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ORIGINAL ARTICLE

Morphological features of the gorgonian *Paramuricea macrospina* on the continental shelf and shelf edge (Menorca Channel, Western Mediterranean Sea)

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ABSTRACT

Morphological variability in gorgonians is frequent and commonly associated with habitat variability, often resulting in segregated morphotypes. *Paramuricea macrospina* is an endemic Mediterranean gorgonian species found on rocky bottoms between 40 and 160 m depth and has recently been reported as one of the most abundant species in continental shelf and shelf edge environments. Three different chromatic forms of *P. macrospina* were observed in the Menorca Channel: a yellow form and a light purple form occurring on maërl beds of the continental shelf, and a dark purple form occurring on rocky substrates of the shelf edge. The objective of the present work is to verify if these *P. macrospina* forms may represent distinct taxonomic units by analysing differences in colony morphology and sclerite size and shape of the three chromatic forms. No significant differences were found in colony shape, suggesting that environmental variability between the continental shelf and the shelf edge is not influential enough to significantly alter colony morphology. Significant differences in sclerite size and shape were found amongst all forms, suggesting that sclerites may be influenced by environmental conditions. However, the co-occurrence of the yellow and light purple forms side by side on the continental shelf may indicate a certain degree of genetic differentiation.

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Introduction

Modularity is a successful strategy widely spread among sessile organisms, as it facilitates adaptation to different environmental conditions (Hughes 1989). Morphological variability is very common, especially among coral and gorgonian species (Bruno & Edmunds 1997; Sánchez et al. 2007; Vermeij et al. 2007). Indeed, these organisms can present a wide plasticity in their growth under different environmental conditions (Todd 2008). Plasticity can affect colonial colour and morphology (Sánchez et al. 2007; Prada et al. 2008), as well as sclerite size and shape (Gutiérrez-Rodríguez et al. 2009) and the presence of specific secondary compounds (Puyana et al. 2004). This can pose an additional challenge for taxonomic, evolutionary and ecological studies (Vermeij et al. 2007).

Coral and gorgonian morphological variability has commonly been related to habitat differences (Bruno & Edmunds 1997; Helmuth et al. 1997), often resulting in segregated morphotypes adapted to different hydrodynamic and/or light conditions (Sebens 1987; Sánchez et al. 2007; Gori et al. 2012). Colony transplant experiments have shown that the same genotype can generate different morphological phenotypes, confirming the importance of phenotypic plasticity (West et al. 1993; Joseph et al. 2015).

During the past 20 years, several studies have addressed morphological variability in shallow gorgonian species (<40 m depth) mainly in relation to the dominant hydrodynamic conditions (Weinbauer & Velimirov 1995; Skoufas 2006; Sánchez et al. 2007).

Studies concerning morphological variability in deep gorgonians are still very scarce (e.g. Mortensen & Buhl-Mortensen 2005; Quattrini et al. 2013; Doughty et al. 2014). However, the increased accessibility to deep environments provided by Remotely Operated Vehicles (ROVs) and manned submersibles has revealed that deep gorgonian species may occur over a wide bathymetric range and through different environmental settings (Stone 2006; Buhl-Mortensen et al. 2015). The increasing observation of deep gorgonian assemblages is showing that, as is the case with

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their shallow counterpart, deep gorgonian species may present a certain degree of morphological variability (Mortensen & Buhl-Mortensen 2005). *Paramuricea macrospina* (Koch, 1882) is an endemic Mediterranean gorgonian mostly found on rocky bottoms at 40–100 m depth (Carpine & Grasshoff 1975; Bo et al. 2012). This species has recently been found to be among the most abundant gorgonians on the Mediterranean continental shelf (Bo et al. 2012; Grinyó et al. 2016). In the Menorca Channel (Western Mediterranean Sea) (Figure 1), *P. macrospina* is the dominant gorgonian species at 65–90 m depth on the continental shelf, but it is also commonly found on the shelf-edge associated with other gorgonians at 110–160 m depth (Grinyó et al. 2016). Two different chromatic forms of *P. macrospina* were observed on the continental shelf, a yellow one (M1) and a light purple one (M2) (Figure 1). Both forms occur on maërl beds, covering vast areas and occasionally reaching very high densities (Grinyó et al. 2016). On the shelf edge, a third dark purple form (M3) was observed on rocky substrates (Figure 1).

In the last few years several studies have started to explore the biology and ecology of deep Mediterranean gorgonian species (e.g. Bo et al. 2012; Topçu & Öztürk 2016). In this context, this study aims to elucidate whether the different *P. macrospina* forms observed in the Menorca Channel represent distinct taxonomic units, by exploring differences in their (1) colony shape and (2) sclerite size and shape.

Material and methods

Colony shape

Pictures of *Paramuricea macrospina* used to analyse colony shape were obtained from videos recorded on the continental shelf (60–80 m depth) and the shelf-edge (110–160 m depth) of the Menorca Channel (39°53′0.73′N, 3°29′51.16′E) in September 2010 and

