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The importance of micro and macro morphological variation in the adaptation of a sublittoral demosponge to current extremes

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Abstract Sponges are known to show morphological acclimation in response to habitat variation. However, previous studies have concentrated on only one aspect of morphological variation, either gross morphology or spicule morphology. *Cliona celata* (Grant) is common in a variety of different habitats on the south-west coast of Ireland and has been investigated with respect to morphological variability on both scales. *C. celata* exhibited six different gross morphological body forms (ridged, burrowing, massive, massive/chimneys, encrusting, encrusting/chimneys). The body form exhibited was correlated to local environment, showing the extent of morphological adaptation in *C. celata*. Sponge size varied (from 548 ± 75 to $2,345 \pm 433$ cm^2) between sites, with the largest ($2,345 \pm 433$ cm^2) being found at the most stable site where flow rates were < 5 cm^{-1} ($F > 23.24$, $P < 0.05$). This may seem paradoxical as growth conditions were considered poor, but mortality and damage from material in suspension was reduced at low energy sites. At the spicule level, morphological variation was also present. Spicules at high energy sites were significantly longer, narrower and less numerous than at low energy sites ($F > 15.36$, $P < 0.05$). Previously, spicule variation has been associated with increased stiffness in hostile environments. However, longer, thinner spicules, as found in *C. celata*, may result in a more flexible sponge. This is the first study to show both gross morphological (macro) and spicule (micro) variation in a single species of sponge. However, this study only reinforces some of the previously produced information on both of these adaptations of sponges to varying environments. This study also illustrates how the results of single studies should not be used to draw conclusions for group level adaptation.

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Introduction

The morphology of any sessile organism is important for a range of reasons including feeding (Vogel 1981; Okamura 1984), competition (Barnes and Rothery 1996), prevention of sediment settlement (Riegl et al. 1996), photo-adaptation (Chappell 1980), water current adaptation (Stearn and Riding 1973; Bell and Turner 2000), reproduction (Wulff 1991, 1995), dispersal (Wulff 1985) and protection against predators (Guida 1976). Sponges are one group of organisms capable of considerable morphological adaptation, with several studies implicating environmental parameters in shaping external shape (e.g. Bell and Barnes 2000a).

Sponge gross morphology is not static. Continual remodelling processes occur, which may allow a sponge to adapt to its environment (Palumbi 1984; Bond and Harris 1988; Gaino et al. 1995). However, phenotypic variation can only occur within a genetically predetermined framework (Bell and Barnes, in press). For example, true arborescent sponges (e.g. *Raspailia ramosa*) cannot become encrusting sponges (e.g. *Paratimea constellata*). In studies of morphology, sponge species have often been found to show a limited number of body forms. These are usually modifications on a common body pattern, often along a continuous gradient (Kaandorp and de Kluijver 1992; Kaandorp 1999). The morphology of a sponge is important in environmental acclimation (Palumbi 1986). For this reason, sponge habitat generalists may employ a variety of morphological phenotypes to survive in a variety of different habitats. *Cliona celata* (Grant) is a common sublittoral sponge, found in a range of habitats attached to rocks and shells (Van Soest et al. 1982; Ackers et al. 1992). *C. celata* has a wide distribution in the eastern Atlantic from Sweden to Gibraltar and the Mediterranean. It is not found on the North Sea coast of the United Kingdom, but is common on the Irish coastline. This species is known to exhibit a massive and a boring form. However, considerable variation exists in these massive forms and controlling factors remain undescribed. Morphological adaptation may occur by other means, including orientation in relation to current flow, as entrained water flow can be induced through sponges under certain conditions (Vogel 1974).

