and the presence or absence of piddocks. Prior to analysis, data were tested for homogeneity of variances using Levene's test. Heterogeneous data were transformed using Log($D-1$) (Nams 1996). However, in most cases this transformation did not remove the heterogeneity. Therefore, analyses were conducted on the untransformed data, but with a more conservative probability ($\alpha = 0.01$; Underwood 1997, Pinn et al. 2005a). Where significant results were obtained, Tukey's post hoc tests were used to compare differences between sites.

Biodiversity. While the piddocks were alive, no other species were observed living within the confines of the burrow. Consequently, burrows no longer occupied by piddocks (hereafter referred to as old piddock burrows) were surveyed to assess which intertidal species used them.

The influence of piddocks on biodiversity was assessed through a comparison of the species richness of 3 microhabitat types: old piddock burrows, crevices and surface rock. However, at the 2 Eastbourne sites and the Newhaven site, the crevice microhabitat was not present and so comparisons were made only between old piddock burrows and surface rock microhabitats. Due to difficulty of sampling the old piddock burrows with standard quadrat techniques, the following methodology was adopted. From existing burrow morphology data (Pinn et al. 2005b), it was estimated that any 5 randomly selected burrows were approximately equivalent in surface

area to 100 cm². The inhabitants of 100 piddock burrows were therefore compared to 20 10 cm × 10 cm quadrats from the crevice and surface rock microhabitat types at each site. The results were analysed using 2-way analysis of similarities (ANOSIM) and multidimensional scaling (MDS; PRIMER, Clarke & Warwick 2001).

These investigations indicated some variation in old burrow usage related to burrow size. Consequently, a further investigation was undertaken, and the occupants of 20 randomly selected burrows for each of 3 different size categories (<6 mm, 8 to 12 mm and >14 mm burrow aperture diameter) were recorded on each shore. Variation in occupancy between burrow sizes and sites were compared using a G-test.

The species spacing (S) methodology of Pennycuick (1992) was used to assess whether any species richness changes observed were area-dependent or independent. Species spacing uses fractal geometry to normalise species richness data (N) in relation to topographical complexity:

$$S = (E/N)^{1/D} \tag{1}$$

where $E = ns^D$ (s is the step length, and n is the number of steps for a particular fractal dimension, D). A reduction in the space between 2 individual species indicates an increase in species richness that is area-independent, i.e. increases in species richness are greater than can be accounted for by the increase in surface area alone. No change in species spacing or an increase in the spacing indicates that any changes in species richness are the result of an increase in the surface area of available substratum.

Because of the way in which the fractal and species richness data were collected, species spacing estimates could only be made at a broad scale, i.e. habitats with and without piddocks. As a consequence, the species richness data collected for the surface rock and crevice microhabitats were considered to represent a non-piddock influenced shore, whereas the complete species richness data set (surface rock, crevice and old burrow microhabitats) represented shores influenced by piddocks.

RESULTS

Substratum hardness and topographical complexity

The rank order of hardness was Eastbourne chalk (5.4), Lyme Regis clay (2.9), Newhaven chalk and Bembridge clay (2.1), Compton clay (1.8) and Eastbourne clay (1.0).

