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Effects of patch shape in intertidal algal mosaics: roles of area, perimeter and distance from edge

Abstract Shape is considered an important attribute of patches, but little attention has been paid to its influence on the structure and dynamics of rocky shore assemblages. Effects of patch shape were investigated from September 1997 to June 1998 in algal assemblages on intertidal shores at Cape Banks, south of Sydney (NSW, Australia). Three experiments were established, in order to separately investigate the importance of three different characteristics of patch shape, namely area, perimeter and distance of the central zone from the edge. In each experiment, responses for sets of replicate patches that differed on average for only one shape characteristic were compared. Patches of different shapes were produced by scraping off all resident organisms, and subsequent colonisation was recorded. The range of shapes naturally occurring at the study sites was also measured over 1 year, and the shapes of plots used in the experiments were chosen to cover this range of natural variability. Shapes of natural patches within assemblages were very variable. Consistent differences were observed in patch size, geometry and characteristics of the substratum among sheltered and exposed shores and among different times of the year, suggesting that different disturbances influence the dynamics of assemblages at these sites. The results of the three experiments showed that shape may have important effects on patch colonisation. Area, perimeter and distance of the central zone from the edge significantly affected growth of algae in experimental clearings. Responses to different patch characteristics were species specific. Effects of different attributes of patch shape also varied over time. This spatial and temporal variability of responses suggests that colonisation processes of patches of different shapes are complex, probably involving effects that can produce contrasting results. Results are relevant to the design and interpretation of field experiments, as they suggest that the shape of plots may affect the perception of patterns and processes in intertidal assemblages.

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Introduction

Patchiness is an important property of many natural assemblages (Sousa 1984a; Pickett and White 1985; Shorrocks and Swingland 1990). Mosaics of patches result from complex interactions between disturbances, climate, substratum heterogeneity and biota, and increased attention among ecologists to spatial heterogeneity has raised awareness about the importance of understanding the nature and causes of patchiness and how organisms respond to patch structure (Wiens 1976; Whittaker and Levin 1977; Johnson et al. 1997). In rocky intertidal and subtidal assemblages, physical and biological disturbances associated with partial or total loss of biomass have been recognised as primary mechanisms that generate mosaics of patches at different stages of recovery and that control abundance and diversity of species (Dayton 1971; Menge 1976; Sousa 1979, 1984a, 2001; Paine and Levin 1981; Menge et al. 1993; Airoldi 2000a, 2003). Waves, excessive heat, scour from sediment and other debris, grazing, predation, diseases and senescence are examples of natural disturbances that cause mortality of organisms and open discrete patches of open space (Southward 1964; Dayton 1971; Hawkins and Hartnoll 1983; Williams 1993; Airoldi and Virgilio 1998). Humans can also increase patchiness through various activities, including collection of a range of organisms for food, bait or aquaria,

trampling and boat anchoring (Kingsford et al. 1991; Dye 1993; Keough and Quinn 1998; Fraschetti et al. 2001; Moreno 2001). Sometimes extreme disturbances can disrupt large portions of the assemblages (McCook and Chapman 1997). More frequently, however, disturbances occur at spatial scales small relative to the area of the habitat, thus creating localised, discrete gaps of open space that are rapidly colonised by recruitment of propagules or lateral extension of surrounding residents (Palumbi and Jackson 1981; Connell and Keough 1985; Dye 1993; Airoldi 1998).

Patches released by variable disturbances may vary in many traits, including size, shape, boundary characteristics, microhabitat structure, position, and time of creation (Paine and Levin 1981). All these traits are believed to influence patterns of recovery of species within patches and to affect the overall structure and diversity of rocky shore assemblages (Connell and Keough 1985; Sousa 1985). Some studies, for example, have observed that the shapes of colonisation curves differed among patches of different sizes, affecting the composition and abundance of species during succession (Jackson 1977; Sousa 1984a; Farrell 1989; Dye 1993; Benedetti-Cecchi and Cinelli 1994; Kim and DeWreede 1996; McCook and Chapman 1997; Anderson 1998; but see Keough 1984 and Airoldi 1998). This has been explained as a consequence of both the greater area per se (e.g. large clearings might sample a greater proportion of available propagules) and changes in the ratio of perimeter length to area (P/A) (e.g. responses of organisms to edges could be more important in smaller patches). No studies have, however, clearly distinguished between the roles of these two factors, probably due to difficulties in designing unconfounded experiments (for a discussion about these problems see "Materials and methods—Field experiments"). The influence of the shape of a patch has been considered an extension of the P/A argument, because the more circular a patch, the lower its P/A (Sousa 1985). Probably, however, the effects of shape are more complex and include factors such as the distance of its central zone from the edge, complexity of edges, orientation, contact with different microenvironments, etc. Shape has been demonstrated to be one of the most important attributes of patches in influencing the abundance and distribution of species in various terrestrial habitats (Game 1980; Gutzwiller and Anderson 1992; Hamazaki 1996; Farina 1998; but see Harper et al. 1993). Observations suggest that shape may be an important factor in influencing the structure of assemblages in marine systems (Raimondi 1990; Oren et al. 1997). So far, however, relatively little attention has been paid to the influence of patch shape on recovery dynamics in marine rocky shore assemblages, and even qualitative observations of patch-shape characteristics are rarely reported.

It is common to use experimentally cleared patches in studies on community structure and dynamics on rocky shores (Osman 1977; Sousa 1979, 1984a; Underwood 1980; Hawkins 1981; Paine and Levin 1981; Keough

1984; Farrell 1989; Dye 1993; Menge et al. 1993; Benedetti-Cecchi and Cinelli 1994; Minchinton 1997; Airoldi 1998, 2000a). In recent studies, increasing attention has been paid to the choice of the appropriate size of clearings, based on surveys of the sizes of naturally occurring patches. It is, in fact, now evident that the variable species composition and dynamic interactions observed among patches may depend on their sizes (Paine and Levin 1981; Keough 1984; Navarrete and Castilla 1990; Kim and DeWreede 1996). The problem that the shape of the plots might affect the outcome of field experiments in rocky shore assemblages has, however, rarely been questioned. The shape of patches is generally chosen based on logistical reasons rather than on similarity to naturally occurring patches, with possible untested consequences in terms of interpretation of field experiments.