Spicules are an important part of the skeletal material of sponges, along with collagen and spongin fibres (Bergquist 1978). The proportion of these spicules within sponges is not static and several studies have shown seasonal changes in the numbers of spicules, resulting in an increased inorganic content (Stone 1970; Schönberg and Barthel 1997; Mercurio et al. 2000). These changes are considered with respect to seasonal differences in wave exposure. This environmental factor is considered a regulatory measure of sponge inorganic content (Palumbi 1986). Increased inorganic content of sponges as a result of tactical acclimation may also be achieved by a decrease in other skeletal components, such as spongin fibres (Stone 1970; Schönberg and Barthel 1997).

Since work by Palumbi (1986), it is considered that sponges show variation in spicule morphologies as an adaptive response to the prevailing environmental conditions. However, evidence for other sponges showing similar relationships appear absent from the literature. Several studies have also described macro-morphological adaptation of sponges in response to varying environmental parameters (Wilkinson and Vacelet 1979; Kaandorp 1999; Bell and Barnes 2000a). These studies have only concentrated on one type of morphological variation (either spicule or gross morphology). Initially this study aims to answer the question, how do micro (spicule) and macro (gross) morphology vary in relation to the degree of water movement? Consideration is also given to other aspects of sponge morphology including the variation in oscule number between sites experiencing different environmental conditions.

Materials and methods

Study site

Lough Hyne Marine Nature Reserve is a small (0.5 km^2) semi-enclosed sea lough situated upon the south-west coast of Ireland (51°29'N, 9°18'W). The lough is connected to the adjacent Atlantic waters by a narrow tidal channel approximately 25 m wide. The topography of this connection results in anomalous tidal movements in which tidal inflow lasts 4 h and outflow lasts 8 h (Bassindale et al. 1957). The consequence of such tidal movements is that water currents are extremely fast during inflow (>300 cm^{-1}), but negligible during outflow. As inflowing water moves across Lough Hyne from Whirlpool Cliff, towards Glannafeen and West Cliff (Fig. 1), water currents decrease rapidly. This results in a sedimentation gradient from east to west. Sublittoral cliff surfaces at Whirlpool Cliff (Fig. 1) are characterised by current-swept, sediment-free surfaces. Surfaces at Labhra Cliff and West Cliff, where currents are slight, are covered in sediment (<5 cm^{-1}). Bullock Island is outside the marine reserve area (Fig. 1). Sublittoral cliffs at this site are subjected to an extremely turbulent, destructive flow regime, with sediment free surfaces. Further information on study sites is given by Picton (1991), Bell and Barnes (2000b) and Bell and Turner (2000).

Measurements and core samples of *Cliona celata* were taken at Bullock Island (high energy, turbulent flow), Whirlpool Cliff (fast unidirectional flow, low sedimentation), Labhra Cliff (slight flow, high sedimentation) and West Cliff (very slight flow, very heavy sedimentation). Photographs were taken of 30 *C. celata* specimens using a Nikonos V (100 ASA film) with a 28 mm lens and strobe at depths between 12 m and 18 m. The camera was attached to a fixed frame allowing the camera-to-sponge distance to be kept constant for all photographs. Slides of each sponge were projected onto graph paper and the surface area was calculated. At the time of taking the photograph, the maximum height and number of exhalent oscula was also recorded. A growth form classification was also constructed (Fig. 2) and each sponge was assigned to one morphological group.

Three core samples (approximately 1 cm diameter, 1 cm depth) were taken from 30 sponges (in July 2000) at each site (4 sites) and were removed immediately for laboratory, spicule and ash weight analysis. In the laboratory, core samples were washed in distilled water and halved. The first halves were placed in pre-weighed vials, dried at 60°C for 48 h, then combusted for 6 h at 450°C. The remaining halves were also placed in pre-weighed vials and dried at 60°C for 48 h. These samples were then dissolved in 10 ml of concentrated nitric acid to remove tissues for spicule analysis (after Ackers et al. 1992). The acid was diluted with 90 ml of distilled water. Samples were agitated, pipetted onto microscope slides and viewed under a compound microscope. The megascleres of *C. celata* are tylostyles, with the heads having swellings just up from the blunt end of the shaft in most spicules. An ocular micrometer was used to measure the length, maximum shaft width and bulb diameter of 50 random spicules. Three different slides for each sponge sample were taken. Estimates of spicule densities were also made (as for Palumbi 1986). Ten dried and pre-weighed pieces of *C. celata* from each site were dissolved in 20 ml of nitric acid to remove all organic material. This was then further diluted with 100 ml of distilled water. The solution was vigorously agitated and 50 μl immediately placed upon a welled slide. The slide was viewed under low power and all spicules were counted. This process was repeated three times for each sample. Estimates of spicule densities were then calculated.