The substratum profiles for areas containing piddocks were topographically more complex than those
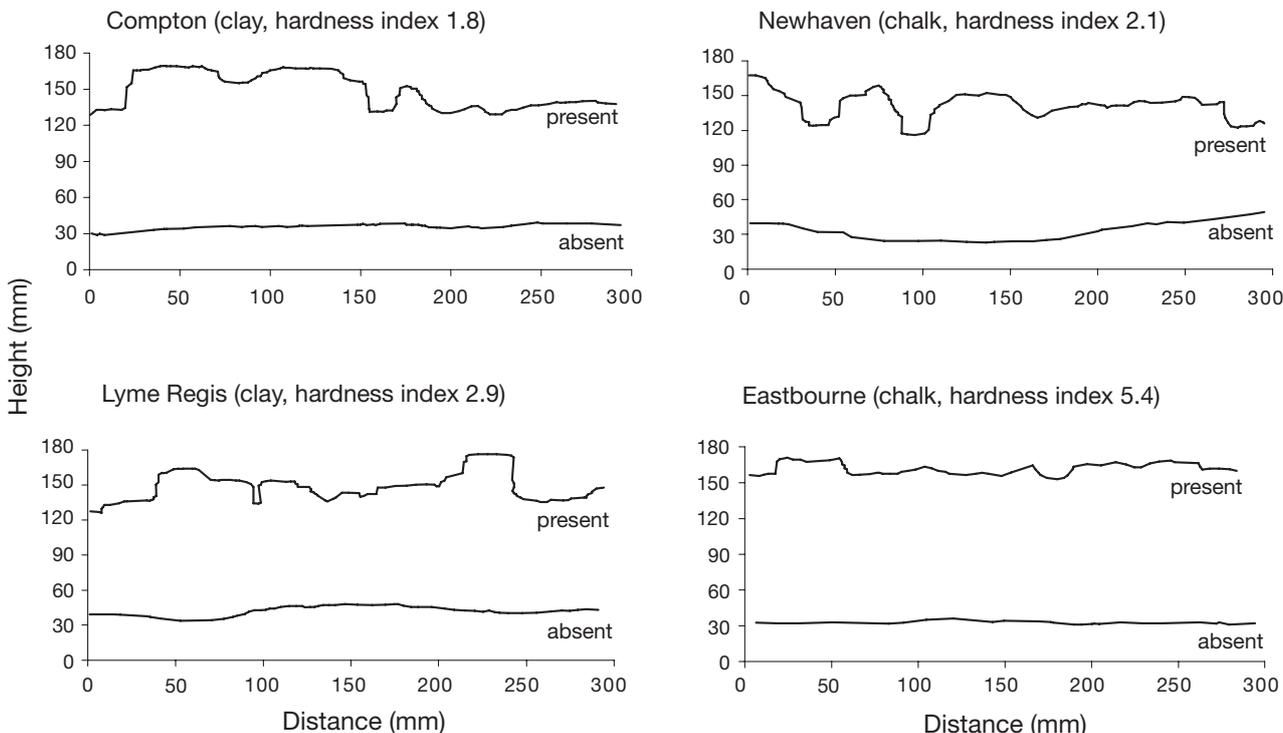
Fig. 2. Examples of substratum profiles (upper profile, with piddocks; lower profile, without piddocks)

without piddocks (Fig. 2). When piddocks were absent, the clay sites were generally smoother than the chalk sites. An example of the log-log plots used to estimate the fractal dimension is given in Fig. 3A. The presence of piddocks increased the fractal dimension, and also made it more variable (Fig. 3B). No significant relation-

ship was observed between topographic complexity and hardness in the absence of piddocks ($p > 0.05$, $p = -0.034$). However, when piddocks were present, a significant negative relationship was observed ($p < 0.001$, $p = -0.254$) indicating that the effect of piddocks was greater on softer rock.
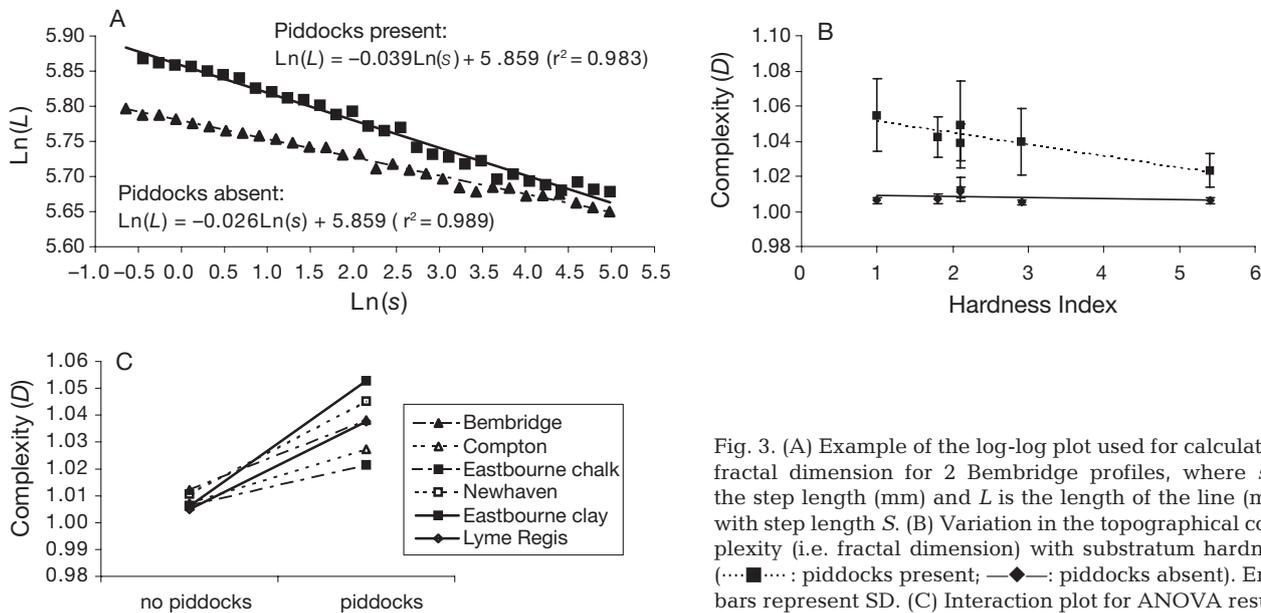

