Marine Biology (1994) 121: 301–307

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Trends in space occupation by the encrusting sponge *Crambe crambe*: variation in shape as a function of size and environment

Received: 13 January 1994 / Accepted: 28 July 1994

Abstract The relationship between sponge size, habitat and shape was studied in the encrusting sponge *Crambe crambe* (Schmidt, 1862), which is distributed widely throughout the shallow Mediterranean littoral. Examination of sponge patches in shaded and well-illuminated habitats showed that the degree of peripheral irregularity of the edges of a patch is directly related to patch size. This relationship is valid only for sponges of >100 mm^2 in area. Photophilic and sciaphilous sponges display different growth forms. The pattern of growth is interpreted in terms of competition for space. The directional growth of sciaphilous sponges may be due to the presence of dominant neighbours that are good space competitors, and the irregular growth of photophilic sponges to the absence of such neighbours.

Introduction

Size and shape are important to encrusting substrate-dependent organisms (Sebens 1987; Stocker 1991), since they determine the extent of contact with neighbours and, consequently, the probability of any interaction (Jackson 1979). Resource acquisition and avoidance of competitors are achieved through the adjustment of growth shapes in modular organisms (Franco 1986). Since resources are not considered to be a limiting factor for sublittoral sponges, even in nutrient-poor tropical waters (Reiswig 1974), the outline of an encrusting (bidimensional) clone in a space-limited habitat would reflect the outcome of the several space-competition pressures it has encountered along its edges.

The growth morphologies of groups of organisms have been compared and ecological strategies inferred by previous investigators (e.g. Warner 1978; Jackson 1979; Coates and Jackson 1985). Nevertheless, due to the wide range of strategies employed by organisms featuring modular growth (Jackson and Coates 1986), more evidence from field studies is necessary.

Previous studies on the growth pattern of modular benthic organisms have mainly concerned cheilostomes (Jackson 1979), hydroids (Buss 1986) and ascidians (Stocker 1991). Studies on sponges have concentrated on branching forms (Wulff 1986, 1990), whereas little is known of the growth strategies of encrusting sponges. Modular organisms with encrusting morphology warrant more detailed studies, since such organisms employ several ecological strategies (Connell and Keough 1985; Turon 1990a; Turon and Becerro 1992). Few studies have examined variations in shape of encrusting sponges as a function of size.

It is controversial as to whether or not sponges are colonial organisms (e.g. Hartman and Reiswig 1973; Fry 1979). Nevertheless, they are included in general studies on the biology of clonal organisms, whereby it is assumed that their ecological functions are similar to those of other "true" modular organisms (Jackson 1977; Ryland and Warner 1986). However, the modules that build the sponge (the elementary canal systems) are not clearly delimited, and change continuously during the sponge's life. This plasticity makes the sponge shape variable over time, adding complexity to the study of its modular organization.

Crambe crambe (Schmidt, 1862) is the most widespread littoral sponge species in the Northwestern Mediterranean, where it competes successfully for the available substrate with other invertebrates and seaweeds. Because of its abundance and wide ecological distribution (Uriz et al. 1992b), it is suitable for comparative studies in different habitats. In this study, using *C. crambe* from two contrasting habitats, we investigated the possibility that sponge shape differs as a function of size and environmental conditions.

Communicated by J. M. Pérès, Marseille

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Materials and methods

Organism and study site

Crambe crambe (Schmidt, 1862) dwells on rocky substrate, forming patches 0.5 to 1.5 cm thick and up to 0.5 m^2 in area. Its known bathymetric distribution ranges from 0 to 60 m (Uriz et al. 1992 b).

The study was carried out in a sublittoral habitat in the locality of Blanes, NE Iberian Peninsula (Western Mediterranean). The site was a 2 to 3 m-wide, 40 m-long gorge, running from east to west; its rocky walls were between 6 and 13 m below the sea surface and faced north and south, respectively. Both walls experienced similar trophic and physical conditions, except for the amount of incident light; this determined the development and existence of very different benthic communities.