Results

Gross morphology

Variation occurred in the gross morphologies of *Cliona celata* found at the different sites (Fig. 3). Bullock Island was dominated by ridged forms (66%) and encrusting forms (28%). Whirlpool Cliff was dominated by massive (63%) and encrusting forms (17%), with smaller numbers of sponges exhibiting body forms with chimneys. High proportions of encrusting sponges occurred at both Labhra Cliff and West Cliff (40% and 30%, respectively) and although burrowing forms (32%) were abundant at West Cliff, they were replaced by encrusting/chimney forms (43%) at Labhra Cliff.

Sponges differed in their surface area, number of oscula (per square metre of surface area) and maximum height between sites (Table 1). Sponges at Whirlpool

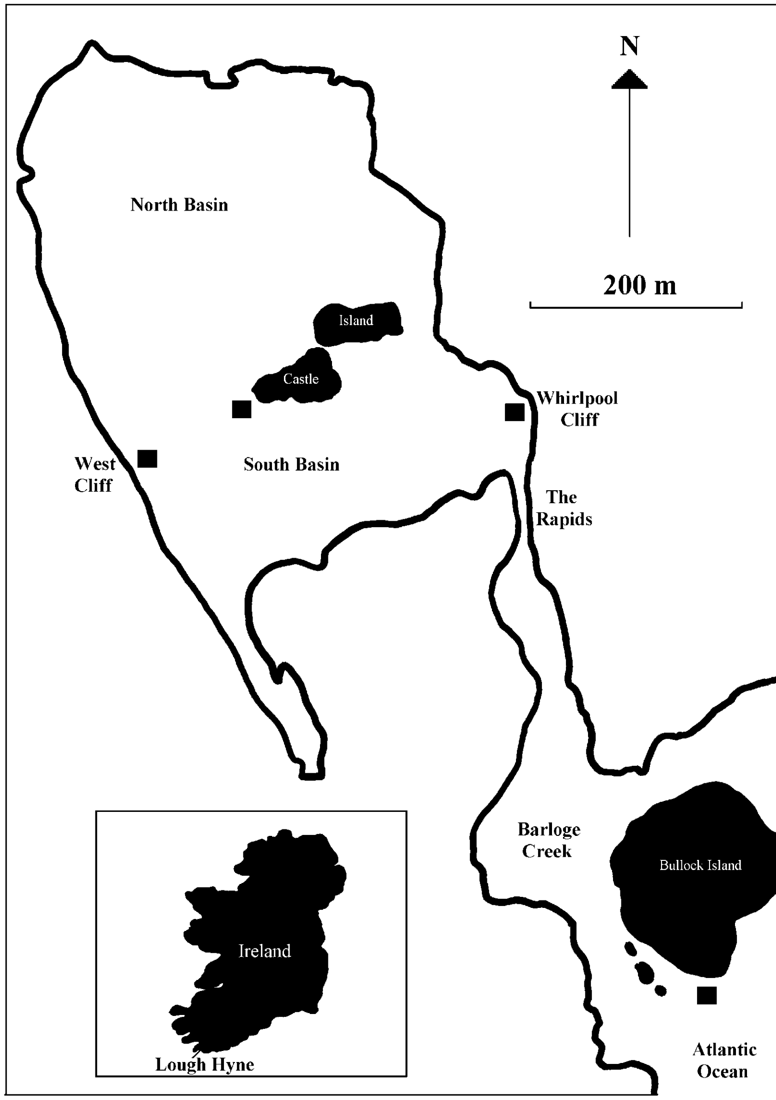

Fig. 1 *Cliona celata*. Lough Hyne Marine Nature Reserve, Co. Cork, Ireland. *Filled squares* indicate sampling stations