Fig. 3. (A) Example of the log-log plot used for calculating fractal dimension for 2 Bembridge profiles, where s is the step length (mm) and L is the length of the line (mm) with step length S. (B) Variation in the topographical complexity (i.e. fractal dimension) with substratum hardness (·····■·····: piddocks present; —◆—: piddocks absent). Error bars represent SD. (C) Interaction plot for ANOVA results

Two-way ANOVA demonstrated statistically significant differences in the fractal dimension due to the presence of piddocks (p < 0.001, F = 1125.95) and between sites (p < 0.001, F = 21.36). Tukey's post hoc tests revealed that Eastbourne chalk and Lyme Regis were significantly different from each other and all other sites, being more topographically complex than the other sites. In addition, these sites were considerably harder than all others (hardness index: Eastbourne chalk = 5.4, Lyme Regis = 2.9, all other sites ≤2.1). Compton, Bembridge, Newhaven and Eastbourne clay were not significantly different from one another. These sites were the softest investigated, with indices ranging from 1.0 to 2.1. In addition, a significant interaction between piddock absence/presence and site was observed (p < 0.001, F = 19.11). Although the fractal dimension was always significantly higher in the presence of piddocks (p < 0.001), the degree of change was not consistently related to the hardness index of the site (Fig. 3C). For example, as might be expected, the highest and lowest degrees of change were observed at the softest (Eastbourne clay) and hardest (Eastbourne chalk) sites, respectively. However, at intermediate levels of hardness, the degree of change observed in the fractal dimension of the site as a consequence of the piddock burrows did not follow the same order as changes in hardness.

Biodiversity

While the piddocks were alive, no other species were observed living within the confines of the burrows. At most sites, approximately 70 to 80% of the burrows contained live piddocks (Eastbourne clay: 73%; Bembridge: 78%; Newhaven: 77%; Lyme Regis: 68%; Eastbourne chalk: 78%). The exception was Compton, where only 8% of the burrows were occupied by piddocks. Approximately 20% of the old piddock burrows were occupied by new species, and the remainder were either empty or filled with sediment.

A range of species was present in the old burrows, the majority of which were vagile rather than sessile; the most common were *Littorina littorea*, *Porcellana platycheles*, *Gibbula cineraria*, *Patella vulgata*, *Eulalia viridis*, Sabellidae and *Lithothamnia* spp. (Table 1).