The north-facing wall was totally covered by a sciaphilous assemblage, mainly composed of encrusting sponges: *Scopalina lophyropoda* Schmidt, 1862, *Phorbas tenacior* (Topsent, 1925), *Pleraplysilla spinifera* (Schulze, 1879), *Chondrosia reniformis* Nardo, 1883, *Cliona viridis* (Schmidt, 1862), *Dysidea avara* (Schmidt, 1862), *D. fragilis* (Montagu, 1918), *Crella elegans* (Schmidt, 1862), with some massive forms such as *Spongia officinalis* Linné, 1759, *Cacospongia scalaris* Schmidt, 1862, *Petrosia ficiformis* (Poiret, 1789), and *Ircinia oros* (Schmidt, 1864). This assemblage is typical of the entrance zone of Mediterranean caves (Uriz et al. 1992 b). The sponge *Crambe crambe*, together with *Scopalina lophyropoda*, were the dominant forms. The substratum was totally covered by organisms.

The south-facing wall received more light. It was dominated by erect seaweeds: *Corallina elongata* Ellis et Solander, *Codium vermilara* (Olivi) Delle Chiajé, *Dictyota dichotoma* (Hudson) and *Halopteris scoparia* (Linné), together with *Crambe crambe*. Patches of free substratum were also present.

In situ photography and slide analysis

A series of 144 photographs of *Crambe crambe* attached to each wall were taken at random in order to obtain a representative sample of sponge sizes and shapes for both sites. Magnifying lens were used for photographing small and medium-sized specimens, while a 35 mm lens (which covered an area of 1×1 m) was used for larger individuals.

Since more than one sponge specimen was visible in most photographs, the 144 slides provided a total coverage of 284 sponge patches, ranging in area from 1 mm^2 to 460 cm^2.

To obtain data for the initial stages of development (< 1 mm^2), a total of 280 rhagons were cultured in the laboratory from larvae collected at sea. These could not be assigned to any specific natural community, but were useful in interpreting general size effects.

Slides were projected onto a DIASTAR-200 (Osram) device, which reflects the image up through a glass sheet. The enlarged images (20×30 cm) were then traced onto transparent paper and measured through a "Genius" digitizer pad using the HiPa2 programme (a modified version of the original design by K. Foreman of Woods Hole Oceanographic Institution).

Estimates of rhagon shape were derived by projecting the image, magnified through a Wild Heerbrug M-8 stereomicroscope and a camera lucida, onto a digitizer pad.

Mathematical indices and data analyses

Four morphometric indices were formulated to describe shape; all were independent of sponge size.

Circularity index (C) (Turon and Becerro 1992)

$$C=\frac{As}{Ap}\,, \tag{1}$$

where As = area of sponge patch, and Ap = area of circle with perimeter equivalent to that of sponge patch; a value of 1 represents a perfect circle, while 0 is approached as the outline becomes more elongated or more irregular. This index is equivalent to the "form factor" mentioned by Russ (1990).

Directional growth index (D)

$$D=1-\frac{P}{M}\,, \tag{2}$$

where M = length of maximum straight line through two sponge points, and P = length of maximum straight line perpendicular to M. This index measures sponge elongation. A value of 0 indicates a perfect circle; 1 is approached as directionality increases.

Convolution index (Cv) (a measure of peripheral irregularity)

$$Cv=1-\frac{Pc}{Ps}\,, \tag{3}$$

where Pc = perimeter of an ellipse, with an area and directional growth index equivalent to those of the sponge patch, and Ps = perimeter of the sponge patch. This index measures the dispersion of the sponge biomass for a given area and directional growth index, thus providing information about the irregularity of the sponge perimeter. A value of 0 indicates a perfect ellipsoid; 1 is approached as the irregularity of the border increases.

Index of relationship (R) between directional growth index and convolution index

$$R=D-Cv\,. \tag{4}$$

This index ranges from -1 to $+1$. Positive values indicate loss of circularity due to the prevalence of directional growth, whereas negative values indicate loss of circularity due to the prevalence of peripheral irregularity.

To detect differences in the morphometric indices as a function of size, sponges were sorted into five size categories: (1) 1 to 100 mm^2 in area, (2) 100 to 1000 mm^2, (3) 1000 to 5000 mm^2, (4) 5000 to 10 000 mm^2, and (5) >10 000 mm^2. Each of these size categories included a similar number of individuals. Moreover, the approximately logarithmic scale used provided more accurate information on the early life stages in which the largest changes in shape could be expected.