Cliff were significantly higher ($H = 78.41$, $df = 3$, $P < 0.001$) and had a greater number of oscules per square metre of surface area ($H = 22.65$, $df = 3$, $P < 0.001$) than at the other three sites. However, the number of oscules per square metre of surface area was significantly lower at Bullock Island ($P < 0.05$) than the remaining sites. The number of oscula per square metre of surface area at Labhra Cliff and West Cliff was twice that of Bullock Island and half that of Whirlpool Cliff.

Ash content

A GLM ANOVA was used to compare the relationship between ash weight (dependent variable) and dry weight (independent variable). This relationship proved to be the same at all three sites (Fig. 4), with no significant difference in the slopes of the relationships ($F = 4.13$, $P = 0.43$). For a unit increase in dry weight, the ash weight (inorganic content) increased by the same amount proportionally at all four sites. Therefore, all data was pooled and a regression line was fitted (with ash weight taken as the dependent variable). Ash weight was positively correlated with dry weight (Pearsons correlation 0.89, $P < 0.001$). The regression was found to be significant ($F = 1{,}015$, $P < 0.001$). The mean inorganic content did not vary significantly ($F = 1.24$, $P = 0.209$) between sites. The *C. celata* specimens at all four sites were composed of approximately 50% inorganic material.

Spicule analysis

Although ash contents did not vary significantly between sites, variation did occur in the density, size and shape of the spicules (Table 2, Fig. 5). The megascleres of *C. celata* are tylostyles, with the heads having swellings just up from the blunt end of the shafts in most spicules (Fig. 5). For all spicule and inorganic content measurements, no significant intra-specimen (between 3 slides or core samples) or intra-site (between 10 sponges)

