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Subindividual variability in sea pens (Octocorallia: Pennatulacea)

Francisco J. García-Cárdenas [1], Carlos M. Herrera [2], Pablo J. López-González [1]

[1] Biodiversidad y Ecología Acuática. Departamento de Zoología, Facultad de Biología, Universidad de Sevilla, Reina Mercedes 6, 41012 Sevilla, Spain.
(FJG-C) (Corresponding author) E-mail: frangarca@us.es. ORCID-iD: https://orcid.org/0000-0002-1503-9552
(PJL-G) E-mail: pjlopez@us.es. ORCID-iD: https://orcid.org/0000-0002-7348-6270
[2] Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas (CSIC), Américo Vespucio 26, 41092 Sevilla, Spain.
(CMH) E-mail: herrera@ebd.csic.es. ORCID-iD: https://orcid.org/0000-0003-2452-3888

Summary: Comparisons between plants and sessile modular colonial invertebrates offer interesting parallelisms between plant and animal body plans after millions of years of divergent evolution. Among these parallelisms might be the existence and distribution of intraindividual heterogeneity in organ traits, also named subindividual variability. Subindividual variability is quantitatively important and has many consequences for plant individuals, populations and communities, and for animal consumers as well. However, could a similar process of subindividual variability occur in sea pens, which have a modular architecture similar to that of plants? In the literature of marine invertebrates very little is known about the presence and magnitude of subindividual variability in modular organisms. This study provides for the first time a quantitative assessment of subindividual variability in sea pens, analysing certain biometric features of reiterated structures that presumably have some ecological function, and offers an initial comparison of quantitative levels of subindividual variation between plants and sea pens.

Keywords: intracolonial variability; Pennatulacea; *Pennatula*; *Ptilella*; coefficient of variation; variance; within-plant variation.

Variabilidad subindividual en plumas de mar (Octocorallia: Pennatulacea)

Resumen: Las comparaciones entre plantas e invertebrados coloniales modulares sésiles ofrecen interesantes paralelismos entre los planes corporales de las plantas y los animales, tras millones de años de evolución divergente. Entre estos paralelismos podría estar la existencia y distribución de la heterogeneidad intraindividual en los rasgos de los órganos, también denominada variabilidad subindividual. La variabilidad subindividual es importante cuantitativamente y tiene múltiples consecuencias para las plantas individuales, las poblaciones y las comunidades, así como para los animales consumidores. Mas, ¿podría ocurrir un proceso similar de variabilidad subindividual en plumas de mar, que tienen una arquitectura modular similar a la de las plantas? En la literatura de invertebrados marinos se sabe muy poco sobre la presencia y la magnitud de la variabilidad subindividual en los organismos modulares. Este estudio proporciona por primera vez una evaluación cuantitativa de la variabilidad subindividual en las plumas de mar, analizando ciertas características biométricas de estructuras reiteradas que presumiblemente tienen alguna función ecológica, y ofrece una primera comparación de los niveles cuantitativos de variación subindividual entre las plantas y las plumas de mar.

Palabras clave: variabilidad intracolonial; Pennatulacea; *Pennatula*; *Ptilella*; coeficiente de variación; varianza; variación intra-planta.

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INTRODUCTION

Most morphological-variability studies on corals have focused on comparing phenotypic characteristics among populations or species, with comprehensive reviews of the phenomenon of phenotypic plasticity, generally ignoring both the existence and quantitative importance of another type of variability below the individual level, or subindividual variability (Kim et al. 2004, Borges 2005, Prada et al. 2008). However, as emphasized by Menezes et al. (2013), the study of intracolony variability in corals deserves more attention as a possible source of criteria for assessing morphological interspecific boundaries. Recent investigations have demonstrated the existence of intracolony genetic variability (IGV) in scleractinian corals, suggesting that the presence of more than one genotype in a single colony may offer advantages for the colony, such as benefits for colony growth, competitive ability, survival and fitness, all of which might be the natural way to produce "super corals" (Oury et al. 2020: 5214).

Colonial marine invertebrates such as bryozoans (Phylum Bryozoa) and cnidarians (Phylum Cnidaria) (Hickson 1916, Harvell 1984, Key 1990) are considered modular animals that are amenable to intra- or intercolony variability studies (O'Dea and Okamura 2000, O'Dea 2003, Wejnert and Smith 2008, among others). However, most studies have focused on intercolony (populations or species) variability levels (Sánchez and Lasker 2003, Sánchez et al. 2007, Schweinsberg et al. 2017). Only a few reproductive studies analysing the sexual content of each autozooid throughout the colony have offered a close view of the phenotypic variability that occurs within the colony (Brito et al. 1997, Orejas et al. 2002; García-Cárdenas and López-González 2022a, b).

Among sessile marine invertebrates, colonial anthozoans (Hexacorallia and Octocorallia) have a modular construction by reiteration of genetically identical subunits (Sánchez and Lasker 2003, Lasker et al. 2003; Sánchez et al. 2007). This modularity can be observed between zones within the colony, between lateral branches, between polyp leaves and, at the lowest level, between polyps of the same individual. Functional or morphological differences in polyp traits within the same colony have sometimes been reported (Foster 1985, Lapid et al. 2004, Finelli et al. 2007, among others). The clonal origin and functional similarity of polyps (autozooids), which are mainly responsible for feeding (resource capture) and reproduction (Williams et al. 2012), make them ideal structures for studying the existence of subindividual variability and its consequences on colony fitness. Depending on the directionality or access to resources, such as food particles, a differentiation in the physicochemical characteristics of polyps might be expected within colonies (Orejas et al. 2002, Finelli et al. 2007). This means that a certain amount of intracolonial variation in polyp traits might be advantageous by optimizing resource exploitation based on a "division of labour" between the different modules of the colony. But has subindividual variability in reiterative morphological traits been proved in modular organisms? Absolutely, but not in animals. Subindividual variability is largely known and widely studied in plants. Like modular marine organisms, plants have a modular construction in which reiterated and clonal structures (such as flowers, seeds, fruits and leaves) show high levels of intra-plant variability (Herrera 2009).

After aeons of divergent evolution, it is difficult to identify parallelisms between the plant and animal kingdoms (Darwin 1859, Haeckel 1869). Parallelisms between the plant and animal body plans, however, might be most likely to arise in comparisons between plants and sessile photosynthesizing colonial invertebrates (Borges 2005). The search for these parallelisms has mainly focused on finding related processes or structures between the two kingdoms that have offered similar solutions to common problems from such different perspectives (Hallé 1999: 268). The interest in finding parallelisms between plants and animals lies in being able to know the consequences of certain natural processes that are known to occur widely in the former of the two kingdoms and infer them in the other (Herrera et al. 2015, 2021, Alonso et al. 2018). It could also generate many applications, such as increasing knowledge and the predictive capacity of certain processes, transfer of techniques and analyses, and the development of new and interesting scientific hypotheses. The ecological consequences of modularity in plants have been widely documented and examined from different perspectives, one of which emphasizes the consequences of a distinctive source of phenotypic variance inherent to this modularity (the "subindividual component"; Herrera 2009, 2017). An inevitable consequence of modularity, or multiplicity of modules within individual plants, is a certain variability in the features of the copies of the same organ (e.g. leaves, flowers, fruits and seeds) that occurs in the different modules within the same individual (Herrera 2009). Many of the traits that vary within individual plants are known for their functional nature (e.g. leaf length and fruit size) and potential effects on the fitness of individuals (Pérez-Harguindeguy et al. 2013). This implies that subindividual variation in functional traits offers the possibility for abiotic environmental conditions (and animal consumers) to perform certain selection at the within-plant level (see Herrera 2009 for more details). Like polyps, plant leaves are reiterated organs that capture resources (e.g. light and carbon dioxide), and their phenotypic variation within single individuals (shape, size, nitrogen content and photosynthetic rates) usually contributes to the exploitation of different segments of a gradient of resources at a spatial scale smaller than the size of the individual (e.g. the vertical light gradient; Herrera 2009). Thus, depending on the directionality or access to resources such as light or food particles, the physicochemical characteristics of leaves are advantageous for optimizing the exploitation of these resources, which is widely known among botanists and ecologists (Pérez-Harguindeguy et al. 2013, Herrera 2017).