In the present study, I investigated the effects of patch shape on recovery dynamics in algal dominated assemblages on intertidal rocky shores south of Sydney (NSW, Australia). I will use the term "patch" to indicate a localised, discrete, uniform gap of rock surface clean of all macroscopic, visible organisms, except encrusting algae, within a continuous stand of non-encrusting macroalgae (possible effects of encrusting algae are discussed in "Materials and methods"). I will use the term "shape" to indicate all possible characteristics connected with the dimensions and spatial configuration of a patch, including, among others, area, perimeter and distance of the central zone from the edge. In this sense the term shape has a broad meaning similar to that used in landscape ecology (Farina 1998), while the term "geometric shape" will be used to refer only to regular shapes, such as a square, circle, triangle, etc. Three experiments were carried out to separate some possible effects of patch shape. The experiments involved the manipulation of patch characteristics, and were specifically designed to test whether colonisation of species differed among patches of different areas, perimeters, or distances of the central zone from the edge, independently of other attributes of shape. The range of shapes naturally occurring at the study sites was recorded over 1 year, and the shapes of plots used in the experiments were chosen to cover such natural variability.

Materials and methods

Study sites

The study was carried out on intertidal rocky shores (hereafter stations) within the Cape Banks Scientific Marine Research Area (hereafter referred to as Cape Banks), on the northern headland at the entrance to Botany Bay, N.S.W., Australia (Fig. 1). The area is a conservation reserve, which provides legislative protection from human disturbance, although enforcement does not appear to be stringent. All stations were gently sloping, sandstone platforms, exposed to low to intensive wave action (Short and Trenaman 1992). Studies were conducted at low tidal levels (0.4–1 m above local datum, Indian low water spring tide level), within dense stands of non-encrusting macroalgae. These were generally < 5 cm

Fig. 1 Map of the study site, with location of the seven stations used in the studies. *Numbers* indicate the stations where patch characteristics were monitored, while *letters* indicate the stations used in the field experiments
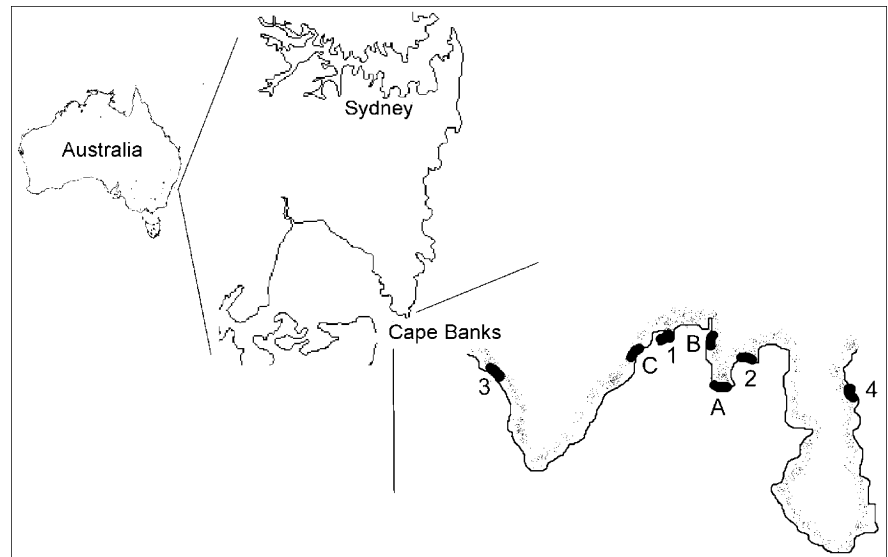
high, did not form a canopy and consisted of mosaics of *Corallina officinalis* Linnaeus, *Ulva lactuca* Linnaeus and other species of Ulvales, *Colpomenia sinuosa* (Mertens ex Roth) Derbés and Solier, *Hormosira banksii* (Turner) Decaisne, *Sargassum* spp. and a variety of filamentous, foliose and coarsely branched algae (sensu Littler and Littler 1984). Other important components of the assemblage were encrusting algae, notably *Hildenbrandia rubra* (Sommerfelt) Meneghini, *Ralfsia verrucosa* (Areschoug) J. Agardh and non-geniculate corallines that were, however, generally masked by overgrowing non-encrusting algae. Various animals were also present, including the solitary ascidian *Pyura stolonifera* Heller, the tubeworm *Galeolaria caespitosa* Lamarck, barnacles, and patellid limpets, mostly *Cellana tramoserica* (Sowerby). Quantitative information on the composition and distribution of assemblages at the study stations will be presented subsequently. Further descriptions of the shores at Cape Banks and its assemblages can be found in Underwood (1980), Minchinton (1997), Chapman and Underwood (1998) and Underwood and Chapman (1998).

Sampling of natural patches

The shape of naturally occurring patches was monitored from September 1997 to June 1998 in replicated plots of 2×2 m at different stations and at different times of the year, in order to obtain quantitative information about the spatial and temporal variability of patch shapes, and to gain information about the possible types of disturbances acting on the assemblage. Three main characteristics of patch shape, i.e. area, geometry and substratum type, were recorded for each patch within each plot. In many cases patches could be approximated to distinctive geometric shapes, such as a circle, square, triangle, ellipse, etc., otherwise patches were defined as irregular. The area of each patch was estimated by measuring the principal axes of their geometric approximation, or, in case of irregular patches, by summing a combination of sub-areas of more regular geometric shape. Estimated areas were gathered into six size categories: < 5 cm^2, 5–50 cm^2, 50–100 cm^2, 100–200 cm^2, 200–300 cm^2 and > 300 cm^2. Patch geometry was recorded only for patches > 5 cm^2, as patches < 5 cm^2 generally resembled circles. The perimeter of patches was not measured directly in the field, because of time constraints, but estimates were calculated for the most regular patches. Often disturbances were not severe enough to completely remove encrusting algae; thus, patches differed in substratum characteristics. Four types of substrata were identified: bare rock (substrate that appeared to be visually free of any sessile macrobiota), encrusting algae, bare rock and encrusting algae, and sediment (a thin layer of fine sand to moderately coarse debris). The hypotheses that shape of patches differs between exposed and sheltered shores and between seasons were specifically tested. Sampling was repeated twice during September and November 1997 (austral spring–summer), and twice during March and June 1998 (austral autumn–winter) at four stations (Fig. 1). Stations 1 and 2 were sheltered, while stations 3 and 4 were moderately exposed to exposed, respectively. Two plots selected at random were sampled each time at each station, except for November 1997 and March 1998 when only one plot could be safely sampled at station 4 due to extremely rough sea conditions. Due to unbalanced number of replicate plots, data were not analysed statistically (Underwood 1997), and patterns were interpreted visually from graphs.