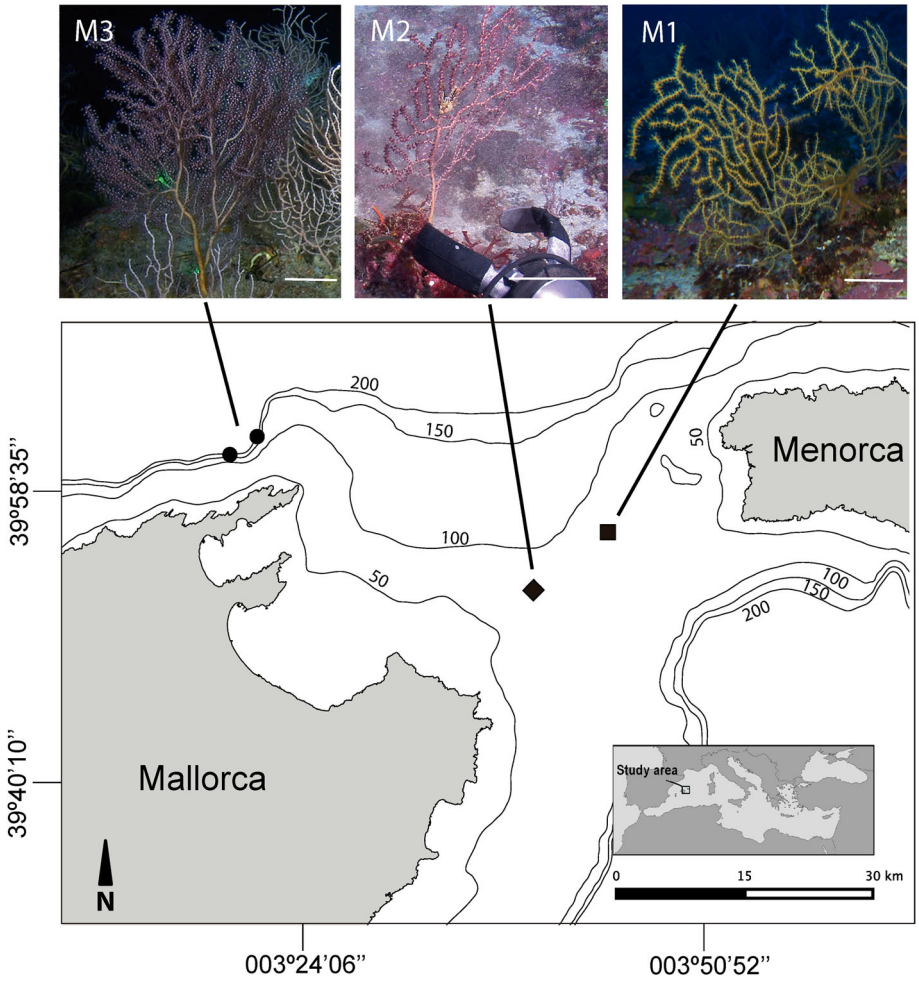

Figure 1. Images of colonies of different chromatic forms of *Paramuricea macrospina*. Collection locations and image captures of each type are shown by: Squares M1, Diamonds M2 and Dots M3.

April 2011. Videos were recorded with the manned submersible JAGO (IFM-GEOMAR) equipped with a 1080 horizontal line colour video camera and two parallel laser beams that provide a scale for the images (50 cm). In each picture, colonies were perpendicular to the camera, and lasers were in the same plane as the colony. Twenty pictures of colonies of each form (M1 and M2 from the continental shelf, and M3 from the shelf-edge) were haphazardly selected for the subsequent analysis. Analyses were performed with the Macnification v. 2.0.1 (Orbicule Enhanced Labs; Schols & Lorson 2008) software and laser beams were used as reference to calibrate each picture.

From each picture, the maximum height and width of the gorgonian colony was measured; mean width was calculated as the mean of three measurements taken at equidistant positions and perpendicular to the height (Gori et al. 2012). Fan surface area was estimated by measuring the area defined by a continuous line that linked the tips of all the branches located on the external perimeter of the colony (Weinbauer & Velimirov 1995). The ramification pattern was determined by establishing a branch ordination pattern following Brazeau & Lasker (1988). Most distal branches were defined as first order branches; second order branches occurred when two first order branches joined (Figure 2). Higher order branches only appear when two branches of equal lower order join. Branches were also classified as 'tributary' or 'source', where source branches are those that join same order branches whereas tributary branches are those that join a higher order branch (Brazeau & Lasker 1988; Gori et al. 2012) (Figure 2). Finally, the length of all first order branches was measured.

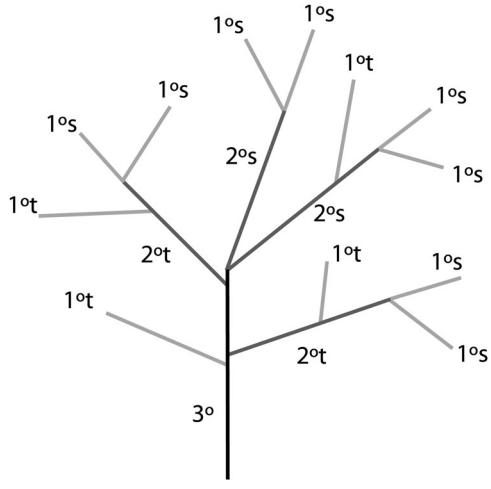

Figure 2. Branching structure showing first (light grey), second (dark grey) and third (black) order branches and source (s) and tributary (t) branches.

For each colony, the following shape features were calculated: height to width ratio, height to mean width ratio, ramification density (number of ramifications/fan surface area), first order branch density (number of first order branches/fan surface area), order of the colony's base, the maximum and mean length of first order branches, the bifurcation ratio

$$R_b = \frac{1}{m} \sum_{i=1}^{m} \frac{n_i}{1 + n_i}$$

where n is the number of branches of order i, and m is the total number of orders, and the tributary to source ratio of first and second order branches.

Sclerite size and shape

Colonies of *Paramuricea macrospina* were collected from the continental shelf (~75 m depth) and shelf-edge (~130 m depth) of the Menorca Channel in April 2011 and July 2012 (Figure 1). Sampling was performed by means of the manned submersible JAGO (IFM-GEOMAR) and the ROV NEMO (Gavin Newman), both equipped with a grabber. Fifteen colonies of each of the two continental-shelf forms (M1 and M2) were sampled, whereas six colonies were sampled for the shelf-edge form (M3). Colonies were fixed in 4% buffered formalin in seawater for two weeks, and finally preserved in 70% ethanol.