Using species richness as a simple measure of diversity, the presence of piddock burrows was found to

Table 1. Percentage of old piddock burrows inhabited by new species

| Site (substratum)	Hardness	Species	%
Eastbourne (clay)	1.0	*Gibbula cineraria* (Mollusca, Gastropoda)	2
		Littorina littorea (Mollusca, Gastropoda)	4
		Pomatoceros lamarcki (Annelida, Polychaeta)	1
		Lanice conchilega (Annelida, Polychaeta)	1
		Eulalia viridis (Annelida, Polychaeta)	6
		Scolelepis foliosa (Annelida, Polychaeta)	3
		Porcellana platycheles (Crustacea, Decapoda)	2
		Lithothamnon (Rhodophyta)	2
		Ulva lactuca (Chlorophyta)	1
Compton (clay)	1.8	*Anemonia viridis* (Cnidaria, Anthozoa)	1
		Porcellana platycheles (Crustacea, Decapoda)	10
		Sabellidae (Annelida, Polychaeta)	8
		Platynereis dumerilii (Annelida, Polychaeta)	3
		Littorina littorea (Mollusca, Gastropoda)	2
		Amphipoda (Crustacea)	4
Bembridge (clay)	2.1	*Gibbula cineraria* (Mollusca, Gastropoda)	4
		Littorina littorea (Mollusca, Gastropoda)	5
		Anemonia viridis (Cnidaria, Anthozoa)	1
		Pilumnus hirtellus (Crustacea, Decapoda)	1
		Pagurus bernhardus (Crustacea, Decapoda)	1
		Carcinus maenas (Crustacea, Decapoda)	6
		Platynereis dumerilii (Annelida, Polychaeta)	3
		Porcellana platycheles (Crustacea, Decapoda)	2
		Lithothamnia spp.	2