Field experiments

Three experiments were established in September 1997, in order to investigate separately the relative importance of three different characteristics of patch shape, namely area, perimeter and distance of the central zone from the edge. All patches used in the experiments were established at random on sheltered, horizontal or gently sloping, uniform rocky surfaces characterised by covers of dense stands of non-encrusting macroalgae (>95%). The minimum distance between patches was 1 m. As shown by the monitoring of natural patches, patches released by disturbances were often partially colonised by encrusting algae. Because encrusting algae can influence the dynamics of colonisation of non-encrusting algae (Airoldi 2000b, and references therein) and in order to avoid potential additional sources of variability, all patches used in the experiments were scraped clean of all resident organisms, including encrusting algae, by using hammer and chisel, to expose virgin substrata. Patches were permanently marked at their edges with epoxy putty (Subcoat S. Veneziani).

The experiments were specifically designed to uncouple the effects related to different attributes of patch shape, i.e. to test whether colonisation of species differed among patches of different areas, perimeters, or distances of the central zone from the edge, independently of other attributes of shape. Patch characteristics are often correlated, making it difficult to unambiguously attribute effects on recovery rates of species to one or the other attribute of patch shape. For example, holding area constant, a patch with a greater perimeter will have a smaller average distance between the central zone and the edge and will be more dissimilar from a perfect circle. To attribute effects to one characteristic of patch shape requires comparison of patches that differ in that characteristic, but do not differ, on average, in proportional representation of other characteristics. This was achieved by: (1) limiting possible patch areas, perimeters, or distances of the central zone from the edge

within ranges that allowed the maintenance of the proportional representation of other characteristics of patch shapes and (2) by using nested designs. This type of design made it possible to compare mean responses for sets of replicate patches of different shapes that differed, on average, for only one shape characteristic. In order to make results more general, shapes included in the experiments were chosen at random from a pool of experimentally feasible geometric shapes within the range of those observed in the natural assemblage (Fig. 2A).

The specific designs of the three experiments are illustrated in Table 1. The first experiment investigated the effects of patch shape on recovery of species as a function of area, defined as the measure of the surface of each patch. It was predicted that, if the influence of patch shape is mostly related to area, colonisation of species would differ among patches of different areas, independently of other attributes of shape. A total of 36 patches were established at station A (Fig. 1), 12 for each of three different measures of areas (150, 280 and 320 cm^2). Areas were selected at random within the range of 50–350 cm^2, which included, on average, 30% of patches of bare rock naturally observed at the study sites (see "Results"). Despite their abundance in nature, areas < 50 cm^2 were excluded; otherwise, it would have been difficult to maintain proportional representation of other characteristics of patch shapes across groups of patches of different areas. The 12 patches of each area were of four different geometric shapes, attributed at random, with three replicate patches for each combination of area and geometric shape (Table 1). The design thus included two factors, area and geometric shape, arranged in a nested design. This design made it possible to separate differences due to area per se from differences due to other possible characteristics related to patch shape. Within each measure of area, in fact, there was a large variability of shape characteristics; the relatively small range of areas included in the experiment (50–350 cm^2) allowed the control of differences in other factors. For example, patches of different measures of areas had perimeter lengths that were largely overlapping (i.e. perimeter lengths varied from 51 to 91 cm in patches of 150 cm^2, from 67 to

97 cm in patches of 280 cm^2 and from 64 to 83 cm in patches of 320 cm^2); thus, differences among patches of different areas could be clearly separated from possible differences in perimeter lengths.

The other two experiments were designed following the same rationale. The second experiment was established at station B (Fig. 1), and investigated the effects of patch shape on recovery of species as a function of perimeter, defined as the length of the contour of each patch. It was predicted that, if the influence of patch shape is mostly related to perimeter, colonisation of species would differ among patches of different perimeters, independently of other attributes of shape. The experimental design included three measures of perimeter (45, 59 and 68 cm), selected at random within a range of perimeters of 45–95 cm. This range was estimated to be representative of the perimeter lengths of about 25% of patches of bare rock naturally occurring at the study sites. Despite their abundance, perimeters < 45 cm were excluded; otherwise, it would have been difficult to maintain proportional representation of other characteristics of patch shapes across groups of patches of different perimeters. As in the previous experiment there were 12 patches for each measure of perimeter. The 12 patches were of four different geometric shapes, attributed at random, with three replicate patches for each combination of perimeter and geometric shape.

The third experiment was established at station C (Fig. 1), and investigated the effects of patch shape on recovery of species as a function of the distance between the central zone and the edge. Edge was defined as the limit between the cleared surface of the patch and the surrounding intact algal bed. For this experiment, the central zone was defined as a fixed central surface of 25 cm^2, the contour of which was separated from the edge of the patch by a border zone of a certain thickness (Fig. 2B). It was predicted that, if the influence of patch shape is mostly related to distance of the central zone from the edge, colonisation of algae at the centre of the patches will differ among patches with different thickness of borders, independently of all other attributes of shape. The experimental design included three measures of thickness of borders (2, 3 and 4 cm), selected at random within a range of border thickness of 2–6 cm. Borders thinner than 2 cm were excluded; otherwise, it would have been difficult to maintain proportional representation of other characteristics of patch shapes across groups of patches of different border thickness. As in the previous experiments, there were 12 patches for each measure of border thickness. The 12 patches were of four different geometric shapes, attributed at random, with three replicate patches for each combination of border thickness and geometric shape.

Sampling and analysis of data

All the patches were cleared in September 1997. Subsequent recovery was followed visually in the field over 1 year from November 1997 until October 1998; during the first 3 months,
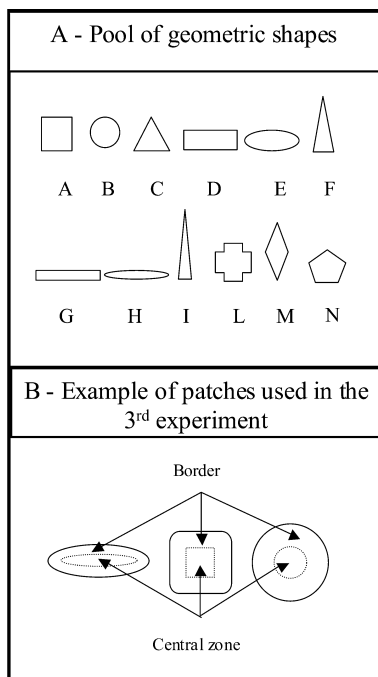

Fig. 2A Pool of geometric shapes used in the three field experiments and **B** example of patches used in the third field experiment. In the third experiment, each patch included a central zone of 25 cm^2 (*dotted line*) and a border zone that varied in thickness (2, 3 or 4 cm). For further explanation see "Materials and methods—Field experiments"