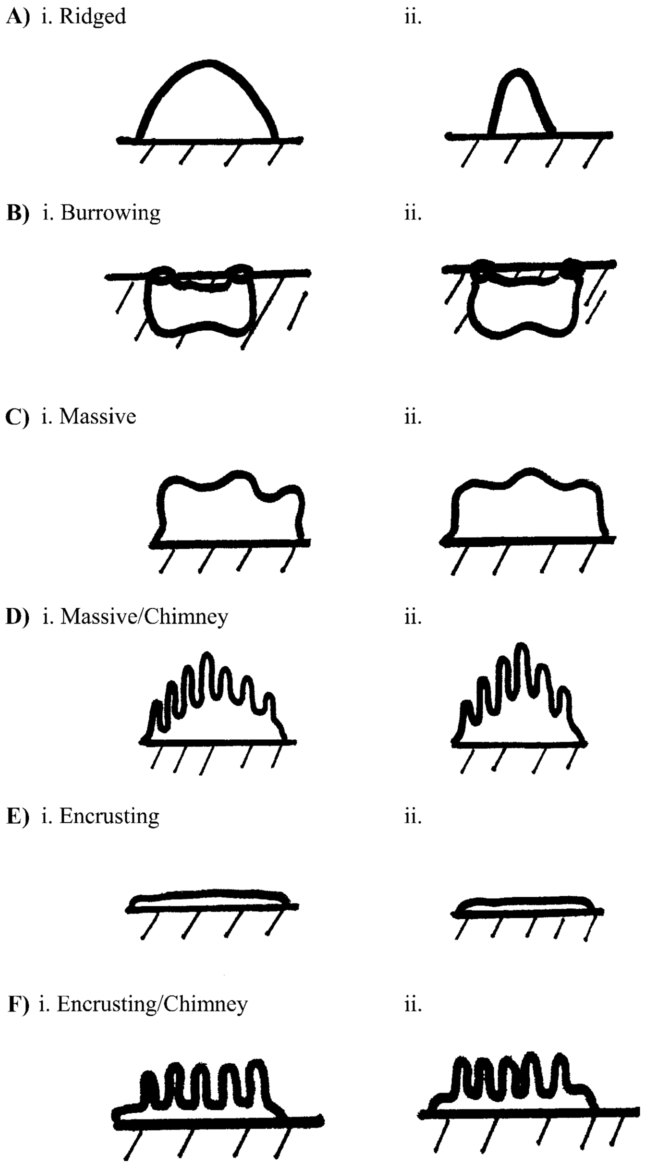

Fig. 2 *Cliona celata*. The side (*i*) and end views (*ii*) of six body forms in to which sponges at Lough Hyne were classified

variation was found between the three sites ($P<0.05$ for each Kruskall Wallis statistic). There was less than 4% and 6% variation in all mean spicule measurements between sponge specimens and within sites respectively. Spicules from Bullock Island and Whirlpool Cliff were significantly longer ($F=15.36$, $P<0.001$) than those from the other two sites (Table 1). The shaft and bulb widths of spicules at Bullock Island and Whirlpool Cliff were not significantly different between these two sites, although both sites had significantly ($F>59.05$, $P<0.001$) narrower spicules and smaller bulb widths than those at Labhra Cliff and West Cliff. Therefore, spicules were longer and thinner at Bullock Island and Whirlpool Cliff, but had a smaller bulb width than at Labhra Cliff and West Cliff. Calculation of spicule density showed differences in the number of spicules per gram of dry tissue (Table 2). Significantly higher spicule densities ($F=8.15$, $P<0.05$) were found in sponges from Labhra Cliff and West Cliff than at Whirlpool Cliff and Bullock Island. Inorganic content differences did not vary between sites, but the spicules sizes were different. Therefore differences in spicule densities must account for the discrepancies in spicule sizes as there was no differences in inorganic content of sponges between sites.

Discussion

Many organisms, including sponges, can exhibit morphological variation in relation to environmental factors (Chappell 1980; Palumbi 1986; Bell and Barnes 2000a). *Cliona celata* showed considerable variation in both gross morphology and spicule characteristics under different flow regimes. Several results reflect those of a previous study on *Halichondria panicea* (Palumbi 1986), but it appears this is the first study to examine both types of variation within a single species. This study illustrates how sponges can show both macro and micro morphological adaptation, within species, to different environmental regimes.

C. celata showed six distinct morphological types at Lough Hyne and on the adjacent Atlantic coast. Many sponge species have the ability to morphologically adapt (Bell and Barnes 2000a). However, few sponges can morphologically adapt to a large range of environments. At Lough Hyne, *C. celata* was observed to morphologically adapt to heavily sedimented (very low current), current-swept and turbulent flow regimes. At Bullock Island where flow conditions were most turbulent, *C. celata* showed ridged forms (Fig. 2). This form is thought to increase the basal to surface area ratio, thereby reducing drag on such basal components. The oscula of these sponges were all lined up along the edge of the ridge, which may enhance entrained flow (Vogel 1974). Several explanations may account for smaller sponges at Bullock Island. Sponges, like most macrobenthos subjected to strong flow, may grow only to an optimal size controlled by a suite of factors. These factors may include competing organisms (such as *Laminaria digitata*), inhibited feeding by turbulent flow (Hiscock 1983), or damage caused by the turbulent flow regime (Barnes and Whittington 1999). Alternatively, age differences alone may account for size differences. Sponges may be younger at Bullock Island where damage and possibly mortality from destructive wave forces may be increased. This is supported by the largest sponges being found at Labhra Cliff where conditions for growth are poor (low water movement), but stable over time (Picton 1991). Size may be considered a function of age, which is in turn controlled by habitat stability as well as growth potential. This hypothesis assumes size is related to longevity, which may not be the case. For example, *C. celata* is believed to grow slowly, but it regenerates quickly when damaged (J. Bell, unpublished data). Although a suite of factors may control the optimum size of a sponge at Bullock Island,