A regression analysis of all data from the two sites and the cultured rhagons was made to reveal any relationships of the various shape parameters with sponge area. To determine environmental effects on these relationships, separate regression analyses were made for each site and compared (Zar 1984). If the regressions were not significantly different, the means of the size classes were pooled across sites and compared by one-way ANOVA and Tukey's (HSD) test (Tukey 1953). If the regressions were significantly different, separate Tukey tests were performed for each site and the means of each size class were compared across sites by Student's *t*-tests. Most indices were normally distributed for each size class (Kolmogorov–Smirnow test) and featured homogeneity of variance (Bartlett test), allowing parametric tests to be performed. Several transformations were attempted in those few instances where these assumptions were not met, but the data did not achieve normality. ANOVA was performed on all data, since it is sufficiently robust for most types of non-normality and even for considerable heterogeneity of variances (Cochran 1947; Box 1953), especially when the number of replicates is large (Underwood 1981; Zar 1984).

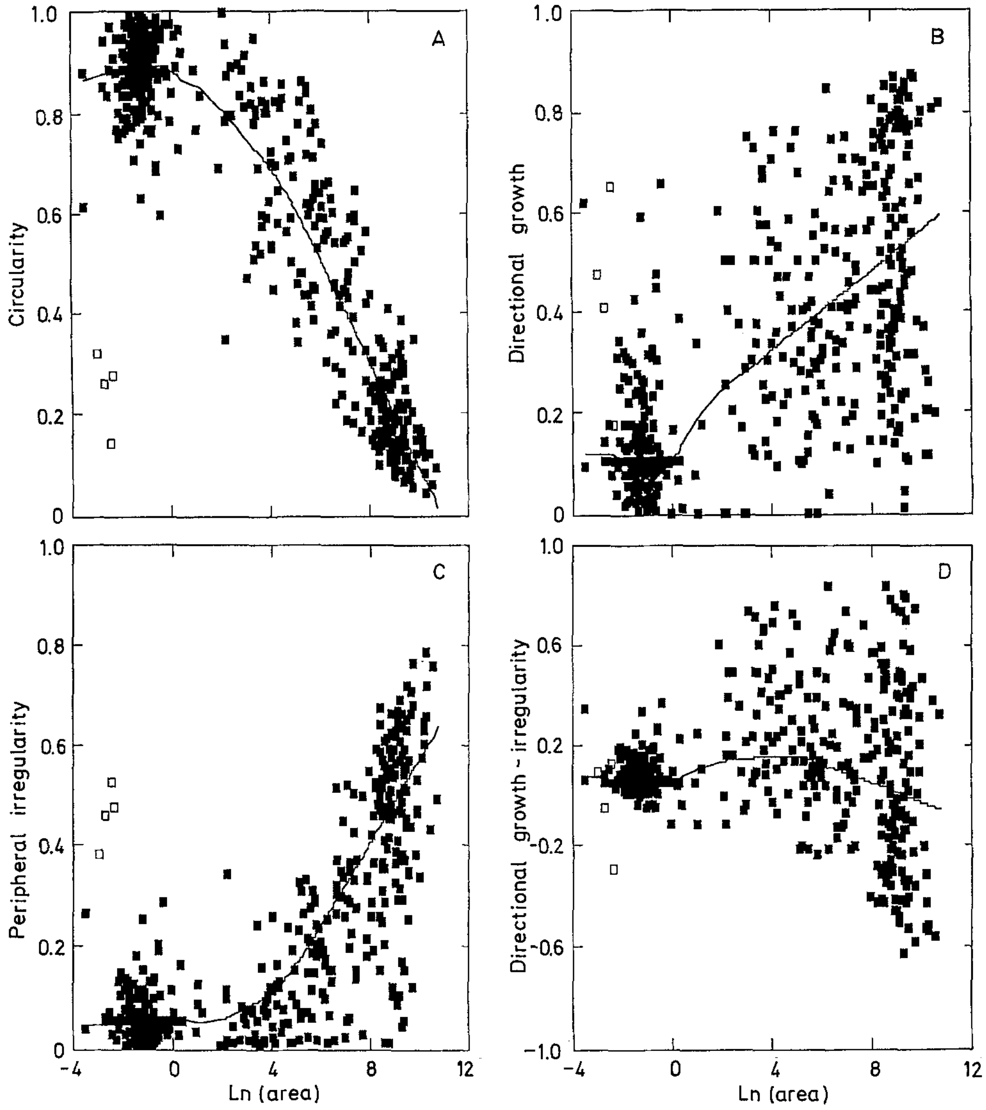

Fig. 1 *Crambe crambe.* Scatterplots of shape index values against ln of sponge area, rhagons included (□ four pre-rhagons (not included in calculations) **A** circularity index; **B** directional growth index; **C** peripheral irregularity (=convolution index); **D** index of relationship between directional growth and peripheral irregularity

Results

Relationships between sponge size and shape parameters