Table 1 Designs of the three experiments used to separate the effects of area, perimeter and distance of the central zone from the edge in intertidal algal assemblages. Geometric shapes are coded as in Fig. 2A

Patch characteristic and measures	Geometric shapes	Replicates
Area		
150 cm^2	C, E, H and I	3
280 cm^2	A, F, G and L	3
320 cm^2	B, D, M and N	3
Perimeter		
45 cm	A, D, G and M	3
59 cm	B, E, F and I	3
68 cm	C, H, L and N	3
Border thickness		
2 cm	H, I, L and M	3
3 cm	A, D, G and N	3
4 cm	B, C, E and F	3

patches were sampled once every month (in November, December and January 1997), while afterwards they were sampled about every 2–3 months (in March, June, August and October 1998), for a total of seven sampling dates. Percentage cover estimates of colonising sessile organisms were obtained by using the "point–intercept" method (Benedetti-Cecchi et al. 1996), while the abundance of mobile species was estimated as the number of individuals per surface unit. In the case of limpets, only individuals larger than about 5 mm diameter were counted, as smaller individuals were sometimes difficult to detect due to cover of algae. The point–intercept method was preferred to the "visual estimation" method (Benedetti-Cecchi et al. 1996) because of technical difficulties in building adequate visual estimation frames for some of the geometric shapes used in the experiments. Patches of different shapes were sampled by using transparent plastic sheets of the corresponding shape. A grid of equally spaced dots was marked on each sheet, and the percentage cover of each species was expressed as the number of hits. The number of dots used in the grids varied, depending on the experiment and patch surface. In the first two experiments, grids were arranged so as to cover the entire surface of the patches except for a border strip of 2 cm, in order to avoid any edge effect that could occur as a result of surrounding algae sweeping into the frame. In these experiments, a constant density of dots of about 0.4 cm^{-2} was maintained. Thus, the number of dots used in the first experiment was 50, 90 and 106 for patches of 150, 280 and 320 cm^2, respectively, while in the second experiment the number of dots ranged from 29 to 105, depending on patch surface area. In the third experiment, the whole central surface of 25 cm^2 was sampled for each patch, by using grids with 25 dots. Species present but not scored under dots were given an arbitrary hit value of 0.5. Algae that could not be identified to species or genus in the field, or that could be confused with other species were grouped into larger taxonomic or morphological groups (see "Results"). Sometimes, small samples of algae were collected from the surrounding assemblage and examined in the laboratory, in order to help identification of species: voucher specimens were retained and are housed at the Centre for Research on Ecological Impact of Coastal Cities (University of Sydney).

Percentage cover and density data were analysed by using two-way ANOVAs, with geometric shape as a random factor nested in area, perimeter and border thickness (three random levels each) for experiments 1, 2 and 3, respectively. It is important to note that in these analyses the relevant hypotheses are those related to the main fixed factors area, perimeter, or border thickness, and not to the factor geometric shape, which is a random factor necessary to separate differences due to the main factors from differences due to other possible characteristics related to patch shape. ANOVAs were run for each species by using as the dependent variable the average abundance of each species in each patch over all sampling dates when abundances were > 0. This procedure allowed estimation of the effects of patch characteristics on the overall colonisation success of each species over the study period (Airoldi 1998, 2000a). Effects of patch characteristics on temporal patterns of colonisation were further examined for each species by running ANOVAs separately on each sampling date when the species was frequent enough for meaningful analyses. This procedure required a large number of tests, which may have potentially increased the risk of type I errors. Repeated measures analyses were, however, not applied, because inspection of the data suggested that the required assumption of no interaction between times and patches was unlikely to be true (Underwood 1997). Cochran's C-tests were used to check for the assumption of homogeneity of variances. When this assumption was violated, angular or logarithmic transformations were applied to the data; homogeneity of variances was always achieved.

Results

Characteristics of natural patches

Density of natural patches varied from 4 to 57 patches m^{-2}. A large proportion of these were of very small sizes (Fig. 3); on average, 33% of the patches were < 5 cm^2, and 35% had an area between 5 and 50 cm^2, while only $< 2\%$ of the patches were > 350 cm^2. Patches were larger at exposed than sheltered stations, particularly during the autumn (Fig. 3). A seasonal trend was also evident: at exposed stations the area of patches tended to be greater during the autumn–winter, while the opposite trend was observed at sheltered stations (Fig. 3).

Patch geometry was extremely variable (Fig. 3). Small patches tended to have more regular shapes that could be approximated to one of nine distinctive geometric shapes, while larger patches were often irregular. Most frequently recognised geometric shapes were circles, triangles, ellipses and rectangles. Squares were

Fig. 3 Area, geometry and substratum type of patches naturally occurring within the algal assemblage at different seasons (*Spring* spring–summer; *Autumn* autumn–winter) and at stations differently exposed to wave action (*Exp* exposed; *Sh* sheltered). Data are mean percentage abundance of six different size classes, ten different geometric shapes and four substratum types, pooled across two sampling times and two stations (n = 8 for sheltered stations and n = 7 for exposed stations). Geometry was recorded only for patches > 5 cm^2. Standard errors are not plotted for clarity of the graphs
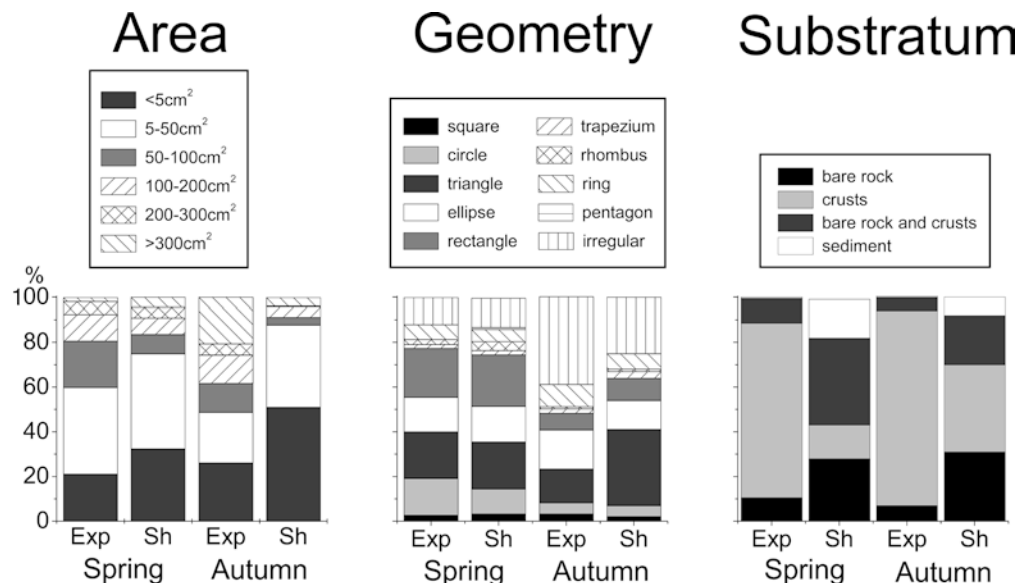
rather scarce, being on average < 3%. Irregular patches were generally more abundant during the autumn–winter, especially at exposed stations (Fig. 3), while circles and rectangles of relatively small sizes (5–100 cm²) were more abundant during the spring–summer.