Newhaven (chalk)	2.1	*Gibbula cineraria* (Mollusca, Gastropoda)	2
		Littorina littorea (Mollusca, Gastropoda)	5
		Patella vulgata (Mollusca, Gastropoda)	2
		Pomatoceros lamarcki (Annelida, Polychaeta)	3
		Nucella lapillus (Mollusca, Gastropoda)	1
		Mytilus edulis (Mollusca, Bivalvia)	6
		Porcellana platycheles (Crustacea, Decapoda)	2
		Actina equina (Cnidaria, Anthozoa)	1
		Owenia fusiformis (Annelida, Polychaeta)	2
		Nephasoma minutum (Sipuncula, Golfingiidae)	3
Lyme Regis (clay)	2.9	*Gibbula cineraria* (Mollusca, Gastropoda)	7
		G. umbilicalis (Mollusca, Gastropoda)	2
		Littorina littorea (Mollusca, Gastropoda)	7
		Patella vulgate (Mollusca, Gastropoda)	1
		Nucella lapillus (Mollusca, Gastropoda)	1
		Pomatoceros lamarcki (Annelida, Polychaeta)	1
		Liparis montagui (Pisces)	2
		Lithothamnion (Rhodophyta)	5
Eastbourne (chalk)	5.4	*Gibbula cineraria* (Mollusca, Gastropoda)	2
		Patella vulgate (Mollusca, Gastropoda)	5
		Porcellana platycheles (Crustacea, Decapoda)	3
		Malacoceros fuliginosus (Annelida, Polychaeta)	3
		Alvania semistriata (Mollusca, Gastropoda)	4
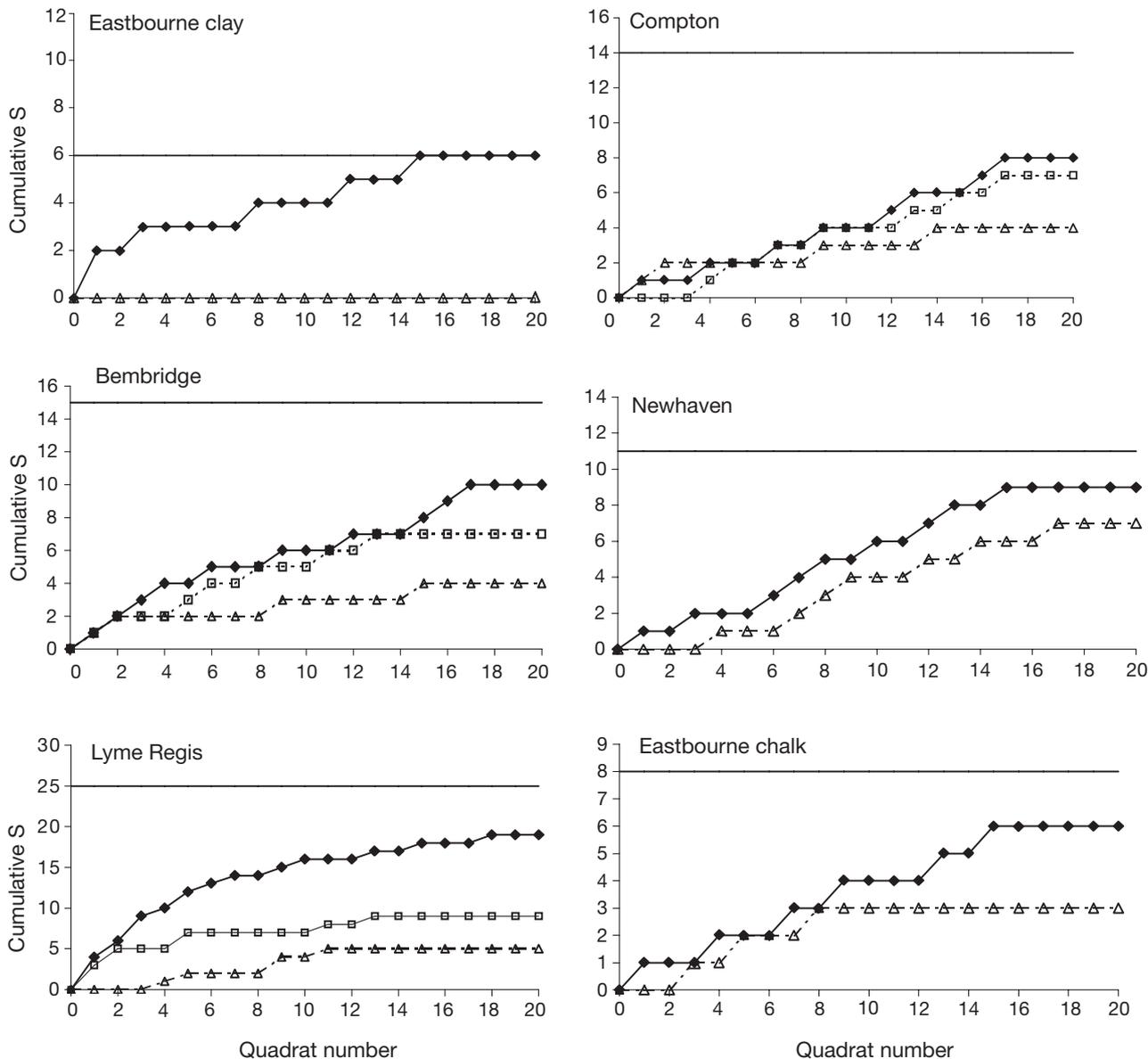
Fig. 4. Comparison of species richness (S) between sampling sites and old piddock burrows (◆), crevices (□) and surface rock (△). Horizontal line without symbols represents total species richness for site