As stated above, colonial anthozoans share with higher plants a modular construction by reiteration of

genetically identical subunits and a sessile adult life (Hallé 1999, Hughes 2005), but this comparative phenotypic perspective has been rarely addressed (Borges 2005). In this hypothetic scenery, could a similar process of subindividual variability occur in anthozoans, which have a modular architecture similar to that of plants?

An ideal candidate for investigating this possible plant-animal parallelism is the sea pen (Octocorallia: Pennatulacea), which is a colonial organism formed from an initial polyp and subsequently constituted by multiple individuals or modules (Kükenthal 1915, Bayer 1956, Tixier-Durivault 1965). The clonal origin and functional similarity of polyps (autozooids) of sea pens suggest an attractive analogy with plant leaves (Hallé 1999), as in both cases they are structures that capture resources. Knowledge on intracolonial variation in pennatulaceans is even scarcer than in other octocorals. Their synapomorphies, such as the origin from the oozooid, the clonal nature of different polyps and their vertical unbranched growing, make them suitable or ideal models for a study of subindividual variability in morphological or functional traits.

As a result, the present contribution provides for the first time a quantitative assessment of subindividual variability in sea pens, analysing certain biometric features of reiterated structures which presumably have some ecological function. We selected six pennatulacean species, including the type-genus *Pennatula* and the recently resurrected genus *Ptilella* (García-Cárdenas et al. 2019). The following specific questions will be addressed: (1) Do congeneric species of sea pens differ with respect to the quantitative distribution of population variance within and between colonies in quantitative polyp traits? (2) If they do, can such differences be related to contrasting ecological conditions? (3) Do different genera, such as *Ptilella* and *Pennatula*, morphologically similar although phylogenetically differentiated, differ in the distribution within and between colonies of population variance in the selected traits? Finally, a brief but interesting comparison of our results with the data collected for years in plants will be made, trying to answer one last question: (4) to what extent do sea pens and terrestrial plants differ with respect to quantitative levels of subindividual variation?

MATERIALS AND METHODS

Sampling

Most material used in this study formed part of a previous taxonomical investigation in which *Ptilella* and *Pennatula* were compared (García-Cárdenas et al. 2019), and complete information about the surveys, the distribution area of the taxa considered and the data collected is contained therein. A preliminary analysis to ensure the existence of variability within and between colonies at polyp and sclerite measurements level was carried out using eight colonies of *Ptilella grayi*. These colonies were collected from several surveys in the northeast Atlantic during the period 2010-2014 (see Table 1), with a bathymetry range of 179 to

Table 1. – Colonies used for the subindividual variability study in sea pens (see García-Cárdenas et al. 2019). Abbreviations: NMS, National Museum of Scotland; MZB, Museu de Zoologia de Barcelona; NHM, Natural History Museum in London; BECA, Biodiversidad y Ecología Acuática of the University of Seville.

Species/ colony	Registration code	Geographic area
Ptilella grayi		
Pt.gy-1*	NMS.Z.2019.2.1	NE Atlantic
Pt.gy-2*	MZB 2018-0761	NE Atlantic
Pt.gy-3*	NMS.Z.2019.2.3	NE Atlantic
Pt.gy-4	NMS.Z.2019.2.2	NE Atlantic
Pt.gy-5	MZB 2018-0763	NE Atlantic
Pt.gy-6	BECA OPEN-338	NE Atlantic
Pt.gy-7	NHMUK 2019.1	NE Atlantic
Pt.gy-8	MZB 2018-0762	NE Atlantic
Ptilella grandis		
Pt.gd-1	MZB 2018-0759	NE Atlantic
Pt.gd-2	NMS.Z.2019.2.6	NE Atlantic
Pt.gd-3	BECA OPEN-334	NE Atlantic
Ptilella inflata		
Pt.in-1	NMS.Z.2019.2.7	SE Atlantic
Pt.in-2	NHMUK 2019.3	SE Atlantic
Pt.in-3	MZB 2018-0760	SE Atlantic
Pennatula rubra		
P.rb-1	BECA OPEN-61	Alborán Sea, Mediterranean
P.rb-2	BECA OPEN-189	Algeciras Bay, Mediterranean
P.rb-3	BECA OPEN-57	Gulf of Cádiz, NE Atlantic
Pennatula phosphorea		
P.ph-1	BECA OPEN-454 (G199)	NE Atlantic
P.ph-2	BECA OPEN-453 (G88)	NE Atlantic
P.ph-3	BECA OPEN-206 (G2776)	NE Atlantic
Pennatula sp.		
P.sp-1	BECA OPEN-152 (G122)	Antarctica
P.sp-2	BECA OPEN-199	Antarctica
P.sp-3	BECA OPEN-198(G84)	Antarctica

261 m depth. All *Ptilella grayi* colonies were collected using a demersal fish trawl with both the cod-end and the full body of the net being thoroughly examined for specimens after each deployment. Total length of preserved colonies ranged from 254 to 572 cm (see García-Cárdenas et al. 2019 for more details).

For the subindividual variability analyses of *Ptilella* and *Pennatula,* we selected three colonies of each of the following species: *Ptilella grayi, Ptilella grandis, Ptilella inflata, Pennatula phosphorea, Pennatula rubra* and *Pennatula* sp. (Table 1). Part of this material was collected over different geographical areas during various benthic surveys: Antarctica (ANT XVII/3, BIOROSS), the northeast Atlantic (Scotia cruises, INDEMARES Chica), the southeast Atlantic (BENGUELA VIII) and the Mediterranean (Bahía de Algeciras project).

Material processing

During the expeditions, the specimens were sorted, labelled and fixed in buffered formalin (5% in seawater). After the fixation period, colonies were preserved in 70% ethanol. The terminology used here follows mainly Bayer et al. (1983). The total length of the colonies was considered from the base of peduncle to the distal top of the rachis. The rachis was divided into three zones of roughly similar length, namely the basal, medial and distal zones, following the methodology used in previous studies of octocorals (see for example Orejas et al. 2002, Soong 2005, Baillon et al. 2014b). The two quantitative morphological traits analysed were sclerite and polyp lengths. Twenty sclerites from the upper and lower area of the rachis-peduncle boundary (10 for each zone) were extracted, measured and compared. From each rachis zone, five autozooids were randomly selected, avoiding those located at the base of the leaf. Comparisons between polyps were carried out within each zone and between zones of different colonies. To estimate the measurement error (ME hereafter), three independent observations were made on different days. All measurements were obtained using the ImageJ 1.38x program (Wayne Rasband, National Institutes of Health, USA).

Data analyses

The statistical analyses were performed using the R computing environment v3.5.0. (R Core Team 2018). The libraries and functions used in each case are specified below. Subindividual variability in the two traits examined was estimated using two methods commonly used in plant studies: the intracolony coefficient of variation (CV hereafter) and variance partitioning (for more details see Herrera 2009). In the first method, the CV (calculated as the intracolony standard deviation/individual mean) is a relative dispersion measure that evaluates the proportion of standard deviation (sd) with respect to the mean (X) and enables a comparison of dispersion between different groups or variables (which may have different measurement units) (Herrera 2009, 2017). In order to test differences between the species and between the interaction of "species per zone of the colony", an ANOVA test was applied to the model. The emmeans 1.4 package was used to calculate the marginal averages (Lenth 2019). The Levene test (Levene 1960) was used to compare the levels of variability between species, the type selected being the Levene median-log test (Schultz 1985). The function used was leveneTest included in the car package (Fox and Weisberg 2019), with the option centre = "median". Variabilities between species were compared using "marginal averages", i.e. the averages of the dependent variable (polyp size) for the different levels of one or more categorical predictor variables (see Herrera 2009).

The second method for assessing intracolony variation in quantitative traits consisted of partitioning the total variance of each trait (VAR_{total}) into its additive between- ($VAR_{between}$) and intracolony (VAR_{within}) components (Herrera 2009). This was carried out using a full random hierarchical mixed model (see below). One drawback of variance partitioning is that the within-individual component of variance may be inflated by ME unless individual reiterated structures are measured repeatedly, thus allowing proper estimation (Herrera 2009). In this approach a precise estimation of ME was performed using repeated measurements from each specimen in order to dissect true within-individual variance and measurement error. Thanks to the analysis of repeatability of measurements through the fully nested random design, the ME component was revealed to be different for both traits, being significantly low in *Ptilella-Pennatula* analyses (0.071%). This means that most "residual" variance in models is actually attributable to differences between polyp lengths, i.e. the within-individual component (see Discussion). As both methods (CV and VAR_{within}) focus on different aspects of intracolony variability which may or may not be related (Pearson 1901), they should ideally be used in combination (Herrera 2009), and this is the approach followed in the analyses carried out in this study.