About 15 h after settlement, attached larvae (pre-rhagons) of *Crambe crambe* were highly irregular in shape. This stage lasted for some hours; immediately after rhagon formation, the young sponges (< 1 mm^2) were more circular in outline. Unfortunately, only four pre-rhagons were photographed and adequately measured so this stage was not included in the numerical analyses; it is included in Fig. 1 for comparative purposes only.

Analysis of the variation in shape descriptors for the whole set of rhagons and field sponges (pooled across sites), revealed the circularity of a sponge patch (Index *C*) to be negatively correlated with the area (ln) of the sponge ($r = -0.86$, $n = 564$, $p < 0.001$), although the values for four pre-rhagons were as low as those for the largest sponges (Fig. 1 A). Directional growth (Index *D*) and peripheral irregularity (=convolution index *Cv*) were significantly and positively related to area ($r = 0.49$, $p < 0.001$; and $r = 0.64$, $p < 0.001$, respectively) (Fig. 1 B, C). As for circularity, the convolution indices of the pre-rhagons were comparable to those of the largest sponges (Fig. 1 C). Index *R* was not correlated with area ($r = 0.001$, $p = 0.566$). It remained close to zero for the rhagons, whereas for larger sponges, despite high variability, the general trend was near zero, indicating that neither the directional growth nor marginal irregularity predominated (Fig. 1 D).

All four indices varied widely with sponge size. Variation in circularity was highest at intermediate sizes, whereas that of directional growth was very high over the whole range of sizes, and variation of the remaining two indices increased with increasing area.

Relationship between habitat and patch shape

Circularity index (C)

When studied separately, sponges from both sites displayed a significant negative correlation of circularity as a