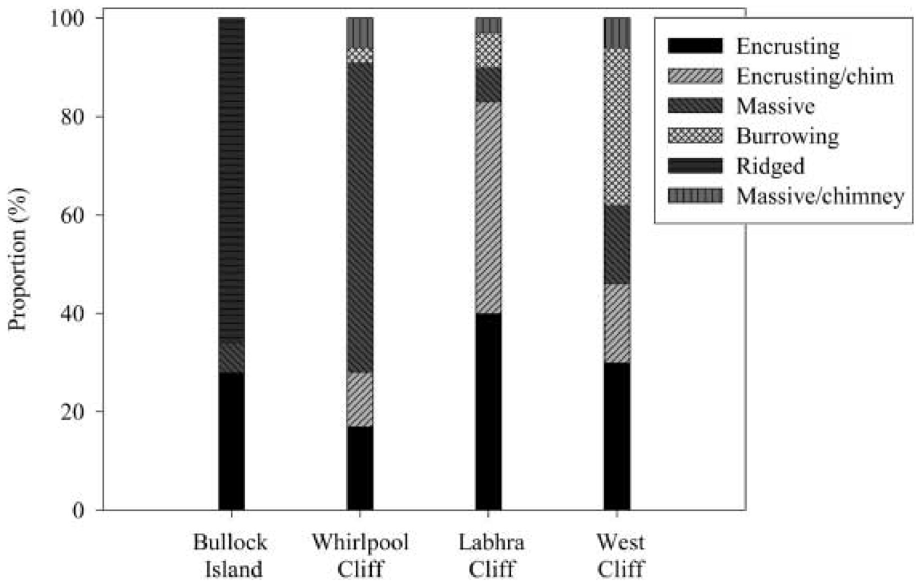

Fig. 3 *Cliona celata*. The proportion of gross external body forms exhibited at four sites of differing flow regime

Table 1 *Cliona celata*. Gross morphological (body shape) measurements (±SE) at four sites at Lough Hyne

Site	Mean surface area (cm^2)	Mean number of oscules per m^2	Mean maximum height (cm)
Bullock Island	548 (±75)	54.8 (±8.8)	9.37 (±0.76)
Whirlpool Cliff	1,330 (±158)	272.8 (±22.2)	14.65 (±1.12)
Labhra Cliff	2,345 (±433)	91.7 (±11.4)	7.06 (±0.68)
West Cliff	1,054 (±196)	93.6 (±7.4)	5.53 (±0.71)

the relative importance of each is unclear. Burrowing forms were only abundant at West Cliff, exclusively on vertical cliff faces. The presence of subsurface inhalent ostia is well suited to West Cliff as this prevents clogging of delicate feeding structures. However, the burrowing form would appear suited to all environments, so it remains unclear why it is absent from other sites. Substratum type is important in the distribution of burrowing sponge species, with this species preferring limestone and other soft rock material, but as substratum type is the same at all sites within Lough Hyne (Holland 1990) it cannot explain the distribution patterns of burrowing types observed.

C. celata showed encrusting and encrusting/chimney forms at Whirlpool Cliff. Although these chimney forms are likely to enhance entrained flow through sponges (Vogel 1974), they have an increased probability (compared to encrusting forms) of being hit and damaged by material being carried in suspension (Hiscock 1983). The encrusting forms cover large areas of cliff face in the circalittoral zone at Whirlpool Cliff, where the large kelps found in the infralittoral zone at Bullock Island are absent. *C. celata* at Whirlpool Cliff had more than double the number of oscules per unit surface area than at Labhra Cliff and West Cliff, and quadruple the number at Bullock Island. These differences conflict with the findings of Palumbi (1986), who suggested a higher energetic cost involved in maintaining stiffer (more inorganic material) tissues in high energy environments requires more oscula for pumping water through the narrower bore aquiferous system associated with sponges in these higher energy environments (Palumbi 1986). However, *C. celata* showed no such differences in inorganic composition between sites and reasons for such oscula differences are unclear. Reduced oscular number at Bullock Island is likely to relate to the dominant ridged body form (Fig. 2) found at this site, in which the oscules are lined up along the ridge edge, whereas at the sedimented areas of Labhra Cliff and West Cliff reduced numbers of oscules may represent an adaptation such that the sponge may have a lower probability of clogging from sediment during periods of reduced pumping (Reiswig 1971).