The preliminary analysis performed in *Pt. grayi* to obtain initial information on the existence and degree of intracolony variability was based on a full random hierarchical mixed model. The required packages were readxl (Wickham and Bryan 2019), dplyr (Wickham et al. 2019), nlme (Pinheiro et al. 2018) and ape 5.0 (Paradis and Schliep 2018). The following more complete analysis using colonies of *Ptilella* and *Pennatula* was based on linear and full random hierarchical mixed models (Herrera 2009). The required packages were readxl 1.3.1 (Wickham and Bryan 2019), dplyr 0.8.3 (Wickham et al. 2019), nlme 3.1-137 (Pinheiro et al. 2018), ape 5.0 (Paradis and Schliep 2018), ggplot2 (Wickham 2016), car (Fox and Weisberg 2019) and emmeans 1.4 (Lenth 2019).

RESULTS

Variation in *Ptilella grayi*

The distribution of mean values revealed that the upper zone of the rachis-peduncle boundary contained larg-

er sclerites (200-300 µm) than the lower zone (100-150 µm). In most colonies the mean polyp length increased from the basal (4-6 mm) to the medial-distal zones of the rachis (approximately 6-8 mm). For both traits variances differed within and between colonies, as shown by differences in interquartile ranges (see Fig. S1). The CV of sclerite size ranged between 0 and 0.02, while the CV for polyp size ranged between 0 and 0.25 (Fig. 1). This indicates that the range of variability of polyp size was higher than that for sclerite size. The CV behaviour of polyp size by zone in the different colonies showed practically antagonistic patterns (e.g. between Pt.gy-1 or Pt.gy-2 and Pt.gy-3, Pt.gy-7 or Pt.gy-8). The colonies Pt.gy-4 and Pt.gy-6 were similar but differed from the rest. Regardless of the numerical results, which can be very marked by Pt.gy-1 and 2 with very high mid-zone CV, in general no clear patterns were observed using CV. However, the model confirmed significant differences for both traits within colonies (p-value <0.001; ANOVA test), and significant differences between colonies only in the case of polyp size (p-value =0.184 for sclerites, p-value <0.001 for polyps; ANOVA test) (see Table S1). Mean, standard deviation and CV values from each colony are summarized in Table S2.

The other approach to quantitatively assessing intracolony variation consisted of partitioning the total population-level variance of the trait (VAR_{total}) into its additive between-colony ($VAR_{between}$) and intracolony (VAR_{within}) components. For the two traits considered, the variance between colonies was negligible ($VAR_{between}$ = 2.56e-04 for sclerite size; 6.20e-08 for polyp size). In contrast, variation of residual values was a substantial source of variation (VAR_{within} = 1.16e03 for sclerites; VAR_{within} = 0.92 for polyps; see Table S3). Expressing variances as percentages of the total (%VAR_{total}) confirmed the negligible variation between colonies for both traits ($VAR_{between}$ <1%) and extensive intracolony variance (VAR_{within} 28% and 49% for sclerites and polyps, respectively) (Table S3).

Variation in *Ptilella* and *Pennatula* species

Coefficient of variation

Comparison of variabilities between colonies of the six species based on CV values showed differences both within and between colonies (Figure 2). The CV for polyp size ranged between 0 and 0.04. There were significant differences between species and between zones within the same colony (p-value <0.01; Levene test) (Table S4). Comparing variabilities between species using "marginal averages" revealed a clearer picture of the distribution of variation within and between colonies (Figure 3; see also Table S5). Differences between species in levels of polyp size variability were statistically significant (p-value <0.001; Levene tests).

Variance partitioning

Variance partitioning of polyp size revealed that the variance between colonies ($VAR_{between}$ = 1.39) was four times the variance between zones (VAR_{zone} = 0.35)

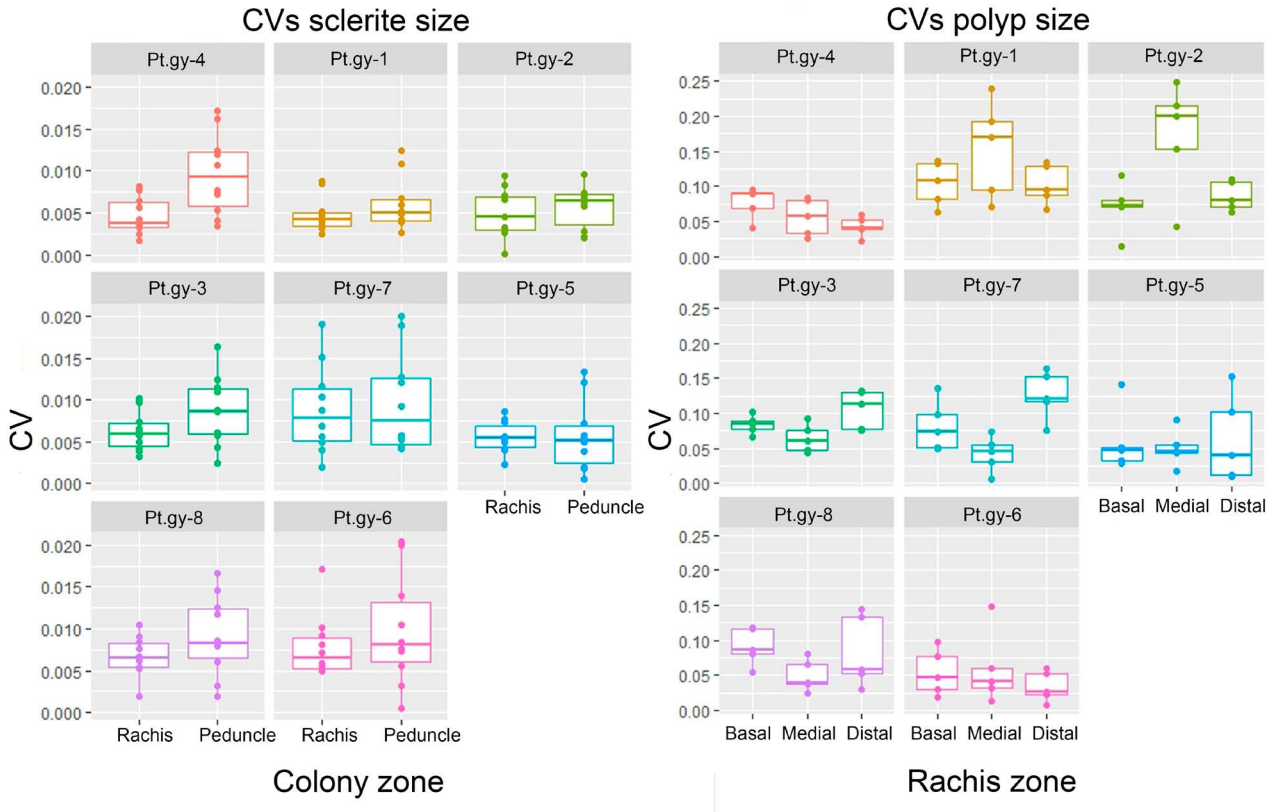

Fig. 1. – Distribution of coefficient of variation (CV) of sclerite and polyp sizes within and between *Ptilella grayi* colonies. CV= x̄/sd [x̄= mean, sd= standard deviation].