Natural patches at exposed and sheltered stations differed markedly in the characteristics of the substratum (Fig. 3). At exposed stations, patches were mostly colonised by encrusting algae, while rocky substratum that appeared totally or partially bare was scarce and mostly confined to relatively small patches. Conversely, at sheltered shores, encrusting algae were not abundant within large patches of open space, and a large proportion of patches appeared to be totally or partially free of any macrobiota, especially during the spring–summer. Further, at sheltered stations, local deposits of sediments were often observed, which never occurred at exposed stations.

Field experiments

Colonisation of experimental patches

Colonisation of experimental patches was quick during all experiments (Figs. 4, 5, 6). Filamentous algae (*Chaetomorpha aerea*, *Cladophora* spp., *Rhizoclonium implexum*, *Sphacelaria* spp., one unidentified Ectocarpacea species and various species of Ceramiales including *Herposiphonia* spp., *Ceramium* spp., *Polysiphonia* spp. and *Antithamnionella tasmanica*) and a few species of Ulvales (*Enteromorpha* sp., *Blidingia minima* and *Ulva lactuca*) were the most abundant species. *Corallina officinalis* grew abundantly in patches cleared at stations A and B for the first and second experiment, but scarcely colonised patches established at station C for the third experiment. Filamentous algae were difficult to identify in the field and generally occurred as a mix of several species; thus, they were grouped in the non-specific morphological category "filamentous". Similarly, young specimens of *Enteromorpha* sp., *B. minima* and *U. lactuca* were sometimes difficult to distinguish; thus, these species were grouped as "Ulvales". Encrusting algae (*Hildenbrandia rubra*, *Ralfsia verrucosa* and non-geniculate corallines) were also abundant, being always among the first colonisers of bare rock, but due to rapid overgrowth by other species they could not be properly quantified, and will not be further considered. Other frequent species were *Colpomenia sinuosa*, *Hormosira banksii*, *Sargassum* spp. and a few unidentified microalgae. Sessile animals were scarce, except for barnacles (mainly *Tesseropora rosea* Krauss), which densely colonised patches established at station A for the first experiment. Patellid limpets (mostly *Cellana tramoserica*) were the most abundant herbivores; they quickly invaded cleared patches, reaching average densities generally greater than those observed in the surrounding algal mosaics (densities of
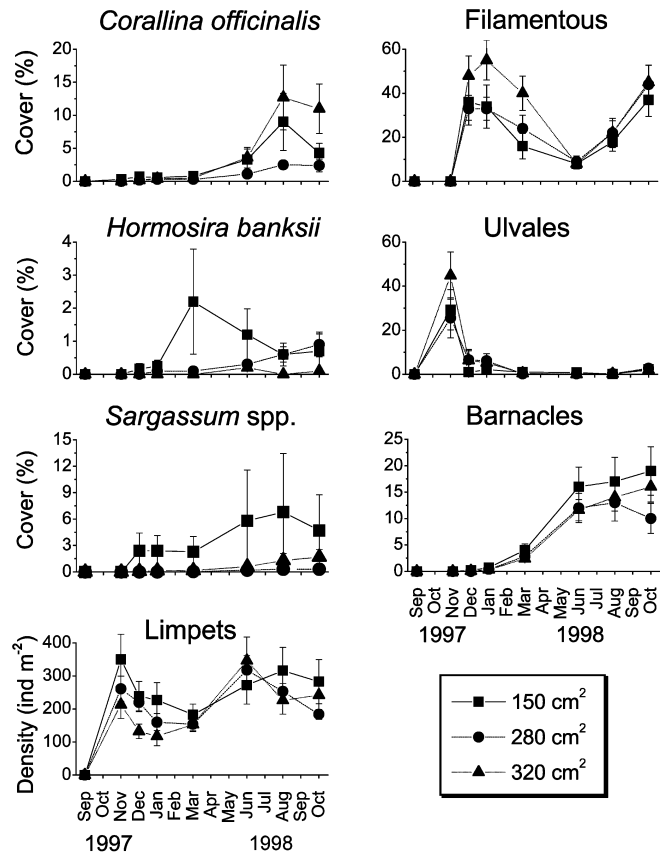

Fig. 4 Percentage cover of *Corallina officinalis*, filamentous algae, *Hormosira banksii*, Ulvales, *Sargassum* spp., barnacles and density of limpets in experimental patches of different areas (150, 280, 320 cm²). Data are averages (± 1 SE) for each patch area and sampling time (*n* = 12) pooled across four geometric shapes (see Table 1)

limpets estimated during the study in unmanipulated areas at the three stations A, B and C averaged 127 ± 103 individuals m⁻²). A few other species were observed, including *Endarachne binghamiae* J. Agardh, *Petalonia fascia* (Müller) Kuntze, *Champia* sp., *Laurencia* spp., *Martensia fragilis*, *Dictyothamnion saltatum* and serpulid worms, but these occurred too sporadically for meaningful analyses.