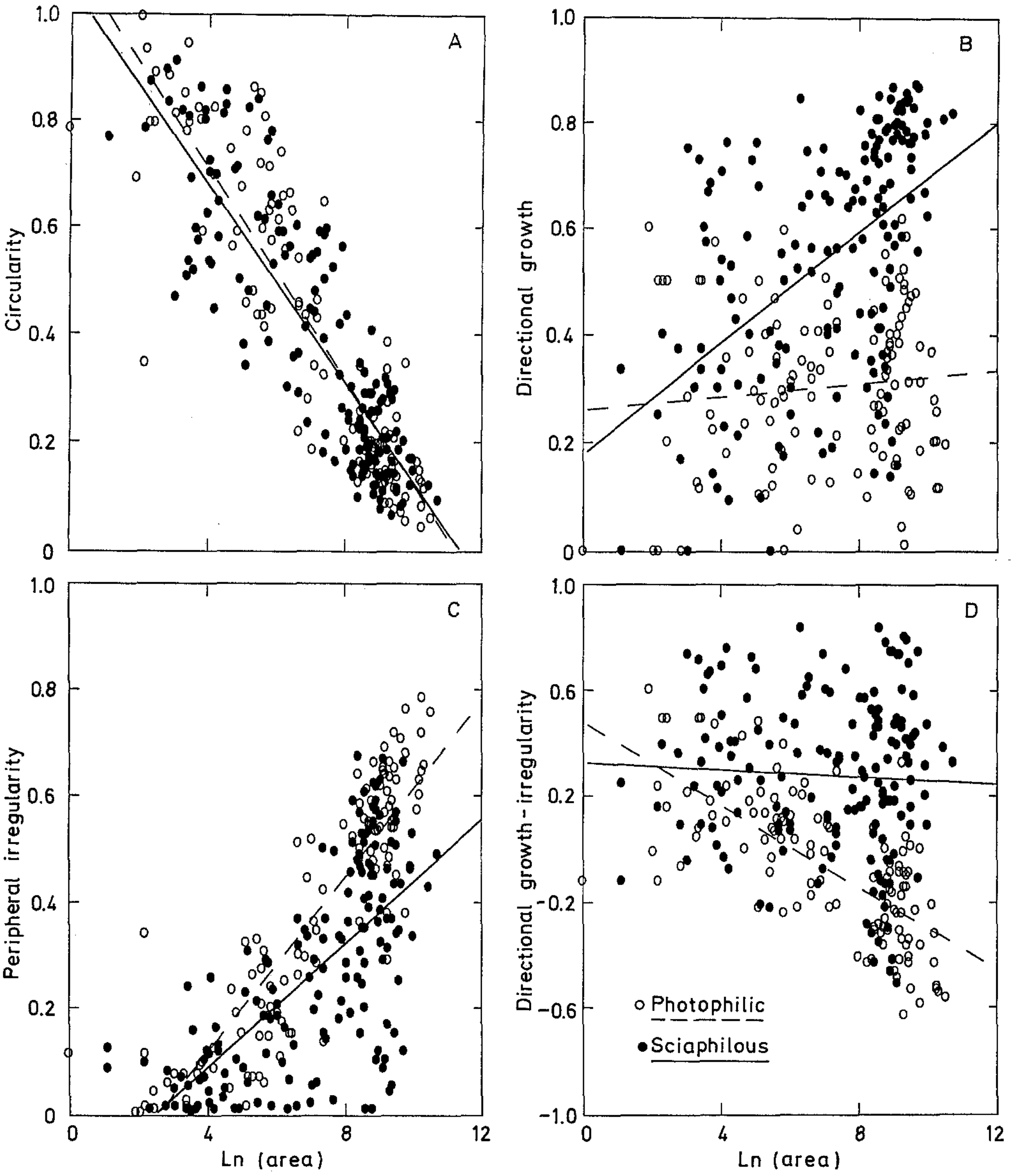

Fig. 2 *Crambe crambe.* Scatterplots of the shape-index values against ln of sponge area for photophilic and sciaphilous specimens. Regressions lines are fitted. Further details as in Fig. 1

function of area ($r=-0.89, n=118, p<0.001$; and $r=-0.86$, $n=161, p<0.001$, for the photophilic and sciaphilous sites, respectively) (Fig. 2A). Tests for slope homogeneity ($p=0.34$) and intercept equality ($p=0.36$) indicated that the regressions were not significantly different. Multiple comparisons (Tukey's test) of the index means of the size classes pooled across sites revealed that the circularity index decreased significantly from Size Class 1 to Size Class 4, whereas it did not differ significantly between size Classes 4 and 5 (Fig. 3A).

Directional growth index (D)

Directional growth did not increase significantly with increasing area in the well-illuminated habitat ($r=0.09$, $p=0.29$), whereas it was positively related to size at the shaded site ($r=0.49, p<0.001$) (Fig. 2B). Comparisons of index means between the five size classes at the shaded site revealed a significantly higher value for Size Class 5 than for the other classes (Fig. 3B). No significant difference was found between the other size classes.

Studend's t-tests between size classes consistently indicated significantly higher mean directional growth in all size classes at the well-illuminated site, except for Size Class 1 (sponge area < 100 mm^2). Directional growth was especially high in sciaphilous sponges of >10000 mm^2, with index values of around 0.8 (Fig. 3B), whereas it barely attained index values of 0.3 to 0.4 in the largest photophilic specimens; this indicates the more frequent occurrence of elongated forms in large sciaphilous sponges.