In all three chromatic forms the collaret was formed by 2–3(4) rows of curved spindles, agreeing with Carpine & Grasshoff (1975). This variability in the number of rows forming the collaret was also observed among polyps of the same colony. The ornamentation was slightly more variable than previously described (Carpine & Grasshoff 1975); however, in all forms the spines of the outer side were usually more developed, while the spination of the inner side could be more or less marked. After examining the sclerites from different parts of the colony, the highest degree of variability among the three chromatic forms was observed in sclerites that formed the calyces. In order to compare sclerites from calyces of a similar size, several first order branches were placed under a binocular stereomicroscope (Olympus SZ-60) and photographed at different angles with a Moticam 2300 camera. Calyx length was measured with the software Macnification v. 2.0.1 as the distance from the base of the calyx to the tips of the most distal calyx sclerites. Measurements were done on fully contracted calyces placed perpendicular to the camera. A total of 200 calyces (19 to 22 calyces per colony) were measured for the M1 and M2 forms, whereas 55 calyces (7 to 12 calyces per colony) could be measured for the M3 form. Calyx

length ranged from 0.3 mm to 1.8 mm. Calyces of 1–1.5 mm were the most abundant, accounting for 62%, 55% and 60% of calyces in M1, M2 and M3 forms, respectively. Consequently, for each sampled colony, a total of 10 calyces 1–1.5 mm in size from the middle section (two cm below the tip) of first order branches were dissected under a binocular stereo microscope (Olympus SZ-60). Collected calyces were immersed in a sodium hypochlorite solution until all organic matter was dissolved and sclerites were disaggregated. Sclerites were rinsed several times with distilled water. A minimum of 20 sclerites were haphazardly selected from each colony, placed on a double stick-tape and subsequently sputter-coated with Au-Pd. Sclerite observations and images were obtained with a HITACHI S-3500 N scanning electron microscope (SEM) at 5.0 KV, and images were obtained at X110. Images were pre-processed with Photoshop C5 (Adobe System) creating a black background, while sclerites were kept grey shaded alongside the scale caption. This procedure facilitated the subsequent measurement by means of the Macnification software. The following measurements were taken for each sclerite: total length, perimeter length, area, maximum width, and bottom, middle and top widths (Kim et al. 2004; Prada et al. 2008; Gutiérrez-Rodríguez et al. 2009; Gori et al. 2012). The number of ramifications at the base of large sclerites was counted and referred to as root number. Mean width was calculated as the mean among bottom, middle and top widths. Sclerite shape was also evaluated by the following ratios: length/maximum width and area/perimeter (Bramanti et al. 2013).

Statistical analyses

Distance-based permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001) was employed to test the null hypothesis of no significant differences among forms in colony shape, and sclerite size and shape. Each term of the analysis was tested using 9999 permutations. Data were standardized with respect to their mean absolute deviation

$$\mathrm{MAD} = \frac{1}{n}\sum_{j=1}^{n}[x_{ij} - \overline{x_i}],$$

where x_i is the value of the i^{th} variable observed in n colonies (García Pérez 2005). Significant relations relevant to the hypothesis were investigated using a posterior pairwise post-hoc test. Finally, an ordination of the analysed colony shape and sclerite size and shape was obtained with a principal component analysis (PCA). PERMANOVA and pairwise post-hoc tests were performed with the Past software (Hammer et al. 2001). PCA was performed with the R-language function princomp, which is available in the Vegan library (Oksanen et al. 2005) of the R software platform.

Results

Colony shape

No significant differences in colony shape (PERMANOVA, *Pseudo-F* = 0.983, *P* = 0.517) were found among the three forms. The first two principal components of the PCA explained 55.4% of the data variance, and the first component accounted for 21.2% of the variance. A strong correlation occurred between first order branch density and ramification density, as well as between height to maximum width and mean width ratios (Figure 3). M1 presented slightly higher first order branch and ramification densities (Figures 3 and 4), whereas M2 presented slightly higher values of height to maximum width ratio and height to mean width ratio (Figures 3 and 4). M3 colonies were characterized by long first order branches, high base orders and a high tributary to source ratio of secondary branches (Figures 3 and 4).

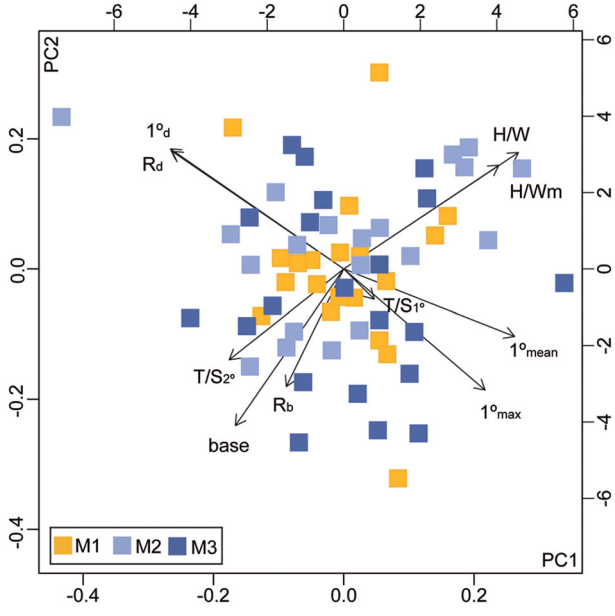

Figure 3. Principal component analysis (PCA) biplot showing the ordination of the studied colonies ($n = 60$) regarding their colony shape, and the role of the analysed features; H/W, height to width ratio; H/Wm, height to mean width ratio; R_d, ramification density; 1°_{d}, first order branch density, base = order of the colony base; 1°_{max}, maximum length of first order branches; 1°_{mean}, mean length of first order branches; R_b, bifurcation ratio; $T/S_{1^{\circ}}$, tributary to source ratio of first order branches; $T/S_{2^{\circ}}$, tributary to source ratio of secondary branches.