increase the number of species present (Fig. 4). Compared to substratum hardness, the increase in species richness was greatest for mid-level hardness and lowest in the softest and hardest substrata (Fig. 5A). However, this was not related to piddock density (Fig. 5B). MDS indicated that the assemblages observed in old burrows were generally different from those found in piddock-like and surface rock microhabitat types (Fig. 5C). Two-way nested ANOSIM of the 3 microhabitat types (old burrows, crevices and surface rock) indicated significant variation between sites and microhabitat type (Table 2).

Of the old piddock burrows occupied, a distinct variation in the degree of occupancy was observed in relation to burrow size. Medium (8 to 12 mm burrow aperture) and larger (>14 mm aperture) burrows were used more regularly, whereas small burrows (<6 mm aperture) were often not occupied (Fig. 6A). These differences were significant (p < 0.001, G [10] = 80.16). Species richness was also highest in the medium and large burrows (Fig. 6B). However, there was no obvious variation in the occupancy or species richness in relation to substratum type or hardness (Fig. 6).
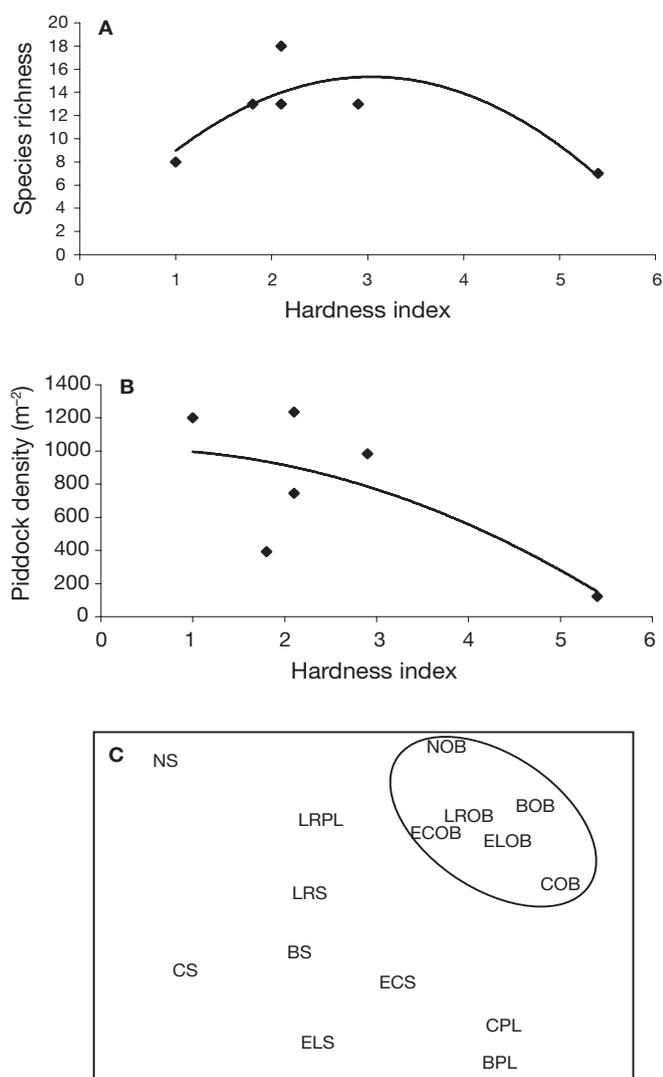
Fig. 5. (A) Species richness and (B) piddock density in relation to substratum hardness and (C) MDS plot. B: Bembridge; C: Compton; EC: Eastbourne clay; EL: Eastbourne chalk; LR: Lyme Regis; N: Newhaven; S: surface rock habitat; OB: old burrow habitat; PL: crevice habitat

Fig. 6. (A) Occupancy of old piddock burrows by other intertidal species and (B) mean (± SD) species richness per burrow in relation to burrow size and site

Species spacing, which uses fractal geometry to normalise species richness in relation to topographical complexity, was used to compare species richness from non-piddock habitats to areas that were influenced by piddocks. Species spacing was approximately 30 to 35% lower in the presence of piddocks, i.e. more species were observed than would be expected for a simple increase in surface area (Table 3). At 1 site, Eastbourne clay, the reduction in species spacing was much greater (83%). In contrast, at Lyme Regis there was a slight increase in species spacing, indicating that there was little change in the distance between species and that any observed increase in species richness was a result of the increased surface
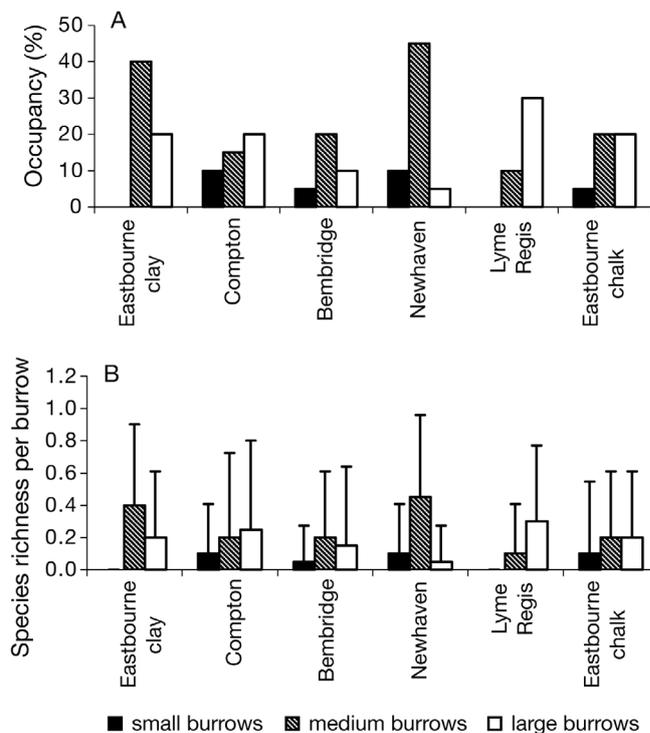
area available (Table 3). With the exception of Lyme Regis, increases in species richness associated with piddock burrows were an area-independent effect and may therefore be considered to be due to greater habitat complexity rather than an increase in surface area alone.