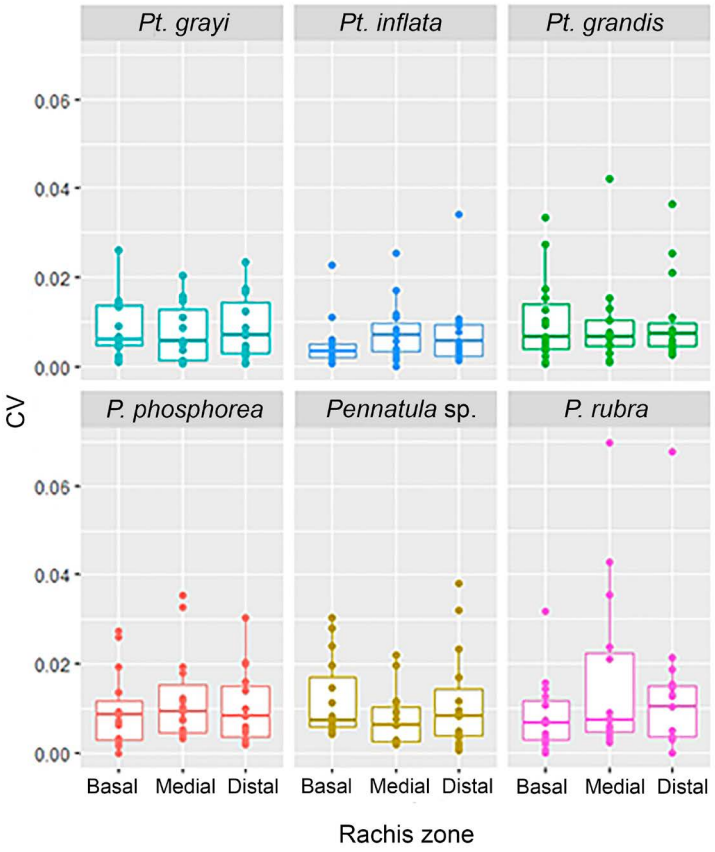

Fig. 2. – Distribution of coefficient of variation (CV) of polyp size within and between *Ptilella* and *Pennatula* colonies. CV= x̄/sd [x̄= mean, sd= standard deviation].

and two times the variance between colonies (VAR_{within} = 0.67) (Table S6). In terms of proportions of the total (%VAR_{total}), the variance component due to variation between colonies ($VAR_{between}$ 57%) was higher than that due to variation within colonies (VAR_{within} 27 %) (Table S6). In other words, individuals from different species had a different distribution of internal variability, regardless of the generic grouping (p-value <0.001; Levene test).

DISCUSSION

In animals with modular organization such as bryozoans, hydrozoans and anthozoans (Sánchez et al. 2007), the study of variation between homologous structures within the same organism is still in its early stages (Harvell 1984, Key 1990, O'Dea and Okamura 2000, O'Dea 2003, Wejnert and Smith 2008, Schweinsberg et al. 2017). Traditionally, hierarchical categories of morphological variation have been the criteria used to investigate the patterns of variation of modular organisms such as corals, intracolony variation being generally neglected in most studies (Menezes et al. 2013). However, functional or morphological differences in polyp traits within the same colony have sometimes been reported (see Foster 1980, 1985, Leuzinger et al. 2003, Ulstrup et al. 2006, among others). This is especially observed in the differential reproductive contribution of the polyps throughout the entire colony (see Jackson and Coates 1986, Harrison and Wallace 1990 and Sakai 1998 for hexacorals; Coma et al. 1995, Brito et al. 1997 and Orejas et al. 2002 for octocorals), and it is frequently found that the polyps located in the proximal zone of rachis show the lowest reproductive effort (García-Cárdenas and López-González 2022a,b).

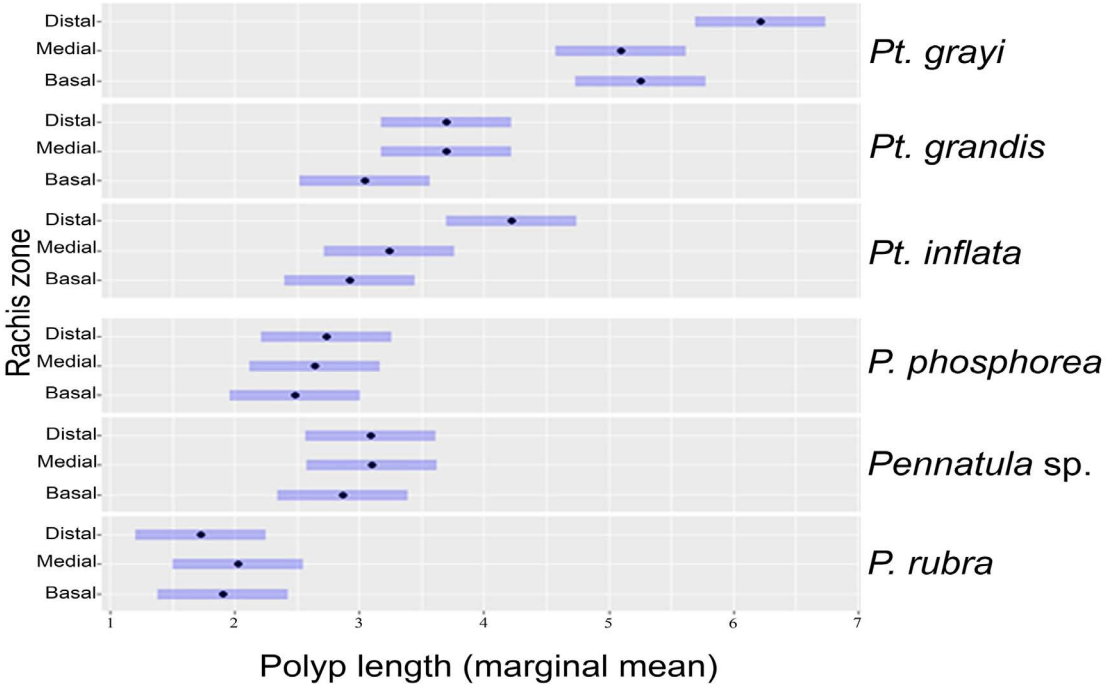

Fig. 3. – Plot box result of marginal mean analysis using the *emmeans* package based on polyp length within and between *Ptilella* and *Pennatula* colonies.

Some studies have also recognized that intracolony variation can sometimes exceed interspecific or environmental morphological variation (Kaandorp and Kübler 2001: 55, Sánchez and Lasker 2003, Sánchez et al. 2007). The recent study of Oury et al. (2020) demonstrated the existence of IGV in *Pocillopora* corals and suggested that mosaicism is the most important process leading to IGV, with some relatively high rates of chimerism (Oury et al. 2020: 5213). Colonies showing IGV should theoretically have a better evolutionary potential than invariable colonies. Multiple genotypes should provide several basic units upon which selection may act. One of the possible morphological, ecological and evolutionary implications of this phenomenon could be intracolony phenotypic variation, as seen in the present contribution.

Some authors using a methodology mainly based on mean and standard deviation have shown the existence of a significant intracolony variation in sea pen colonies (Edwards and Moore 2008, 2009, Baillon et al. 2014a,b). Our results are based on two of the most robust methods for comparing variabilities (Brown and Forsythe 1974, Van Valen 1978, Conover et al. 1981), which are largely used in plant variability comparisons (Schultz 1983, 1985, Herrera 2009) but have not been applied previously in corals as far as we know. However, one limitation of this methodology is that it requires a suitable estimation of ME (Herrera 2009), which is commonly not acknowledged (e.g., Sherwood et al. 2008, Baillon et al. 2016). Without estimation of ME or its complementary approach, repeatability of measures, a hidden variation source could be inflating the actual intracolony variance levels (Herrera 2009). In our analyses, a certain ME was suspected in the intracolony component for polyps of *Ptilella grayi*. After detecting and correcting that ME, we can confirm that the within-individual variance component (VAR_{within}) was clearly higher than the between-colony variance component (VAR_{within} >25%; $VAR_{between}$ <1%), which demonstrates that the elevated within-individual variance component found in pennatulacean species is real and not an artefact derived from measurement problems offered by the material studied.

Spatial distribution of trait variability

The functional nature of sclerites and polyps is directly related to the structure, feeding and fitness of the colony (Hickson 1916, Williams et al. 2012). However, as shown here, spatial distribution of variability in some of their features (e.g. length) was not homogeneous along the vertical axis of colony, suggesting a certain "sectoriality", as has also been reported in plants (Herrera 2009). For example, sclerites of *Pt. grayi* exhibited a higher variation above the rachis-peduncle boundary (mud-water gradient) in the basal portion of the rachis. Menezes et al. (2013) suggested that the rachis is a higher environment pressure zone than the peduncle (buried) due to competitive contact with surrounding organisms. In a similar way, Herrera (2009) observed differences in variability distribution of certain traits in aquatic plants related to the water-air gradient. In most colonies analysed here, the polyp length showed higher variation levels at the medial-distal than the basal zone of the rachis. Among the factors that may modulate intracolonial variation, some authors have suggested the feeding source, fecundity investment, continuous burial by sediment or competitive contact with surrounding organisms (Soong and Lang 1992, Goffredo et al. 2011, Menezes et al. 2013). This has been suggested for *Anthoptilum grandiflorum*, *Balticina finmarchica* and *Pennatula aculeata* (Baillon et al. 2016). Thus, polyps located in the medial-distal zone of the rachis, far from the substrate, might be subject to higher environmental stress conditions than polyps located in the basal zone.