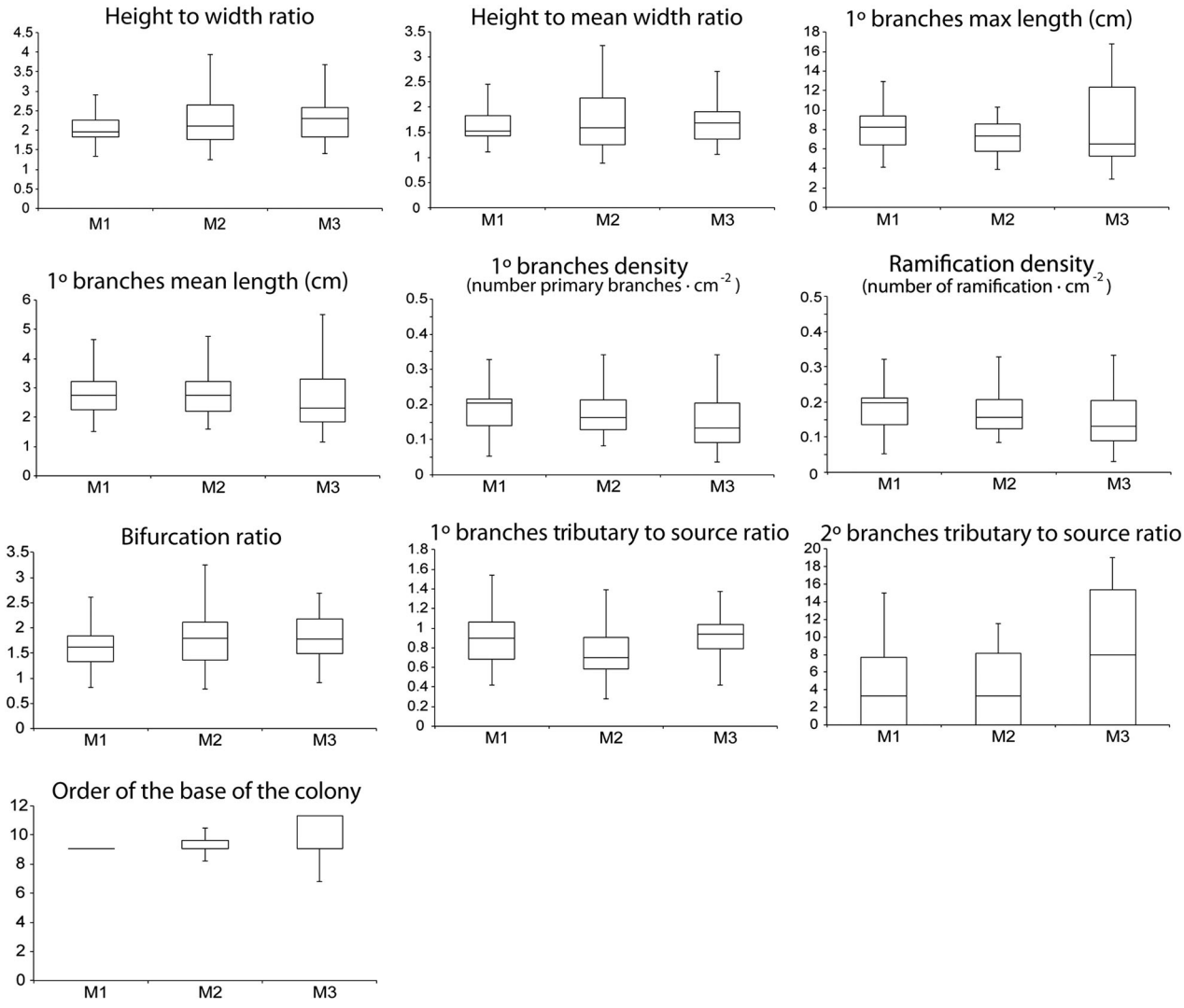

Figure 4. Colony shape features; box indicates first and third quartiles, line within the box indicates the mean value, and upper and lower lines indicate the range between minimum and maximum values.

Sclerite size and shape

Two different types of sclerites were observed to form the *Paramuricea macrospina* calyces: thornscales and spindles (Figures 5–7). Significant differences among the three forms were observed in the thornscales (PERMANOVA, *Pseudo-F* = 6.812, $P < 0.001$) as well as in the spindles (PERMANOVA, *Pseudo-F* = 6.586, $P < 0.001$). The largest differences in both thornscales and spindle morphology were observed between *P. macrospina* M1 and M3 (Table I). The first two principal components of the PCA explained 84% of the data variance for thornscales, and 88% for spindles; first components accounted for 65% and 64% of the variance, respectively. Thornscale size and shape was larger in M1, intermediate in M2, and smaller in M3 (Figure 8). Spindle size and shape presented less variability among forms (Figure 9). M1 colonies were characterized by thornscales and spindles with high mean and maximum width, as well as by a high number of thornscales roots (Figures 8–11). M2 colonies presented intermediate values (Figures 8–11), whereas M3 colonies were mainly characterized by thornscales and spindles with high length and high length to width ratios (Figures 8–11).

Discussion

The results of this study show that the three chromatic forms of the gorgonian *Paramuricea macrospina* observed on the continental shelf and slope of the Menorca Channel significantly differ in terms of sclerite size and shape, but not in terms of colony shape.

Most colonial morphological features barely changed among the three forms (Figure 3). Therefore,