This is not the first study to demonstrate differences in spicule morphology and size between habitats of different environmental conditions (Palumbi 1986). However, considerable differences occur between the results of this and previous studies. Palumbi (1986) found spicules of *Halichondria panicea* to be wider at high energy sites. However, no differences were found in spicule length. Spicule content was also much higher in *H. panicea* from high energy environments. Here, longer, thinner spicules were found in *C. celata* at the sites of higher energy (Whirlpool Cliff and Bullock Island). Palumbi (1984) suggested that stiffness of sponges increased with the total percentage of sponge dry mass devoted to the spicules, with stiffer sponges being more suited to hostile, high energy environments. However, no difference was found in the body mass of *C. celata* devoted to spicules between sites, with differences that

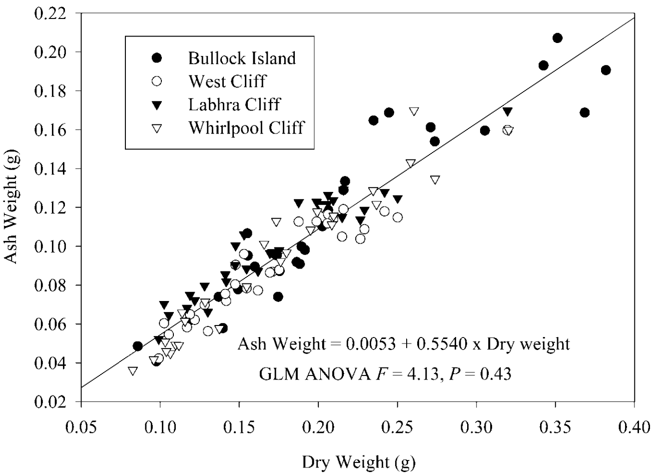

Fig. 4 *Cliona celata*. The dry weight (g) to ash weight (g) relationship for core samples taken from four sites at Lough Hyne

would be expected from spicules sizes being accounted for by higher densities. The longer, more numerous spicules at Bullock Island and Whirlpool Cliff may not make stiffer tissues (Payne 1966; Koehl 1982) at the high energy sites, but they may provide a degree of flexibility (more flexible spicules). This may also be important in helping sponges adapt to hostile environments in a different manner to that exhibited by *H. panicea* (Palumbi 1986). The significance of larger bulbs at the heads of the spicule shafts is unclear, but the reduction in size of these bulbs in high energy environments may mean the loss of a potential structural weakness point, making the spicules stronger and more flexible. Previous studies have shown correlations between ambient water silica content and spicule size, with larger spicules being associated with higher silica concentrations (Mercurio et al. 2000). Silica concentrations are expected to be the same at all sites sampled within the present study due to the small geographic distances separating sites and the periodic mixing of Lough Hyne and coastal waters (Bassindale et al. 1957).