Comparison between subindividual variability of sea pens and plants

The study of the continuous variation in quantitative features of homologous organs within the same plant remains relatively unexplored from an ecological perspective despite being a quintessential plant feature. However, the few studies that have been carried out have provided an enormous amount of information and suggested manifold biological and ecological implications (Herrera 2009, 2017). The study of marine modular organisms, including sea pens (such as number of features, individuals and species analysed), is even more limited, but some noteworthy parallelisms can be inferred when the distribution of variability is compared.

When the levels of subindividual variability of reiterated structures obtained here for *Ptilella* and *Pennatula* colonies are compared with the subindividual variability reported for certain plant organs (Figure 4), we can see that polyps (more intracolonially variable than sclerites) show lower levels of variability than leaves (fruits or seeds) but comparable levels to flowers (Fig. 4). Like polyps, flowers are the organ responsible for reproduction (perhaps the burden of reproduction may be exerting more influence on the distribution of variability levels of polyps than the capture of resources). In any case, in both reiterated structures (flowers and polyps), there is an important source of variability that must be considered. What might this parallelism involve for pennatulaceans from an ecological point of view? The similar organization of phenotypic variation in pennatulaceans to that observed in plants supports the hypothesis that subindividual variability is an emergent property of individual organisms caused by their modular construction and the reiteration of homologous structures with the same function (leaves, fruits, flowers or seeds in plants, sclerites or polyps in sea pens), regardless of their evolutionary origin. Parallelisms like this between plants and animals allow us to determine the consequences of certain natural processes that are known to occur in one of the two kingdoms and infer them in the other (Herrera et al. 2015, Alonso et al. 2018). Following this idea, the influence exerted by the associated fauna (e.g. animal consumers) in the organization of within-individual variance in plants (Herrera 2009), could have similar effects between predators and sea pens (Clippele et al. 2015), opening a new field of study. For example, it has been suggested that subindividual variability in

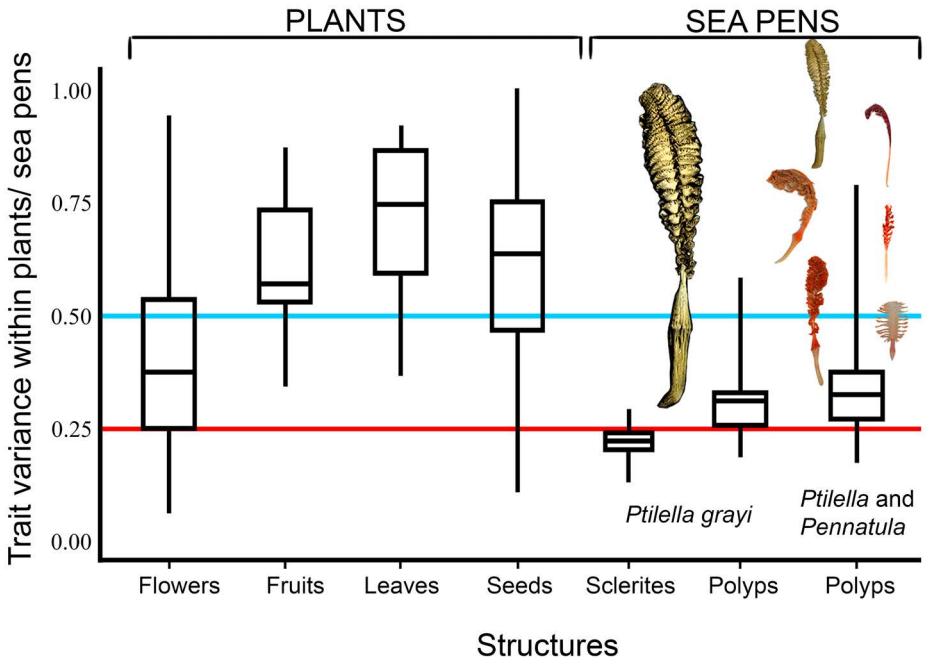

Fig. 4. – Within-plant variability comparison between plant and sea pen traits. Modified partially from Herrera et al. (2017: Fig. 1a). The horizontal dashed line denotes the level above which subindividual variance is greater than variance between individual means (blue line) or which involves an important source of variance (red line).

some functional traits of leaves may be advantageous to individuals by enhancing whole-plant photosynthetic performance and optimizing the exploitation of environmental variation (Osada et al. 2014, Herrera 2017). It is known that some animal consumers have the opportunity to discriminate between not only individual plants but also the multiplicity of non-identical organs borne by each of them, affected by the distribution of variability of reward offered by plants (Herrera 2009, 2017). In the same way, subindividual variability of polyp traits could be related to the optimization of resource exploitation via "division of labour" within the individual (Sides et al. 2014, Siefert et al. 2015). In this hypothetical case, sea pen predators (such as *Tritonia* sp. on *Pteroeides* sp. in Duncan 1998, García-Matucheski and Munian 2011; or *Armina* sp. on *Veretillum cynomorium* or *Ptilosarcus guerneyi* in Birkeland 1974, Jones et al. 2000, Buhl-Mortensen et al. 2010, among others) would exert a certain discrimination between colonies and could likewise be influenced by levels of subindividual variation, an interesting hypothesis that could be tested by future studies on pennatulaceans. Perhaps in this hypothetical scenario, following the parallelism with plants, the term heterozooidy (analogous to the term heterophylly, see Herrera 2009) may be considered appropriate to refer to this subindividual variation within the same zooid type.

CONCLUSIONS

In summary, though our results must be taken with caution, the parallelism found between pennatulaceans and plants promotes a multitude of biological questions. On this point, we can offer answers to the questions listed in the Introduction:

(1) Congeneric species of sea pens (*Pt. grandis*, *Pt. grayi* and *Pt. inflata*) differed with respect to the quantitative distribution of population variance within and between colonies in quantitative polyp traits. However, (2) additional factors such as contrasting environmental conditions between the collecting areas could offset and conceal the effect of this distribution. (3) In a similar way, species from *Ptilella* and *Pennatula*, similar morphologically although phylogenetically differentiated, showed differences in distribution within and between colonies of population variance, but not related to taxonomic grouping at genus level. Finally, (4) this study suggests, as a parallelism between plant and animals, that the organization of phenotypic variation in pennatulaceans is quite similar to that observed in terrestrial plants.

This study therefore serves as a first step towards future studies that improve our knowledge of possible ecological implications and generate more suitable criteria for the delimitation of interspecific morphological limits, more efficient experimental designs, and new and interesting biological hypotheses that have already been formulated and discussed in plants but are unknown in sea pens and other marine modular colonial organisms.

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REFERENCES

Alonso C., Pérez R., Bazaga P., et al. 2018. Within-plant variation in seed size and inflorescence fecundity is associated with epigenetic mosaicism in the shrub *Lavandula latifolia* (Lamiaceae). Ann. Bot. 121: 153-160. https://doi.org/10.1093/aob/mcx140

Baillon S., Hamel J.-F., Mercier A. 2014a. Diversity, distribution and nature of faunal associations with deep-sea pennatulacean corals in the Northwest Atlantic. PLoS ONE 9: e111519. https://doi.org/10.1371/journal.pone.0111519

Baillon S., Hamel J.-F., Wareham V.E., Mercier A. 2014b. Seasonality in reproduction of the deep-water pennatulacean coral *Anthoptilum grandiflorum*. Mar. Biol. 161: 29-43. https://doi.org/10.1007/s00227-013-2311-8

Baillon S., English M., Hamel J.F., Mercier A. 2016. Comparative biometry and isotopy of three dominant pennatulacean corals in the Northwest Atlantic. Acta Zool. 97: 475-493. https://doi.org/10.1111/azo.12141

Bayer F.M. 1956. Octocorallia. In: Moore, R.C. (ed). Treatise on invertebrate paleontology. Part F. Coelenterata. Geol. Soc. America Univ. Kansas Press. New York and Lawrence Kansas, pp. 166-231.