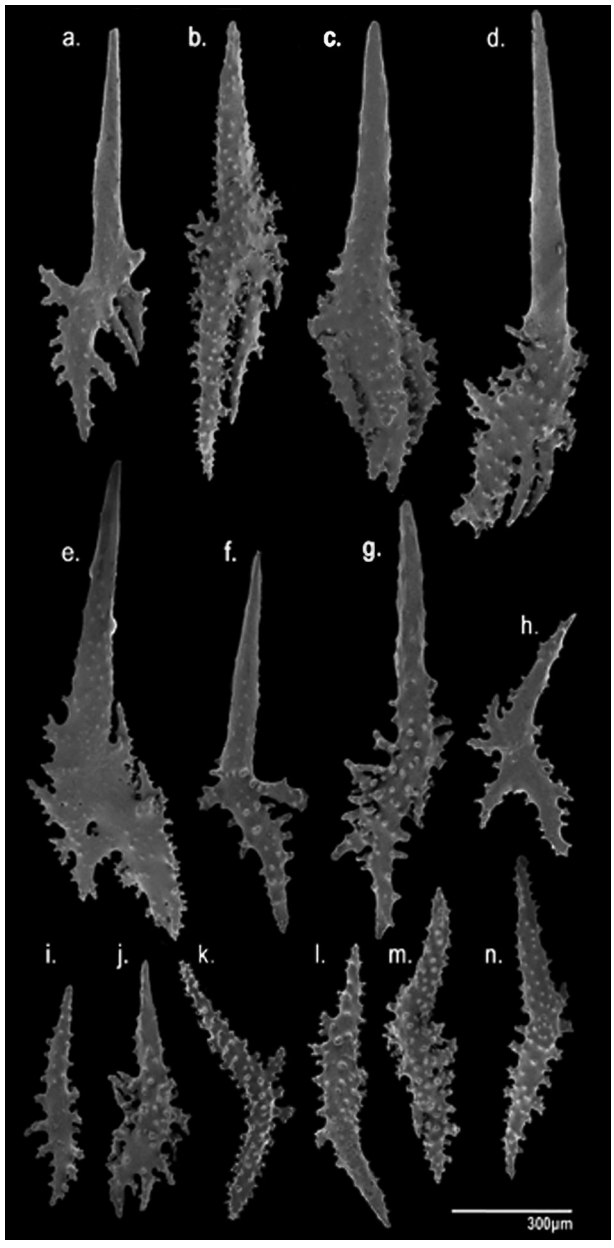

Figure 5. Thornscales (a–h) and spindles (i–n) from the calyx of *Paramuricea macrospina* M1.

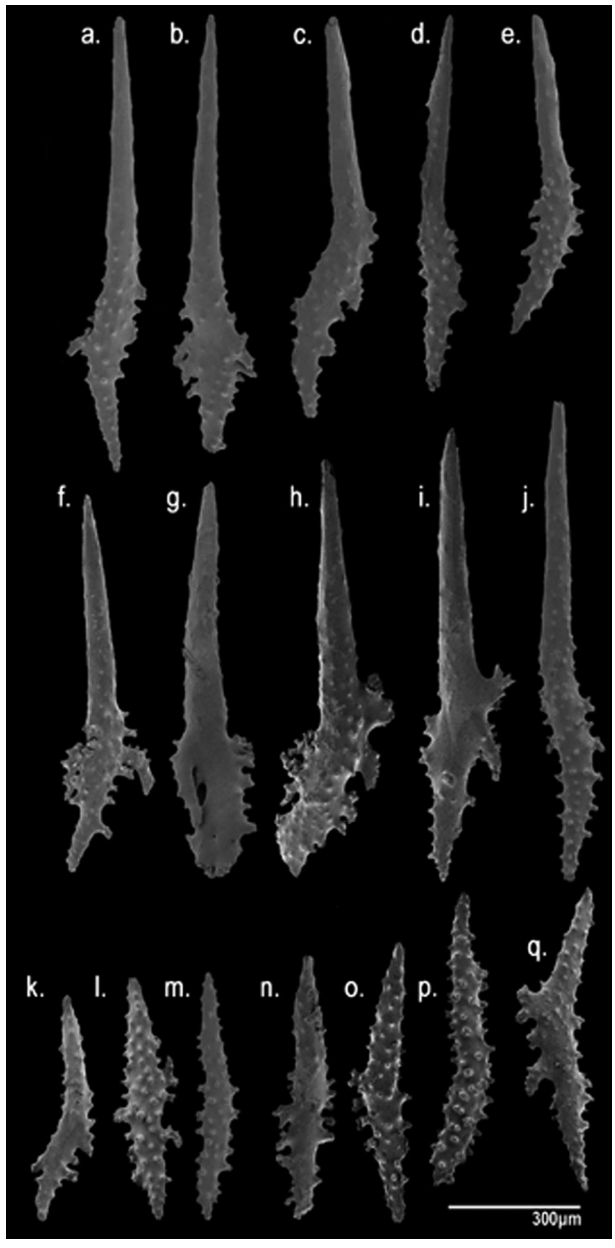

Figure 6. Thornscales (a–j) and spindles (k–q) from the calyx of *Paramuricea macrospina* M2.

P. macrospina's colonial morphology is a conservative character that experiences little variation across different environments in the Menorca Channel, as also observed in species of the genus *Leptogorgia* in the Gulf of Mexico (Mitchell et al. 1993). This invariability contrasts with other studies, where depth-related changes in environmental conditions result in significant morphological variation in shallow anthozoan species (e.g. Helmuth & Sebens 1993; Prada et al. 2008; Nir et al. 2011; Gori et al. 2012). However, most research has been conducted in shallow littoral environments, where environmental conditions change considerably over a narrow depth range (Garrabou et al. 2002). Conversely, the increased stability of environmental conditions at greater depths (>50 m) (e.g. Puig et al. 2000; Fernández de Puelles et al. 2007), may explain the lack of variability in the colonial morphology of the three chromatic forms of *P. macrospina*. Only the shallow forms (M1 and M2) occurring on maërl beds on the continental shelf may suffer the effects of sporadic intense hydrodynamic events (Puig et al. 2001; Teixidó et al. 2013) that have been shown to cause damage to sessile organisms at similar depths (Woodley et al. 1981; Bongaerts et al. 2013). Based on Grinyó et al. (2016), the structural stability of shelf-break rocky bottoms sheltered from strong