Bare space was colonised predominantly by recruitment of sexual propagules and subsequent vegetative growth and/or increase in size of settled individuals. Lateral vegetative invasion by surrounding specimens was observed frequently for filamentous species and occasionally for *Corallina officinalis*. Some species, such as Ulvales, showed marked seasonal trends, with reduced abundance during the autumn and winter months (Figs. 4, 5, 6). Also filamentous species showed seasonal peaks of abundance. Patterns, however, differed between patches cleared at station A (Fig. 4) and those cleared at stations B and C (Figs. 5, 6), possibly reflecting a major abundance of green algae (*Chaetomorpha aerea*, *Cladophora* spp., *Rhizoclonium implexum*) at station A with respect to stations B and C, where red and brown
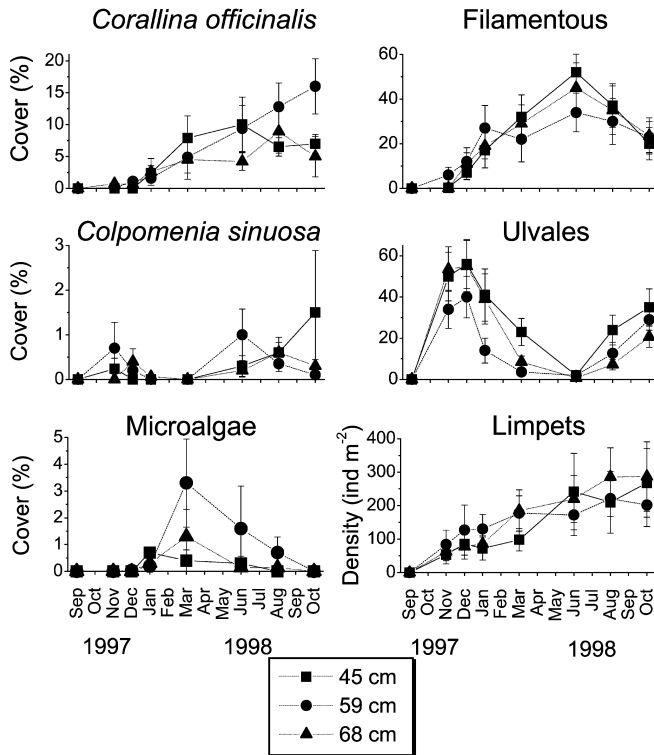
Fig. 5 Percentage cover of *Corallina officinalis*, filamentous algae, *Colpomenia sinuosa*, Ulvales, microalgae and density of limpets in experimental patches of different perimeters (45, 59 and 68 cm). Data are averages (±1 SE) for each patch perimeter and sampling time (*n* = 12) pooled across four geometric shapes (see Table 1)
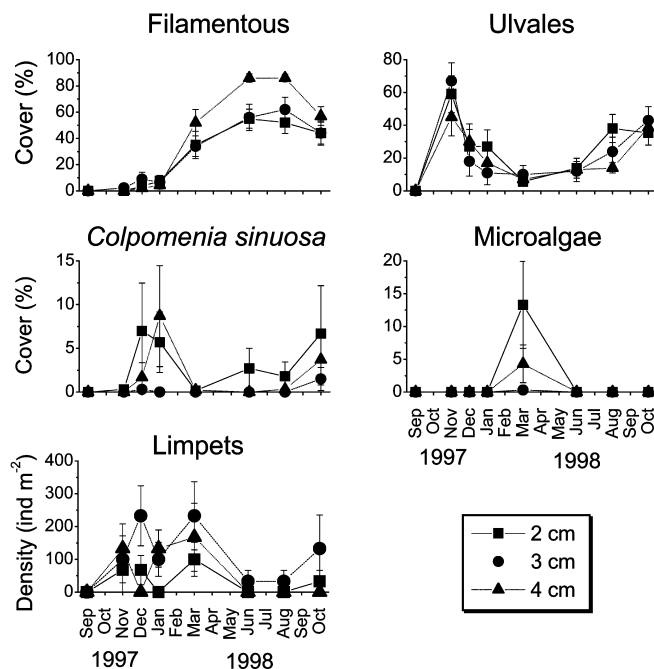

Fig. 6 Percentage cover of filamentous algae, Ulvales, *Colpomenia sinuosa*, microalgae, and density of limpets in experimental patches of different border thickness (2, 3 and 4 cm). Data are averages (±1 SE) for each border thickness and sampling time (*n* = 12) pooled across four geometric shapes (see Table 1)

filamentous algae were dominant components of the surrounding assemblage.

Effects of patch area, perimeter and distance of the central zone to the edge

Patch area significantly influenced colonisation of *Corallina officinalis* (Table 2). Recruitment of this calcareous articulated alga became conspicuous after June 1998 and was greatest in the largest patches (Fig. 4). A similar trend of greatest abundance in largest patches was also observed for filamentous algae from December 1997 to March 1998, when cover of these species peaked (Fig. 4; Table 2). Differences, however, disappeared in June 1998, when cover of filamentous algae declined. Cover peaked again during the following months, but no differences became visible among patches of different areas, thus resulting in non-significant effects of patch area on average abundance of filamentous algae over time (Table 2). *Hormosira banksii*, *Sargassum* spp. and barnacles showed a tendency towards greatest cover in the smallest patches (Fig. 4), in contrast to the patterns observed for *C. officinalis* and filamentous algae. Within each level of patch area, however, recruitment of *H. banksii* and barnacles was very variable among patches of different geometric shapes, thus resulting in non-significant effects of patch area (Table 2). Recruitment of *Sargassum* spp. was also very variable among replicate plots, and this species colonised few experimental patches (Fig. 4). No effects of patch area were observed on recruitment of Ulvales or on densities (standardised as number of individuals per m²) of limpets (Fig. 4; Table 2).

Patch perimeter significantly influenced colonisation of Ulvales (Table 3). These species were, on average, most abundant in patches with the smallest perimeters, this trend becoming most noticeable in March 1998 (Fig. 5). Initially, Ulvales also heavily colonised patches with the largest perimeters; their abundance in these patches, however, decreased markedly after January 1998, and towards the end of the experiment patches with the largest perimeters supported less Ulvales than all other patches (Fig. 5). *C. officinalis* and unidentified microalgae showed a tendency for greatest abundance in patches with an intermediate perimeter of 59 cm, but within each level of patch perimeter patterns differed greatly among patches of different geometric shapes (Fig. 5; Table 3). No consistent effects of patch perimeter were observed on colonisation of any other species of algae or on density of limpets (Fig. 5; Table 3).

Distance between the central zone and the edge significantly influenced colonisation of filamentous algae (Table 4). In particular, patches with the thickest borders supported notably greater abundances of filamentous species than other patches (Fig. 6). Unexpectedly *C. officinalis* was very scarce in patches used in this experiment, despite being abundant in the surrounding assemblage. Distance between the central zone and the edge did not affect colonisation of any other species of algae or density of limpets.