Bayer F.M., Grasshoff M., Verseveldt J. 1983. Illustrated trilingual glossary of morphological and anatomical terms applied to Octocorallia. E. J. Brill/ Dr. Backhuys, Leiden. 75 pp.

Birkeland C. 1974. Interactions between a sea pen and seven of its predators. Ecol. Monogr. 44: 211-232. https://doi.org/10.2307/1942312

Borges R.M. 2005. Do plants and animals differ in phenotypic plasticity? J. Biosci. 30: 41-50. https://doi.org/10.1007/BF02705149

Brito T.A.S., Tyler P.A., Clarke A. 1997. Reproductive biology of the Antarctic octocoral *Thouarella variabilis* Wright and Studer 1889. Proc 6th Int Conf Coelenterate Biology, Natural History Museum of Leiden, The Netherlands. 63-69 pp.

Brown M.B., Forsythe A.B. 1974. Robust tests for the equality of variances. J. Am. Stat. Assoc. 69: 364-367. https://doi.org/10.1080/01621459.1974.10482955

Buhl-Mortensen L., Vanreusel A., Gooday A.J., et al. 2010. Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. Mar. Ecol. 31: 21-50. https://doi.org/10.1111/j.1439-0485.2010.00359.x

Clippele L.H., Buhl-Mortensen P., Buhl-Mortensen L. 2015. Fauna associated with cold water gorgonians and sea pens. Cont. Shelf Res. 105: 67-78. https://doi.org/10.1016/j.csr.2015.06.007

Coma R., Ribes M., Zabala M., Gili J.M. 1995. Reproduction and cycle of gonadal development in the Mediterranean gorgonian *Paramuricea clavata*. Mar. Ecol. Prog. Ser. 117: 173-183. https://doi.org/10.3354/meps117173

Conover W.J., Johnson M.E., Johnson M.M. 1981. A comparative study of tests for homogeneity of variances, with applications to the outer continental shelf bidding data. Technomet. 23: 351-361. https://doi.org/10.1080/00401706.1981.10487680

Darwin C. 1859. On the origin of species. Murray, London.

Duncan J.C. 1998. Biology of the sea pen *Pteroeides* sp. in Fiordland, New Zealand. PhD dissertation, Univ. Otago (New Zealand), 88 pp.

Edwards D.C.B., Moore C.G. 2008. Reproduction in the sea pen *Pennatula phosphorea* (Anthozoa: Pennatulacea) from the west coast of Scotland. Mar. Biol. 155: 303-314. https://doi.org/10.1007/s00227-008-1028-6

Edwards D.C.B., Moore C.G. 2009. Reproduction in the sea pen *Funiculina quadrangularis* (Anthozoa: Pennatulacea) from the west coast of Scotland. Estuar. Coast. Shelf Sci. 82: 161-168. https://doi.org/10.1016/j.ecss.2009.01.006

Finelli C.M., Helmuth B.S., Pentcheff N.D., Wethey D.S. 2007. Intracolony variability in photosynthesis by corals is affected by water flow: role of oxygen flux. Mar. Ecol. Prog. Ser. Ser. 349: 103-110. https://doi.org/10.3354/meps07101

Foster A.B. 1980. Environmental variation in skeletal morphology within the Caribbean reef corals *Montastraea annularis* and *Siderastrea siderea*. Bull. Mar. Sci. 30: 678-709.

Foster A.B. 1985. Variation within coral colonies and its importance for interpreting fossil species. J. Paleontol. 59: 1359-1381.

Fox J., Weisberg S. 2019. An {R} Companion to Applied Regression, Third Edition. Thousand Oaks CA: Sage. https://socialsciences.mcmaster.ca/jfox/Books/Companion/

García-Cárdenas F.J, López-González P.J. 2022a. Growth and reproductive traits of deep-sea pen *Anthoptilum murrayi* Kölliker, 1880, from Iceland (North Atlantic). Mar. Biol. Res. 18: 7-8, 448-465. https://doi.org/10.1080/17451000.2022.2147949

García-Cárdenas F.J, López-González P.J. 2022b. Some observations on the reproductive biology of the Mediterranean pennatulacean *Pteroeides spinosum* (Ellis and Solander, 1786) (Cnidaria: Octocorallia: Pennatulacea). Thalassas https://doi.org/10.1007/s41208-022-00505-6

García-Cárdenas F.J, Drewery J., López-González P.J. 2019. Resurrection of the sea pen genus *Ptilella* Gray, 1870 and description of *Ptilella grayi* n. sp. from the NE Atlantic (Octocorallia: Pennatulacea). Sci. Mar. 83: 261-276. https://doi.org/10.3989/scimar.04845.26A

García-Matucheski S., Muniain C. 2011. Predation by the nudibranch *Tritonia odhneri* (Opisthobranchia: Tritoniidae) on octocorals from the South Atlantic Ocean. Mar. Biodivers. 41: 287-297. https://doi.org/10.1007/s12526-010-0063-y

Goffredo S., Caroselli E., Gasparini G., et al. 2011. Colony and polyp biometry and size structure in the orange coral *Astroides calycularis* (Scleractinia: Dendrophylliidae). Mar. Biol. Res. 7: 272-280. https://doi.org/10.1080/17451000.2010.492222

Haeckel E.H.P.A. 1869. Ueber Den Organismus Der Schwamme und Ihre Verwandtschaft Mit Den Coralen.

Hallé F. 1999. Éloge de la plante. Pour une nouvelle biologie. Éditions du Seuil, Paris, France. 356 pp.

Harrison P.L., Wallace C.C. 1990. Reproduction, dispersal and recruitment of scleractinian corals. In: Dubinsky Z (ed). Ecosystems of the World. Vol. 25. Coral Reefs. Amsterdam: Elsevier. 133-207 pp.

Harvell D. 1984. Why nudibranchs are partial predators: intracolonial variation in bryozoan palatability. Ecology 65: 716-724. https://doi.org/10.2307/1938043

Herrera C.M. 2009. Multiplicity in unity. Plant subindividual variation and interactions with animals, Univ. Chicago Press, Chicago, USA. 437 pp. https://doi.org/10.7208/chicago/9780226327952.001.0001

Herrera C.M. 2017. The ecology of subindividual variability in plants: patterns, processes, and prospects. Web Ecology 17: 51-64. https://doi.org/10.5194/we-17-51-2017

Herrera C.M., Medrano M., Bazaga P. 2015. Continuous within plant variation as a source of intraspecific functional diversity: patterns, magnitude, and genetic correlates of leaf variability in *Helleborus foetidus* (Ranunculaceae). Am. J. Bot. 102: 225-232. https://doi.org/10.3732/ajb.1400437

Herrera C.M., Bazaga P., Pérez R., Alonso C. 2021. Lifetime genealogical divergence within plants leads to epigenetic mosaicism in the shrub *Lavandula latifolia* (Lamiaceae). New Phytol. 231: 2065-2076. https://doi.org/10.1111/nph.17257

Hickson S.J. 1916. The Pennatulacea of the Siboga Expedition, with a general survey of the order. Siboga Expeditie Monographs 14, Livr. 77: 1-265.