Most studies of sponge morphology or acclimation cite the pivotal work of Palumbi (1986), showing how a sponge species can adapt to hostile environments by means of change in skeletal components. However, others describe how gross sponge morphology may adapt sponges to different environments (Kaandorp and de Kluijver 1992; Kaandorp 1999; Bell and Barnes 2000a). This is the first study to show how both of these

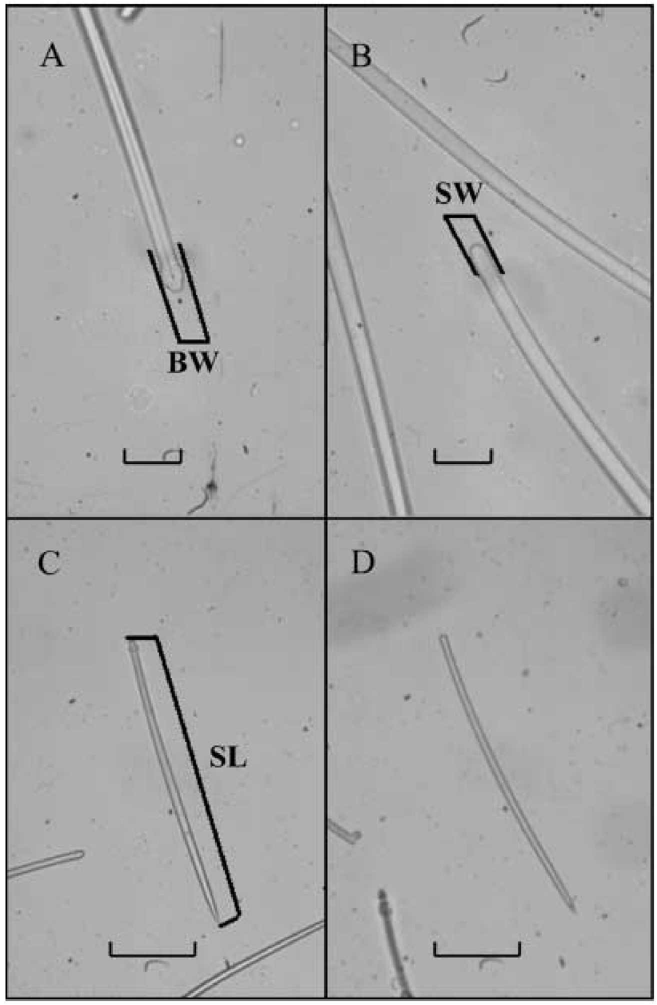

Fig. 5 *Cliona celata*. Measurements of spicule lengths (*SL*), widths (*SW*) and bulb widths (*BW*) at low (*A*, *B*) and high energy sites (*C*, *D*). *Bars* 10 μm

factors are important in the environmental acclimation of a single sponge species. *C. celata* appears to exhibit a different adaptation than that described for *H. panicea* by Palumbi (1986). *C. celata* showed a much lower inorganic content than *H. panicea*, found at both low and high energy sites. The lowest numbers of oscula (per unit surface area) for *C. celata* were found at high energy sites, with the converse being true for *H. panicea*. The structure of *C. celata* may allow the species to adapt to high energy environments by increased flexibility, accounting for reduced organic material and lower num-

Table 2 *Cliona celata*. Micro morphological (spicule dimensions ±SE) variation at four sites at Lough Hyne. Inorganic (silica) content is also shown

Site	Mean length (μm)	Mean width (μm)	Bulb width (μm)	Density (spicule 10^7/g dry wgt)	Inorganic content (%)
Bullock Island	321 (±2.08)	12.3 (+0.14)	12.3 (±0.15)	1.59 (±0.13)	54 (±1.43)
Whirlpool Cliff	323 (±1.96)	12.3 (+0.11)	12.3 (±0.15)	1.31 (±0.14)	52 (±0.91)
Labhra Cliff	312 (±1.79)	13.9 (+0.10)	16.5 (±0.13)	2.01 (±0.14)	51 (±1.20)
West Cliff	313 (±1.88)	13.9 (+0.12)	16.5 (±0.14)	1.98 (±0.14)	51 (±1.19)

bers of oscula (as pumping pressures are reduced). This study illustrates how universally accepted studies may not be applicable to all species within any given group, and that each species needs to be considered individually before general group level patterns and trends can be examined or presented.

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