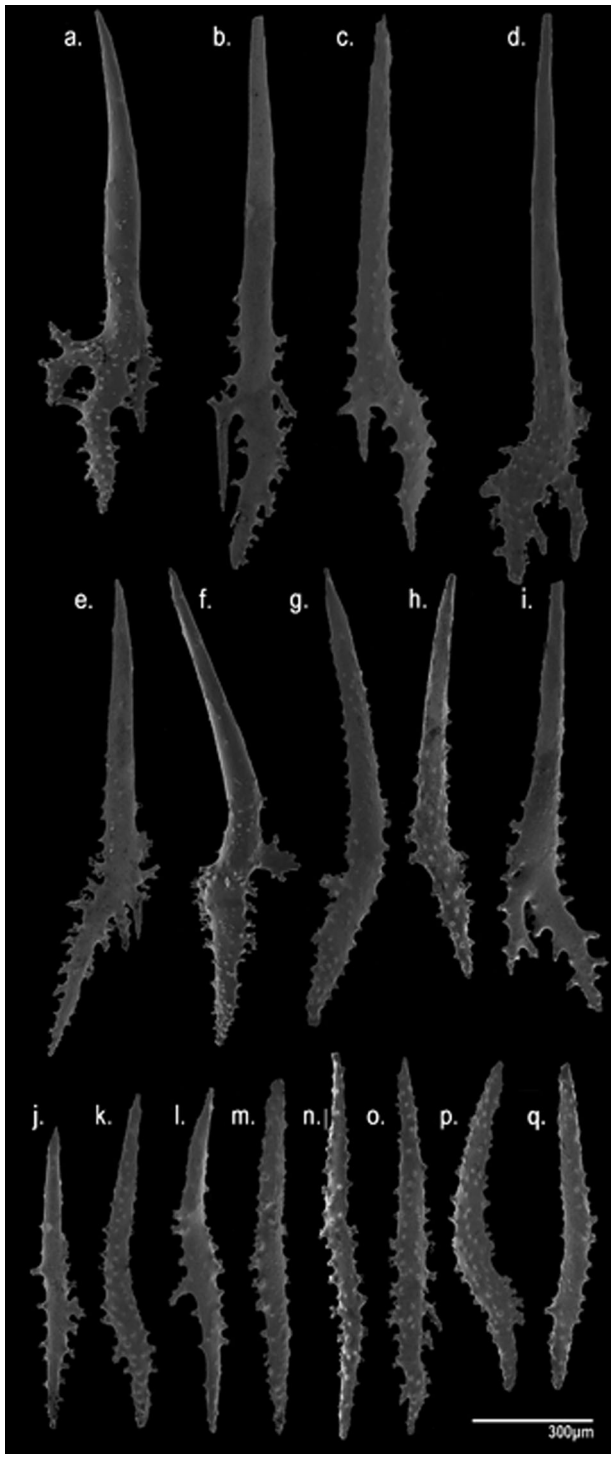

Figure 7. Thornscales (a–i) and spindles (j–q) from the calyx of *Paramuricea macrospina* M3.

Table I. Pairwise test for thornscale and spindle forms.

Forms	Thorns		Spindles	
	P-value	Significance	*P*-value	Significance
M1 vs. M2	0.0158	*	0.0237	*
M1 vs. M3	0.0002	***	0.0009	***
M2 vs. M3	0.0423	*	0.0366	*

Significance is indicated with one ($P < 0.05$) or three asterisks ($P < 0.001$).

hydrodynamic events may allow deep M3 colonies to grow larger, as previously observed in other gorgonian species (West et al. 1993; Gori et al. 2012). This may explain why M1 and M2 colonies are significantly (PERMANOVA $P < 0.05$) smaller (23 ± 8.7 SD and 22 ± 9.1 SD cm, average height respectively) than deeper M3 ones (34 ± 15 SD cm, average height). Furthermore, trammel net fishing (a common practice on the continental shelf of the Menorca Channel) may be particularly detrimental to large colonies, since smaller colonies are probably less susceptible to getting entangled and broken by the nets used by artisanal fishermen in the area (Grinyó et al. 2016). Finally, it has been observed that in deep environments exposed to unidirectional currents, gorgonians may develop larger colonies, maximizing the surface exposed to perpendicular flow and increasing prey capture efficiency (Sebens & Johnson 1991). However, these differences in substrate stability and the possible exposure to intense hydrodynamic events of *P. macrospina* on the continental shelf and the shelf-edge are evidently not influential enough to cause any significant changes in its colonial morphology.

Unlike colony shape, thornscale and spindle size and shape significantly differed among the three forms. Differences in *P. macrospina* sclerite shape mostly derived from width rather than length, unlike those more frequently observed in other gorgonian species (e.g. West 1997; Gori et al. 2012). Both thornscales and spindles had the same length but were much wider and heavily rooted in M1 and M2 than in M3 colonies. Other Mediterranean coastal gorgonian species also had larger sclerites in shallow environments than in deeper ones (Velimirov 1976; Skoufas 2006; Gori et al. 2012). It has been suggested that larger sclerites would confer higher flexion capacity to gorgonian colonies in shallow or exposed habitats (Skoufas 2006). However, shallow colonies of Caribbean gorgonians had shorter sclerites than in deeper colonies (West et al. 1993; Kim et al. 2004; Prada et al. 2008) as a possible adaptation to high water motion, since large sclerites are more susceptible to breakage than smaller ones (West 1998). This would agree with studies reporting a negative correlation between sclerite size and water motion (West et al. 1993; Kim et al. 2004). In this regard, the less robust morphology of M3 sclerites could be an adaptation to less intense hydrodynamic conditions. In addition to their structural role, sclerites can also act as a structural defence against predators (Van Alstyne et al. 1992; Puglisi et al. 2002), with larger sclerites being more effective than smaller ones in deterring predators (West 1998). Therefore, the larger sclerites in M1 and M2 could