Convolution index (C_V)

When plotted against area, the degree of peripheral irregularity followed a linear regression in both photophilic ($r=0.89$, $p<0.001$) and sciaphilous ($r=0.66$, $p<0.001$)

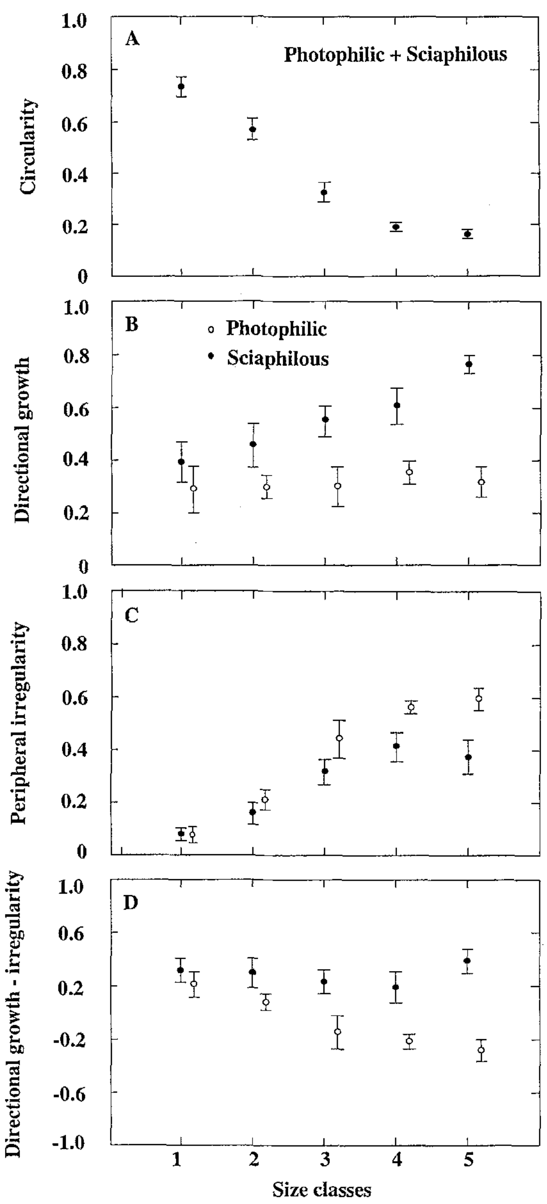

Fig. 3 *Crambe crambe.* Mean values of indices (with 95% confidence intervals) in five size classes. Data for photophilic and sciaphilous sponges are presented separately except for the circularity index, for which no habitat effect was found (see Fig. 2A)

sponges (Fig. 2C). The slope of the regressions was significantly different ($p<0.001$; covariance analysis).

Multiple comparisons of means (Tukey's test) showed no significant differences between Size Classes 4 and 5 (sponge area >5000 mm^2) in photophilic sponges (Fig. 3C). Consequently, the recorded significant change in peripheral irregularity must have been due to the smaller sponges. For sciaphilous sponges, no significant differences were found between Size Classes 1 and 2, 3 and 5, or between 4 and 5 (Fig. 3C), indicating a shift of the values of this index between the two smaller size classes and the three larger size classes.

Comparisons of index means of the size classes for photophilic and sciaphilous specimens (Student's t-tests) indicated significant differences between sites except for Size Class 1 (sponge area < 100 mm^2), the mean index values always being higher in photophilic sponges (indices ranging from 0.2 to 0.6) than in sciaphilous ones (0.1 to 0.45) (Fig. 3C), with the strongest differences in sponges >10000 mm^2.

Relationship (Index R) between directional growth index and convolution index

This index (Eq. 4) was negatively related to sponge area in the photophilic specimens ($r=-0.69$, $p<0.001$) (Fig. 2D). Multiple comparisons of size-class means (Tukey's test) showed that Size Classes 3, 4 and 5 had significantly lower indices than Size Classes 1 and 2 (Fig. 3D). This index did not vary with sponge size in the sciaphilous specimens ($r=-0.04, p=0.537$) (Fig. 2D), nor was a significant class effect detected by ANOVA (Fig. 3D). The index values were always positive in this environment for all size classes, indicating a prevalence of directional growth over peripheral irregularity for sciaphilous sponges of all sizes.

Comparisons of the index means between photophilic and sciaphilous specimens for each size class (Student's t-tests) revealed significant differences between sites except in Class 1 (sponge area < 100 mm^2). As for directional growth, the highest mean values of Index R were displayed by sciaphilous sponges of >10000 mm^2 in area (Size Class 5), and the lowest mean values by photophilic sponges from the same size class.