Hughes R.N. 2005. Lessons in modularity: the evolutionary ecology of colonial invertebrates. Sci. Mar. 69S1: 169-179. https://doi.org/10.3989/scimar.2005.69s1169

Jackson J.B.C., Coates A.G. 1986. Life cycles and evolution of clonal (modular) animals. Philos. Trans. R. Soc. Lond. B. 313: 7-22. https://doi.org/10.1098/rstb.1986.0022
Jones L.A., Hiscock K., Connor D.W. 2000. Marine habitat reviews, a summary of ecological requirements and sensitivity characteristics for the conservation and management of Marine SACs. UK Marine SACs Project Report. Peterborough: Joint Nature Conservation Committee. 178 pp.
Kaandorp J.A., Kübler J.E. 2001. Environmentally driven plasticity. In: The Algorithmic Beauty of Seaweeds, Sponges and Corals. Springer, Berlin, Heidelberg. 15-66 pp. https://doi.org/10.1007/978-3-662-04339-4_2
Key M.M. 1990. Intracolony variation in skeletal growth rates in Paleozoic ramose trepostome bryozoans. Paleobiology 16: 483-491. https://doi.org/10.1017/S0094837300010204
Kim E., Lasker H.R., Coffroth M.A., Kim K. 2004. Morphological and genetic variation across reef habitats in a broadcast-spawning octocoral. Hydrobiologia 530: 423-432. https://doi.org/10.1007/s10750-004-2646-8
Lapid E.D., Wielgus J., Chadwick-Furman N.E. 2004. Sweeper tentacles of the brain coral *Platygyra daedalea*: Induced development and effects on competitors. Mar. Ecol. Prog. Ser. 282: 161-71. https://doi.org/10.3354/meps282161
Lasker H.R., Boller M.L., Castanaro J., Sánchez J.A. 2003. Modularity and determinate growth in a gorgonian coral. Biol. Bull. 205: 319-330. https://doi.org/10.2307/1543295
Lenth R. 2019. emmeans 1.4: Estimated Marginal Means, aka Least-Squares Means. R package version 1.4. https://CRAN.R-project.org/package=emmeans.
Leuzinger S., Anthony K.R.N., Willis B.L. 2003. Reproductive energy investment in corals: Scaling with module size. Oecologia 136: 524-31. https://doi.org/10.1007/s00442-003-1305-5
Levene H. 1960. Robust tests for equality of variances. In: Olkin I. et al. (eds), Contributions to probability and statistics: Essays in honor of Harold Hotelling. Stanford, CA: Stanford University Press. 278-292 pp.
Menezes N.M.D., Neves E.G., Barros F., et al. 2013. Intracolonial variation in *Siderastrea* de Blainville, 1830 (Anthozoa, Scleractinia): taxonomy under challenging morphological constraints. Biota Neotropica 13: 108-116. https://doi.org/10.1590/S1676-06032013000100012
O'Dea A. 2003. Seasonality and zooid size variation in *Panamanian encrusting* bryozoans. J. Mar. Biol. Ass. U. K. 83: 1107-1108. https://doi.org/10.1017/S0025315403008348h
O'Dea A., Okamura B. 2000. Intracolony variation in zooid size in cheilostome bryozoans as a new technique for investigating palaeoseasonality. Palaeogeogr. Palaeoclimatol. Palaeoecol. 162: 319-332. https://doi.org/10.1016/S0031-0182(00)00136-X
Orejas C., López-González P.J., Gili J.M., et al. 2002. Distribution and reproductive ecology of the Antarctic octocoral *Ainigmaptilon antarcticum* in the Weddell Sea. Mar. Ecol. Prog. Ser. 231: 101-114. https://doi.org/10.3354/meps231101
Osada N., Yasumura Y., Ishida A. 2014. Leaf nitrogen distribution in relation to crown architecture in the tall canopy species, *Fagus crenata*. Oecologia 175: 1093-1106. https://doi.org/10.1007/s00442-014-2966-y
Oury N., Gélin P., Magalon H. 2020. Together stronger: Intracolonial genetic variability occurrence in *Pocillopora* corals suggests potential benefits. Ecol. Evol. 10: 5208-5218. https://doi.org/10.1002/ece3.5807
Paradis E., Schliep K. 2018. ape 5.0: an environment for modern phylogenetic and evolutionary analyses in R. Bioinformatics 35: 526-528. https://doi.org/10.1093/bioinformatics/bty633
Pearson K. 1901. Mathematical contributions to the theory of evolution: 9, On the principle of homotyposis and its relation to heredity, to the variability of the individual, and to that of the race; part 1, homotyposis in the vegetable kingdom. Philos. Trans. R. Soc. Lond. A. 197: 285-379. https://doi.org/10.1098/rsta.1901.0020
Pérez-Harguindeguy N., Díaz S., Garnier E., et al. 2013. New handbook for standardised measurement of plant functional traits worldwide. Aust. J. Bot. 61: 167-234. https://doi.org/10.1071/BT12225
Pinheiro J., Bates D., DebRoy S., Sarkar D., R Core Team. 2018. nlme: Linear and Nonlinear Mixed Effects Models_. R package version 3.1-137.
Prada C., Schizas N.V., Yoshioka P.M. 2008. Phenotypic plasticity or speciation? A case from a clonal marine organism. BMC Evol. Biol. 8: 47. https://doi.org/10.1186/1471-2148-8-47
R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.
Sakai K. 1998. Effect of colony size, polyp size, and budding mode on egg production in a colonial coral. Biol. Bull. 195: 319-25. https://doi.org/10.2307/1543143
Sánchez J.A., Lasker H.R. 2003. Patterns of morphologic integration in branching colonies of marine modular organisms: supramodule organization in gorgonian corals. Proc. R. Soc. Lond. B. 270: 2039-2044. https://doi.org/10.1098/rspb.2003.2471
Sánchez J.A., Aguilar C., Dorado D., Manrique N. 2007. Phenotypic plasticity and morphological integration in a marine modular invertebrate. BMC Evol. Biol. 7: 122. https://doi.org/10.1186/1471-2148-7-122
Schultz B.B. 1983. On Levene's test and other statistics of variation. Evol. Theory 6:197-203.
Schultz B.B. 1985. Levene's test for relative variation. Syst. Zool. 34: 449-456. https://doi.org/10.1093/sysbio/34.4.449
Schweinsberg M., Tollrian R., Lampert K.P. 2017. Inter-and intracolonial genotypic diversity in hermatypic hydrozoans of the family Milleporidae. Mar. Ecol. 38: e12388. https://doi.org/10.1111/maec.12388
Sherwood O.A., Jamieson R.E., Edinger E.N., Wareham V.E. 2008. Stable C and N isotopic composition of cold-water corals from the Newfoundland and Labrador continental slope: Examination of trophic, depth and spatial effects. Deep-Sea Res. I. 55: 1392-1402. https://doi.org/10.1016/j.dsr.2008.05.013
Sides C.B., Enquist B.J., Ebersole J.J., et al. 2014: Revisiting Darwin's hypothesis: Does greater intraspecific variability increase species' ecological breadth? Am. J. Bot. 101: 56-62. https://doi.org/10.3732/ajb.1300284
Siefert A., Violle C., Chalmandrier L., Albert C.H., et al. 2015: A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. Ecol. Lett. 18: 1406-1419. https://doi.org/10.1111/ele.12508
Soong K. 2005. Reproduction and colony integration of the sea pen *Virgularia juncea*. Mar. Biol. 146: 1103-1109. https://doi.org/10.1007/s00227-004-1509-1
Soong K, Lang J.C .1992. Reproductive integration in reef corals. Biol. Bull. 183: 418-431. https://doi.org/10.2307/1542018
Tixier-Durivault A. 1965. Quelques octocoralliaires australiens. Bull. Mus. Natl. Hist. Nat. 37: 705-716.
Ulstrup K.E., Ralph P.J., Larkum A.W.D., Kühl M. 2006. Intra-colonial variability in light acclimation of zooxanthellae in coral tissues of *Pocillopora damicornis*. Mar. Biol. 149: 1325-1335. https://doi.org/10.1007/s00227-006-0286-4
Van Valen L. 1978. The statistics of variation. Evol. Theory 4: 33-43.
Wejnert K.E., Smith A.M. 2008. Within-colony variation in skeletal mineralogy of *Adeonellopsis* sp. (Cheilostomata: Bryozoa) from New Zealand. N. Z. J. Mar. Freshw. Res. 42: 389-395. https://doi.org/10.1080/00288330809509967
Williams G.C., Hoeksema B.W., van Ofwegen L.P. 2012. A fifth morphological polyp in pennatulacean octocorals, with a review of polyp polymorphism in the genera *Pennatula* and *Pteroeides* (Anthozoa: Pennatulidae). Zool. Stud. 51: 1006-1017.
Wickham H. 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York. https://doi.org/10.1007/978-3-319-24277-4
Wickham H., Bryan J. 2019. readxl: Read Excel Files. R package version 1.3.1. https://CRAN.R-project.org/package=readxl
Wickham H., Romain F., Lionel H., Kirill M. 2019. dplyr: A Grammar of Data Manipulation. R package version 0.8.3. https://CRAN.R-project.org/package=dplyr

SUPPLEMENTARY MATERIAL

Fig. S1. – Distribution of mean ($\bar{X}$) and variance components of sclerites and polyps within and between *Ptilella grayi* colonies.