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Table 2 ANOVAs of the percent cover of *Corallina officinalis*, filamentous algae, *Hormosira banksii*, Ulvales, *Sargassum* spp. and barnacles and the density of limpets in experimental patches of different areas and geometric shapes. Factors are: area (three areas, random) and geometric shape (*Geom.*; four geometric shapes, random, nested in area). Analyses were run: (1) on average abundance in each patch measured over those sampling dates when abundances were > 0 and (2) separately on each sampling date when species were frequent enough for meaningful analyses (in the latter case results are only reported for those dates when significant effects of factor area were detected). For further details see "Materials and methods". Significant *P* values are in *bold*

Source of variation	df	Average abundance			By sampling date		
		MS	F	P	MS	F	P
C. officinalis							
Area	2	107	4.31	**0.049**	August 1998		
					2.39	4.87	**0.03**
Geom. (Area)	9	25	0.60	0.78	0.49	0.42	0.9
Residual	24	41			1.15		
					October 1998		
					274	4.50	**0.04**
					61	0.75	0.66
					81		
Filamentous					March 1998		
Area	2	193	2.22	0.16	1,052	5.70	**0.02**
Geom. (Area)	9	87	1.15	0.37	184	0.54	0.8
Residual	24	76		339			
H. banksii							
Area	2	1.63	0.66	0.54			
Geom. (Area)	9	2.48	3.58	**< 0.01**			
Residual	24	0.69					
Ulvales							
Area	2	212	0.82	0.47			
Geom. (Area)	9	258	1.04	0.44			
Residual	24	248					
Sargassum spp.							
Area	2	3.58	1.16	0.36			
Geom. (Area)	9	3.11	0.48	0.87			
Residual	24	6.47					
Barnacles							
Area	2	63	0.52	0.61			
Geom. (Area)	9	120	2.17	**0.06**			
Residual	24	56					
Limpets							
Area	2	12,644	2.78	0.11			
Geom. (Area)	9	4,542	0.49	0.86			
Residual	24	918					

Table 3 ANOVAs of the percent cover of *Corallina officinalis*, filamentous algae, *Colpomenia sinuosa*, Ulvales and microalgae and the density of limpets in experimental patches of different perimeters and geometric shapes. Factors are: perimeter (three perimeters, random) and geometric shape (*Geom.*; four geometric shapes, random, nested in perimeter). Analyses were run: (1) on average abundance in each patch measured over those sampling dates when abundances were > 0 and (2) separately on each sampling date when species were frequent enough for meaningful analyses (in the latter case results are only reported for those dates when significant effects of factor perimeter were detected). For further details see "Materials and methods". Significant *P* values are in *bold*

Source of variation	df	Average abundance			By sampling date		
		MS	F	P	MS	F	P
C. officinalis							
Perimeter	2	1.02	0.66	0.541			
Geom. (Perimeter)	9	1.56	2.32	**0.048**			
Residual	24	0.62					
Filamentous							
Perimeter	2	17	0.11	0.90			
Geom. (Perimeter)	9	160	1.21	0.33			
Residual	24	133					
C. sinuosa							
Perimeter	2	1.02	0.15	0.86			
Geom. (Perimeter)	9	6.69	0.73	0.68			
Residual	24	9.18					
Ulvales					March 1998		
Perimeter	2	0.81	4.38	**0.047**	1,199	6.15	**0.02**
Geom. (Perimeter)	9	0.18	0.35	0.95	194	0.87	0.56
Residual	24	0.52			223		
Microalgae							
Perimeter	2	32.6	1.88	0.21			
Geom. (Perimeter)	9	17.4	2.42	**0.04**			
Residual	24	7.1					
Limpets							
Perimeter	2	1,916	0.24	0.8			
Geom. (Perimeter)	9	8,135	0.54	0.83			
Residual	24	15,201					

Table 4 ANOVAs of the percent cover of filamentous algae, Ulvales, *Colpomenia sinuosa* and microalgae and the density of limpets in experimental patches of different border thickness and geometric shapes. Factors are: border thickness (three thicknesses, random) and geometric shape (*Geom.*; four shapes, random, nested in border thickness). Analyses were run: (1) on average abundance in each patch measured over those sampling dates when abundances were > 0 and (2) separately on each sampling date when species were frequent enough for meaningful analyses (in the latter case results are only reported for those dates when significant effects of factor border thickness were detected). For further details see "Materials and methods". Significant *P* values are in **bold**

Source of variation	df	Average abundance			By sampling date		
		MS	F	P	MS	F	P
Filamentous							
					June 1998		
Border	2	2,314	4.28	**0.049**	4,956	4.37	**0.047**
Geom. (Border)	9	541	2.02	0.081	1,135	2.63	**0.03**
Residual	24	268			432		
					August 1998		
					2,768	4.32	**0.049**
					641	4.05	**< 0.01**
					158		
Ulvales							
Border	2	101	0.28	0.764			
Geom. (Border)	9	364	2.72	**0.024**			
Residual	24	134					
C. sinuosa							
Border	2	108	2.69	0.12			
Geom. (Border)	9	40	0.46	0.89			
Residual	24	87					
Microalgae							
Border	2	443	2.21	0.16			
Geom. (Border)	9	200	1.06	0.43			
Residual	24	190					
Limpets							
Border	2	6.47	0.87	0.45			
Geom. (Border)	9	7.44	1.37	0.25			
Residual	24	5.42					

Discussion

Habitat patch variety

Literature on patchy assemblages in terrestrial systems has devoted attention to patch-shape variability in natural and human-managed landscapes (e.g. Krummel et al. 1987; Farina 1998; Helzer and Jelinski 1999). Quantifying the size–shape relationship of patch mosaics has, in fact, helped greatly not only in understanding how spatial heterogeneity relates to a number of important ecological processes that generate patterns of species diversity (Gutzwiller and Anderson 1992), but also in determining the appropriate spatial scales to use in studying such systems (Krummel et al. 1987).

In comparison, far less attention has been devoted to measure patch-shape variability in marine habitats, in spite of the recognised potential relevance of this factor (Paine and Levin 1981; Sousa 1985). The large range of patch shapes observed at Cape Banks suggests that shape is more variable in intertidal algal mosaics than recognised previously. Further, consistent differences observed in patch size, geometry and characteristics of the substratum among sheltered and exposed stations and among different times of the year indicate that patch shape is likely influenced by the magnitude and type of disturbances, and by the mechanism by which the disturbance agents operate. For example, patches released by the harvesting of *Pyura stolonifera*, which is illegally collected at Cape Banks by recreational fishermen to be used as bait, were different and easily recognisable from those resulting from other types of disturbances; they looked like rather regular patches, about 30–50 cm² large, mostly circular or elliptical, of clean rock surface (author's personal observations). This type of patch was more frequent at sheltered stations, where probably *P. stolonifera* is easier to collect. At exposed stations, large, irregular patches, covered by encrusting algae, were frequent during the autumn and winter, suggesting that the dynamics of patch formation at those sites was influenced by autumn storms (see also Minchinton 1997). Similarly, at sheltered stations, the large amount of patches of bare rock, or rock only partially covered by encrusting algae, which were especially frequent during the spring–summer, suggests that the dynamics of patch formation at sheltered shores was likely influenced by desiccation events, which burn-off both erect and encrusting algae (author's personal observations). Further studies are necessary to identify and predict relationships between the regime of disturbance and patch shape in algal mosaics. Nevertheless, present results suggest that observing patch shapes may give useful information about the mechanisms of patch formation and the regime of disturbance in an area.