Table 2. ANOSIM results with significant effects presented in bold. OB: old burrows; C: crevice habitat; SR: surface rock only

Microhabitat types	R	p
OB vs. SR		
Microhabitat	0.664[a]	**0.001**
Sites	0.202[a]	**0.001**
Eastbourne Chalk vs. Eastbourne Clay	0.132	**0.001**
Eastbourne Chalk vs. Newhaven	0.216	**0.001**
Eastbourne Clay vs. Newhaven	0.302	**0.001**
OB vs. SR vs. C		
Microhabitat	0.339[a]	**0.001**
Piddock-like vs. surface	0.121	**0.001**
Piddock-like vs. old burrows	0.444	**0.001**
Surface vs. old burrows	0.603	**0.001**
Sites	0.176[a]	**0.001**
Lyme Regis vs. Compton	0.211	**0.001**
Lyme Regis vs. Bembridge	0.143	**0.001**
Compton vs. Bembridge	0.200	**0.001**
[a]Global R		

Table 3. Influence of piddock presence on species spacing, a statistic that uses fractal geometry to normalise species richness in relation to topographical complexity

Site	Species spacing		% reduction due to the presence of piddocks
	Piddocks absent (mm)	Piddocks present (mm)	
Eastbourne clay	261.71	44.49	83.0
Compton clay	25.52	23.61	7.5
Bembridge clay	24.60	17.14	30.3
Newhaven chalk	37.53	26.38	29.7
Lyme Regis clay	24.14	24.76	−2.5
Eastbourne chalk	69.00	42.97	37.7

DISCUSSION

Our work clearly demonstrates the importance of piddocks as habitat modifiers and their subsequent influence on intertidal biodiversity. In recent years, a considerable volume of work has been devoted to the influence of habitat complexity on species richness (e.g. Chapman 2000, Diaz et al. 2003). Although the influence of habitat complexity is positive for many species (e.g. Bradshaw et al. 2003), some negative influences have also been observed (e.g. Kelaher 2003).

The majority of species observed using old piddock burrows were vagile rather than sessile, and it is likely that the friable nature of the substratum, which makes it very easy to erode by both physical and biological means, prevented the successful colonisation by sessile species that are some of the main space-occupying species in the intertidal. Vagile species are often limited in their diversity and abundance in the intertidal because of the lack of available shelter during low tide. Biodiversity, in terms of species richness, is therefore higher when suitable microhabitats for vagile species are present in addition to those available for sessile species. Piddock burrows provide more shelter for vagile species than irregularities in the naturally occurring substratum such as crevices and thus enhance the abundance and diversity of intertidal species low on the shore.

Increases in species richness associated with greater topographical complexity could be due simply to the increased area of substratum available for colonisation (i.e. an area-dependent effect) or due to an increase in habitat complexity (i.e. an area-independent effect). On 5 of the 6 shores investigated, we demonstrated that the increase in species richness associated with piddock borings was area-independent, i.e. the increase in species richness was greater than would be expected for the increase in surface area alone. In

addition, on all shores, the preferential use of medium and larger old piddock burrows by new occupants was observed, with small burrows rarely being occupied. This is most likely due to the size distribution of the species observed on the shore.