Discussion

Circularity of a patch of *Crambe crambe* decreases with increasing sponge size, irrespective of habitat. This characteristic, also described for other modular encrusting organisms (Stocker 1991; Turon and Becerro 1992), could be interpreted in terms of physical or biological spatial heterogeneity (Turon and Becerro 1992). Accordingly, an initially circular sponge (rhagon) would be unable to grow uniformly around its whole perimeter, resulting in a loss of circularity. Nevertheless, there is a short period during which the newly settled sponges do display a circularity index which is as low as that for the largest sponges. Characteristic irregular forms in newly settled sponges have also been reported for other encrusting sponge species (Borojevic 1971; Uriz 1982; Misevic et al. 1990) and for ascidians (Cloney 1978; Turon 1990b). These forms could represent a genetically-determined strategy common to the first growth stage of many encrusting modular organisms. Interpretation of this growth strategy is, however, difficult. The search for a suitable microhabitat or spatial refuge (Buss 1979) before growth may contribute to species' survival. Moreover, the increased surface:biomass ratios involved in these forms (they are merely a few cells thick), may favour water exchange (Borojevic 1971) before the canal system becomes functional (rhagon).

For the smallest sponge size class (< 100 mm^2 area), no differences in shape indices were evident between sites and no significant regression was found between area and shape parameters within individuals of this class. These results may indicate that the factors affecting sponge shape (sponge size or environment) become apparent only after the sponge has attained a certain size.

The species *Crambe crambe* appears to adjust its shape in response to the environmental conditions of the two habitats studied. Since the communities studied occupied both side of a gorge, environmental conditions were similar in all physical respects except for incident light. Therefore, the "habitat effect" may result from either a direct response to the amount of light received or from the different specific composition of the assemblages, which determines different space-competition pressures. The former hypothesis seems unlikely in a sponge in which no photosynthetic symbionts have been found (authors' unpublished research). An interpretation in terms of space competition seems more probable.

Circularity can be lost as a result of directional growth or of irregular growth in the form of pseudopod-like formations on the margin of the patch. Directional growth of *Crambe crambe* seems to be more usually associated with sciaphilous specimens, especially in large sponges. As in other invertebrates (e.g. cheilostomes: Stebbing 1973), encounters with good space competitors may cause cessation of growth on a given zone of the sponge and direct sponge growth towards a space occupied by more vulnerable organisms, thus resulting in an elongated growth form. Such resistant neighbours are far more frequent among sciaphilous, long-lived organisms which are provided in many cases with chemical defences (Uriz et al. 1991; 1992a). Redirection of growth has been considered one of the advantages of organisms with indeterminate growth over those with determinate growth, as it improves their chances of finding a refuge (Buss 1979).

The non-directional growth of *Crambe crambe* living in well-illuminated habitats may be enhanced by the absence or low levels of true space competition in such environments. New patches of bare substratum are continuously formed in this habitat by the death of short-lived organisms (e.g. opportunistic seaweeds, ascidians) and grazing (much more intense in well-lit habitats) (Zabala and Ballesteros 1989), and would provide space for colonization by *C. crambe*, whose growth shape may not be strongly influenced by neighbours in this environment.

Size is positively correlated with peripheral irregularity (=convolution index, *Cv*) of the sponge patch in both habitats. Large sponges, however, featured more irregular perimeters in photophilic than in sciaphilous specimens. In fact, some sponges in the shaded habitat, even those of the largest size class, displayed very low degrees of peripheral irregularity (Fig. 2C). These corresponded to specimens in contact with good space competitors with an even border (e.g. the sponge *Chondrosia reniformis*) which determined the outline of *Crambe crambe*.

In summary, the prevalence of directional growth over pseudopod-like formations in sciaphilous sponges in contrast to photophilic specimens may be due to spatial competition. Nevertheless, experimental approaches would be desirable to verify these inferred relationships between size, shape, and habitat in encrusting sponges.

Acknowledgements The authors are indebted to J. M. Tur, who took part in the field work. This study was funded via Projects CICYT MAR91-0528 (Spanish Marine Resources and Aquaculture Programme) and MAST-CT91-004 (Commission of the European Communities) and a Basque Government fellowship to M.A.B.

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