The most frequent geometric shapes of patches at Cape Banks were circles, ellipses, triangles, rectangles or irregular shapes. In general, larger patches tended to be more irregular, while smaller patches approximated more circular shapes. Interestingly, square patches were rare at any shore and at any time of the year. This is important as a square is the most frequent shape of patches used to investigate small-scale colonisation processes and dynamic interactions in rocky shore assemblages (Menge 1976; Underwood 1980; Sousa

1984a; Dye 1993; Menge et al. 1993; Williams 1993; Benedetti-Cecchi and Cinelli 1994; Kim and DeWreede 1996; Anderson 1998; Airoldi 2000a). This implies that current models of community structure and dynamics have been developed by using experimental patches which may not necessarily reflect natural patch distributions.

Effects of patch shape on algal dynamics

Most hypotheses formulated about the possible effects of patch shape in marine habitats generally attribute such effects to variations in the perimeter to area ratio. For example, Sousa (1984b, p. 371) indicated that "the more irregularly shaped a clearing of a given area is, the higher the ratio of perimeter length to area and the greater the influence (both positive and negative) organisms in the immediate neighborhood of the patch will have on its recolonization". Similarly, Raimondi (1990, p. 305) suggested that observed greater "... recruitment of *Chthamalus* to narrow sites than to wider sites of the same area ...[probably indicated] ... a gregarious response to the adults on the clearing perimeters". Results of the present experiments support the hypothesis that algal colonisation is influenced by patch shape. Patterns of recovery, however, were more complicated than generally supposed, and appeared to be regulated by additional factors to the perimeter to area ratio.

Responses to different patch characteristics (i.e. area, perimeter and distance of the central zone from the edge) were species specific. Colonisation of *Corallina officinalis* was faster in patches with a greater area independent of other attributes of shape, while no effects were observed in relation to length of perimeter or distance of the central zone from the edge. Ulvales were more abundant in patches with a smaller perimeter length and were not affected by either area or border thickness. Growth of filamentous algae was enhanced by an increasing distance of the central zone from the edge, and to a lesser extent by a greater area. Results also indicated that the effects due to different attributes of patch shape may vary over time, as observed for example for filamentous algae during the colonisation of patches of different areas. At present, the mechanisms by which different patch-shape attributes affect colonisation of species are not well understood. The variability of responses observed in the present study suggests that colonisation processes of patches of different shapes are complex, probably involving direct and indirect effects that may produce contrasting results. Further, for less abundant species, responses to patch area, perimeter and distance of the central zone from the edge were often not consistent among patches of different geometry, suggesting that colonisation is likely regulated by additional attributes to those included in the present experiments. Studies from terrestrial systems suggest that other important attributes of patch shape probably include patch orientation, substratum heterogeneity, complexity of edges, contacts with different microenvironments and interconnections of patches by corridors (Game 1980; Gutzwiller and Anderson 1992; Hamazaki 1996).

Observations from other assemblages suggest that variable colonisation of algae among patches of different shapes could be related to uneven distributions of herbivores, which would tend to be more abundant in patches with a greater percentage of edge habitat (Sousa 1984a; Farrell 1989). Such effects, however, appeared unimportant at Cape Banks, where the distribution of limpets and other herbivores was not influenced by any attribute of patch shape. This is consistent with the results of another experiment carried out at Cape Banks, where no relevant differences were observed in the distribution of limpets between the edges and central zones of circular patches of different sizes (Airoldi and Underwood, unpublished data). The component species of algal assemblages at Cape Banks had generally a small size (< 5 cm height) and did not form a canopy, which might explain the lack of relevant responses of herbivores to edge effects.

Differences among patches of different areas were overall less evident than suggested by other authors for some rocky intertidal assemblages (Sousa 1984a; Farrell 1989; Dye 1993; Benedetti-Cecchi and Cinelli 1994; Kim and DeWreede 1996; Minchinton 1997). This may have been because constraints in the logical design of the experiments only allowed a limited range of possible patch sizes (see "Materials and methods—Field experiments"). Nevertheless, the differences among patches of the same area, but different geometric shapes, and the effects of perimeter length and border thickness identified in the present experiments suggest that in other studies effects of patch size may have been overestimated by effects in fact related to patch shape. Possible confounding effects due to variations in perimeter length or in percentage of edge habitat have often been discussed by authors, and some studies have suggested that patterns of recruitment may be more closely related to patch shape than area, especially if patches are small (Paine and Levin 1981; Raimondi 1990; Minchinton 1997). The potential role of patch shape, however, is still ignored by most models of species dynamics on rocky shores. In the present study, differences as large as those generally attributed to patch area were observed among patches of constant area, but of different geometric shapes. This result has methodological implications. While much attention is devoted to the choice of the appropriate size of patches in field experiments, little attention is generally paid to the choice of the appropriate shape of patches. Many current models of community structure and dynamics have been developed based on colonisation processes and dynamic interactions measured in square plots, implicitly assuming that shape of plots does not matter. In light of the present results, and of the demonstrated range of natural patch shapes, this assumption does not seem realistic.

Conclusions

Given the complexity of responses to different attributes of patch shape observed in the present experiments, predicting quantitative differences in colonisation of patches of different shapes is probably difficult. Moreover, at present there is no mechanistic explanation for the responses observed, and further research is necessary to elucidate how different attributes of patch shape can affect colonisation of species. The results of this study, however, show that shape is an important property of patches in intertidal algal assemblages and can affect their structure and dynamics, even within the relatively small range of scales covered by this study. This conclusion has implications not only for current models of community structure and dynamics, but also for the conservation and management of rocky shores, as human-induced perturbations can largely alter the shape of patches in natural landscapes. Results also suggest that attention should be devoted to the choice of the shape of patches in field experiments, and that care is necessary when interpreting experiments where, for reasonable logistic constraints, only a limited range of naturally occurring patch shapes has been considered.

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