Johnson et al. (2003) noted similar area-independent effects on rocky shores in the Isle of Man but not in southwest England, while Kostylev et al. (2005) reported that changes in surface area alone accounted for the increase in species diversity on rocky shores in Hong Kong. Similar area-dependent results were obtained for Lyme Regis in the current study. Johnson et al. (2003) concluded that regional differences in the effect of topographical complexity on biodiversity were related to environmental conditions, citing variation in crevice microclimate as the most likely explanation; crevices maintained a microclimate on the Isle of Man, whereas in the warmer southwest England, crevices dried out completely during the tidal cycle and so did not provide any effective form of refuge. At the centimetre topographical scale, piddock burrows are relatively deep (maximum recorded depth = 8.1 cm; Pinn et al. 2005b). Hence, by comparison to most crevices, they are much more likely to maintain a damp microclimate throughout the tidal cycle. As a consequence, piddock-influenced shores in southern England usually showed an increase in habitat complexity leading to an area-independent positive effect on species richness.

In the current study, there was variation in the degree to which species richness was affected by topographical complexity. For example, in clay at Eastbourne, an 83% reduction in species spacing was observed, whereas at most other sites this was 30 to 40%. Pinn et al. (2005b) reported that the Eastbourne clay site had one of the highest densities of piddocks (1200 ± 488 m^{-2}) and was dominated by larger, older individuals of all 3 species, particularly *Pholas dactylus*, the largest of the northern European species. As a result, the burrows available for colonisation were numerous and medium to large in size, i.e. those favoured for occupation by new species. In addition, this site was comprised of the softest rock of all sites investigated and, consequently, was likely to be subject to the greatest rate of physical wave erosion, which would increase burrow aperture and hence their suitability for colonisation.

Conversely, only a small decrease (7%) in species spacing was observed at Compton. The piddock population of this site was much less dense (391 ± 110 m^{-2}) and dominated by *Barnea candida*, the smallest of the British piddock species (Pinn et al. 2005b). Despite being comprised of the second softest rock, the burrows available for colonisation were relatively small

even taking physical erosion into account, and few were utilised.

In contrast to the other sites, the increase in species richness associated with piddock burrows at Lyme Regis was area-dependent, i.e. purely the result of increased surface area for colonisation. Piddock density (986 ± 295 m^{-2}) and dominating species (*Pholas dactylus*) cannot explain this difference, nor can substratum hardness or the rates of physical erosion (other sites had both higher and lower index values). One major difference was observed in the nature of the substratum at Lyme Regis compared to the other sites. At Lyme Regis, the clay was overlaid with a layer of hard limestone. As a result of physical wave erosion at the site, the limestone often overhangs and shades the clay. Consequently, piddock burrows were less likely to provide additional habitat diversity beyond that found in shaded crevices.

The current study has clearly demonstrated that piddocks are allogenic ecosystem engineers. Through their rock-boring activities, piddocks significantly increased the topographical complexity of the shore. Associated with this increase was a significant increase in species richness. At 5 of the 6 sites, the increase in species richness was area-independent. Consequently, piddocks increase intertidal biodiversity, while at the same time contributing to the erosion of the substratum (loss in volume of approximately 41.1 % of the top 8.5 cm layer of rock over a 12 yr period; Pinn et al. 2005b). Many of these soft rock shores are of particular conservation importance due to their rarity within Europe. For example, the UK has an international responsibility to conserve littoral and sublittoral chalk habitats, as this country has 57 % of the European total and many of the best examples of this habitat type.

Crain & Bertness (2006) advocated the use of ecosystem engineers as target species for conservation, since the management of such species will ultimately protect numerous associated species. They proposed that ecosystem engineers alleviate biotic and abiotic stresses, expand the distributional limits for many species and often form the foundation for community development. For example, human exploitation of a related rock-boring bivalve, the date mussel *Lithophaga lithophaga*, has led to significant desertification and loss of biodiversity on large stretches of the coastline in the Mediterranean (Fanelli et al. 1994, Fraschetti et al. 2001, Guidetti et al. 2003). Conversely, the cold winter of 1962/63 had a dramatic effect on intertidal fauna in southern Britain, including piddocks (Crisp 1964). Piddocks are now abundant again throughout much of the eastern English Channel (Pinn et al. 2005b). Concurrent with this increase will be a parallel increase in intertidal species richness.

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