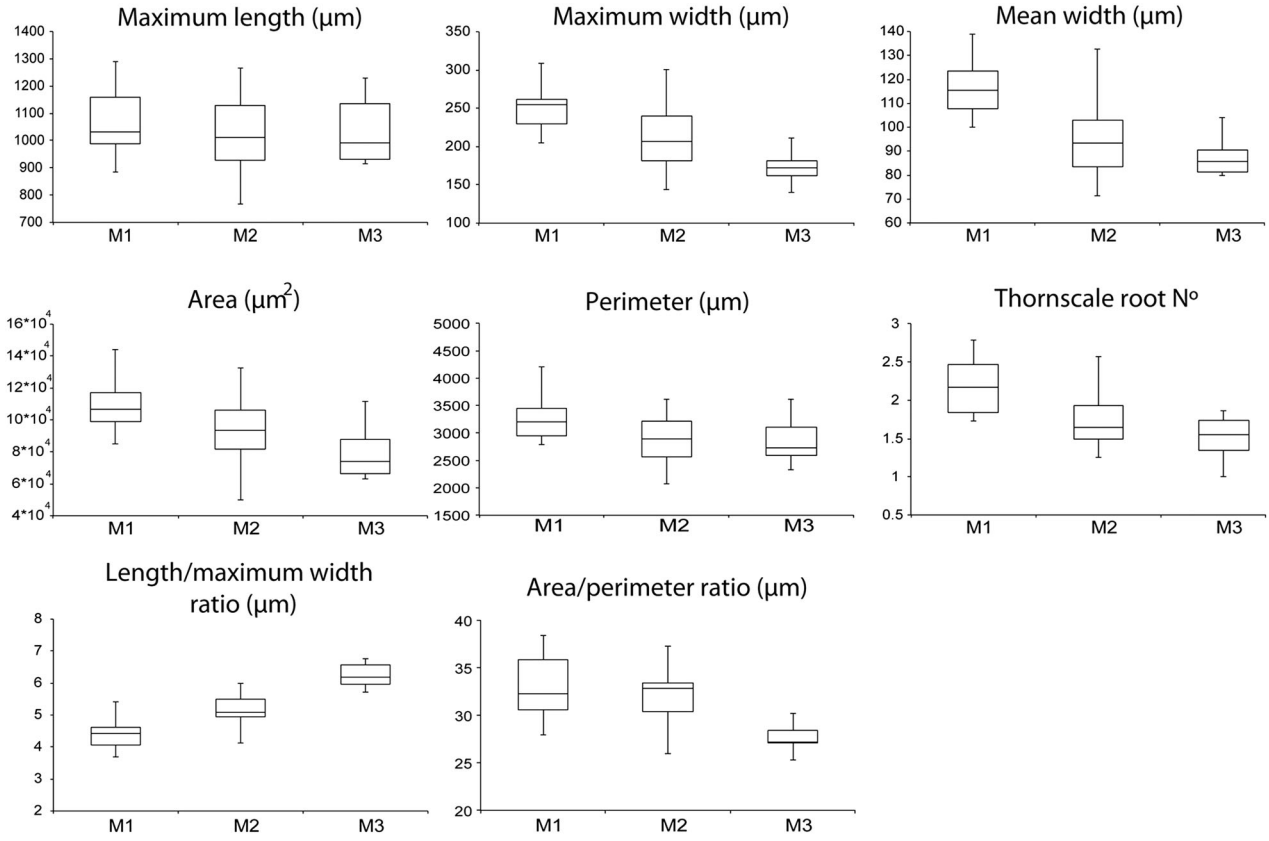

Figure 8. Thornscale features; box indicates the first and third quartile, line within the box indicates the mean value, and upper and lower lines indicate the range between minimum and maximum values.

also be an adaptation to higher predator pressure. This would agree with previous studies that generally reported higher predation pressure in shallow than in deeper areas (West et al. 1993). However, predation processes on deep-water gorgonians are still largely unknown.

Overall, it could be supposed that differences in environmental conditions on the continental shelf and shelf-edge are not enough to induce any change in the colony shape of *P. macrospina*, but may be influential enough to affect sclerite size and shape. However, this is not supported by the significant differences observed among the two continental shelf forms (M1 and M2), which occur side by side on the same mäerl beds (Grinyó et al. 2016). In this sense, differences between M1 and M2 sclerites could indeed suggest a genetically controlled process rather than an environmentally driven one. M2 sclerites present intermediate values between M1 and M3 forms (Figures 8 and 9). However, the differences between M2 and M3 sclerites were less pronounced than between M2 and M1 (Table I). Considering the similar colouration in M2 and M3 colonies and the less marked differences in sclerite size and shape, it could alternatively be suggested that M2 and M3 are shallow and deep forms of a single morphotype occurring over a wide depth range comprising both the continental shelf and slope, whereas M1 is a different morphotype only occurring on the continental shelf.

Overall, the colony morphology of the three forms of *P. macrospina* observed in the Menorca Channel did not show any clear relation with possible changes in environmental conditions with depth on the continental shelf versus shelf-edge. However, it would be interesting to extend the morphological comparisons to also include shallow coastal areas, where the species has recently been reported (20–40 m depth, Topçu & Östürk 2015) and where hydrodynamic conditions may have greater contrast. Conversely, the observed differences in sclerite size and shape probably suggest that both environmental and genetic factors are conditioning sclerite size and shape. Transplant experiments between depths would be desirable to further explore the possible role of phenotypic plasticity and genetic divergence on the morphological variability of this very abundant Mediterranean deep gorgonian species (Grinyó et al. 2016). Gorgonians are able to adapt to different environmental settings

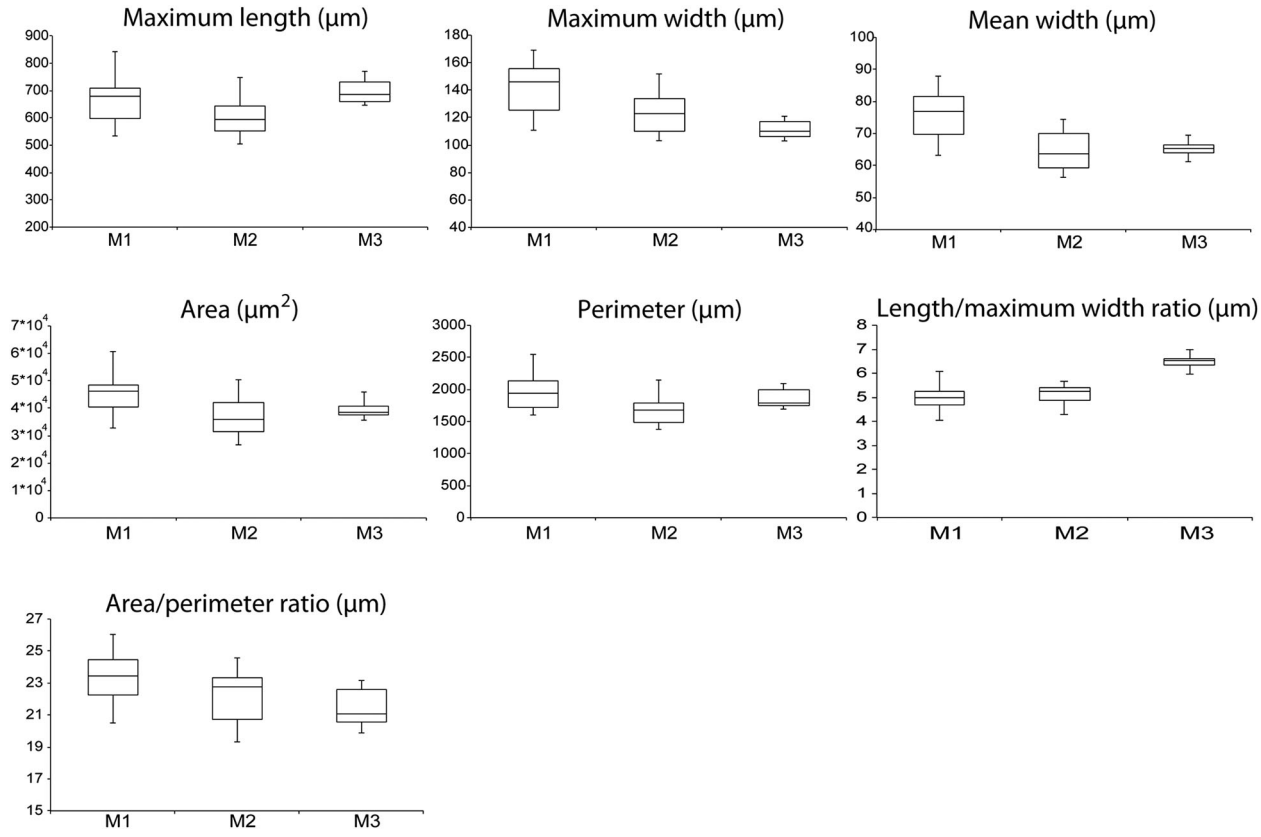

Figure 9. Spindle features; box indicates the first and third quartile, line within the box indicates the mean value, and upper and lower lines indicate the range between minimum and maximum values.

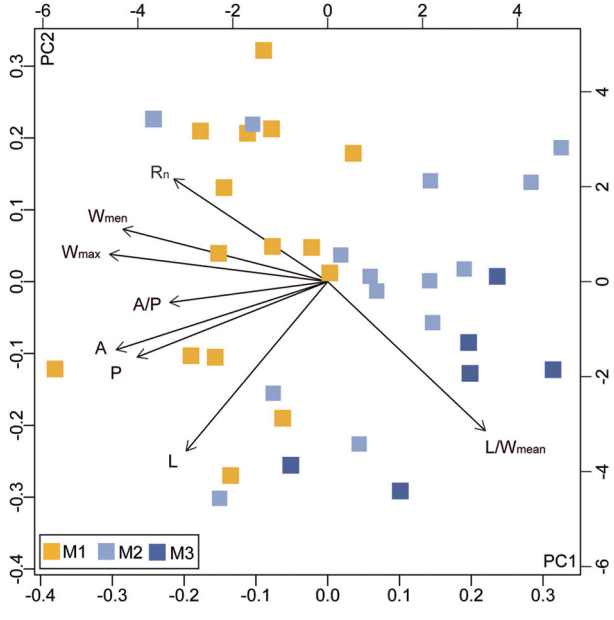

Figure 10. Principal component analysis (PCA) biplot showing the ordination of the studied colonies ($n = 36$) regarding their thornscale size and shape, and the role of the analysed features; L, thornscale length; P, thornscale perimeter; A, thornscale area; W_{max}, thornscale maximum width; W_{mean}, thornscale mean width; Rn, number of thornscale roots; L/W_{mean}, thornscale length to mean width ratio; A/P, thornscale area to perimeter ratio.

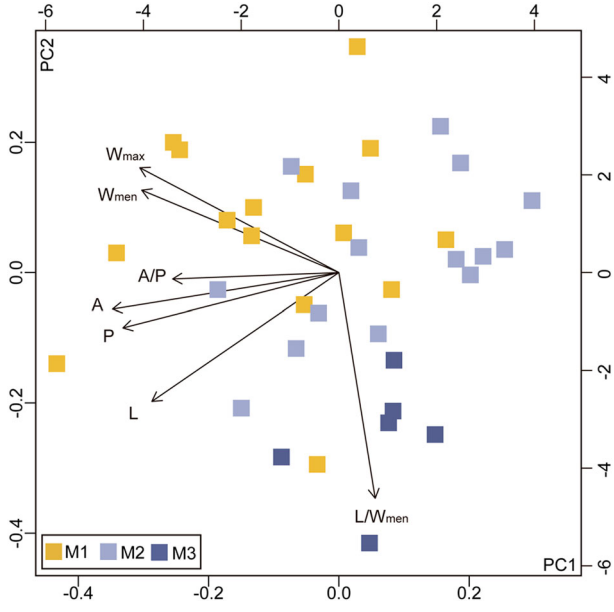

Figure 11. Principal component analysis (PCA) biplot showing the ordination of the studied colonies ($n = 36$) regarding their spindle size and shape, and the role of the analysed features; L, spindle length; P, spindle perimeter; A, spindle area; W_{max}, spindle maximum width; W_{mean}, spindle mean width; L/W_{mean}, spindle length to mean width ratio; A/P, spindle area to perimeter ratio.

that can lead to morphological variability (Weinbauer & Velimirov 1995; Gori et al. 2012). In this regard, *P. macrospina*'s broad bathymetric distribution and occurrence in very different environments reflect its wide adaptability (Bo et al. 2012; Topçu & Öztürk 2015; Grinyó et al. 2016). While it is clear that morphological variability can be driven by environmental features, we hypothesize that morphological variability could also be reflecting a more complex speciation process occurring in the studied species. A preliminary genetic analysis was carried out, revealing that all three *P. macrospina* forms shared the same mitochondrial sequence for mtMutS (msh1). Igr1 + COI analyses were also attempted; however, extraction was only successful in M3. In this regard, new genetic markers are needed to further explore evolutionary differentiation and morphological variation among Mediterranean gorgonians.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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