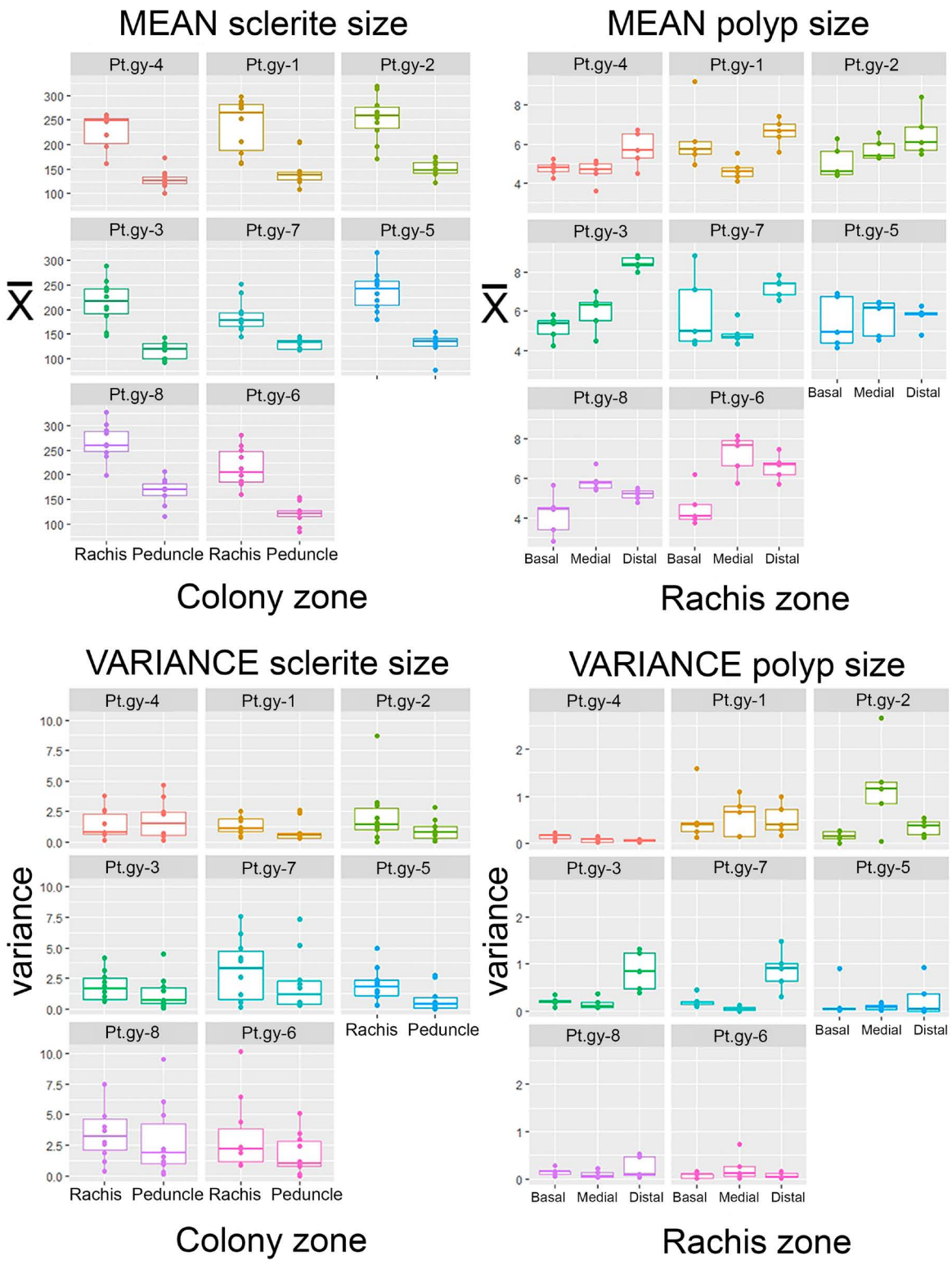

Table S1. - Results of ANOVA test applied to the model based on the CV of sclerite and polyp sizes for the eight colonies of *Ptilella grayi*. Sum sq., sum of squares; Gf, degrees of freedom. Code Signif.: ***= <0.001.

	Sclerites					Polyps				
ANOVA	Sum sq.	Gf	F value	Pr (>F)	Signif.	Sum sq.	Gf	F value	Pr (>F)	Signif.
Colonies	60937	7	6.9474	3.97e-07	***	27.459	7	4.6625	1.57e-04	***
Zones	378639	1	302.1793	<2.2e-16	***	37.303	2	22.1693	1.21e-8	***
Colony: zones	12837	7	1.4635	0.184		53.277	14	4.5233	3.40e-06	***
Residuals	180436	144				80.766	96			

Table S2. – Coefficient of variation of *Ptilella grayi* colonies. X, mean; sd, standard deviation; CV, coefficient of variation. Based on 360 observations.

	Sclerites						Polyps								
Ptilella grayi colony	Rachis			Peduncle			Basal			Medial			Distal		
	X (µm)	sd (µm)	CV	X (µm)	sd (µm)	CV	X (mm)	sd (mm)	CV	X (mm)	sd (mm)	CV	X (mm)	sd (mm)	CV
Pt.gy-1	238.57	52.27	**0.219**	146.72	32.40	**0.216**	6.29	1.67	**0.265**	4.68	0.81	**0.172**	6.61	0.88	**0.133**
Pt.gy-2	269.27	62.05	**0.230**	151.32	15.78	**0.104**	5.08	0.86	**0.169**	5.72	1.06	**0.186**	6.49	1.19	**0.184**
Pt.gy-3	215.35	43.58	**0.202**	116.63	17.23	**0.148**	5.16	0.69	**0.134**	5.97	0.97	**0.163**	8.46	0.84	**0.099**
Pt.gy-4	230.30	32.71	**0.142**	129.18	18.43	**0.143**	4.76	0.46	**0.096**	4.58	0.60	**0.132**	5.75	0.87	0.151
Pt.gy-5	247.25	43.61	**0.176**	130.12	20.18	**0.155**	5.43	1.27	**0.234**	5.67	0.91	**0.160**	5.72	0.68	**0.119**
Pt.gy-6	215.08	38.06	**0.177**	120.68	21.01	**0.174**	4.52	0.95	**0.211**	7.23	1.03	**0.142**	6.58	0.65	**0.099**
Pt.gy-7	187.07	32.14	**0.172**	130.76	9.89	**0.076**	5.95	1.86	**0.313**	4.86	0.56	**0.116**	7.22	0.92	**0.127**
Pt.gy-8	266.62	35.16	**0.132**	165.75	25.20	**0.152**	4.17	1.07	**0.256**	5.85	0.55	**0.095**	5.16	0.49	**0.096**

Table S3. – Summary of the results of the analyses of sclerite and polyp sizes using a full random hierarchical mixed model (lme); lme, result of the lme analysis; VAR, variance; ape, result of the ape analysis; $\%VAR_{total}$, total variance (%). ME, measurement error. Based on 360 observations.

	Sclerite			Polyp		
	$VAR_{between}$	VAR_{zone}	VAR_{within}	$VAR_{between}$	VAR_{zone}	VAR_{within}
lme VAR	2.56e-04	2.97e03	1.16e03	6.20e-08	0.9604	0.9216
lme intervals	9.14e-34 - 3.06e+29	37.97- 78.40				
Within Std Error			32.04 – 36.44			
ape	6.75e-08	0.718	0.281	3.25e-08	0.506	0.493
$\%VAR_{total}$	**<1%**	71%	**28%**	**<1%**	50%	**49%**
ME			0.04%			16%
Repeatability			99%			84%

Table S4. – Levene test applied to the lme model based on the CV for polyp size in *Ptilella* and *Pennatula* colonies. Sum sq., sum of squares; Gf, degrees of freedom. Code Signif. : ***= <0.001; **= <0.01.

Levene	Sum sq.	Gf	F value	Pr (>F)	Signif.
Species	338.99	5	64.0906	<2.2e-16	***
Zones	13.13	2	6.2073	0.0023	**
Species: zones	17.65	10	1.6680	0.088	
Residuals	266.58	252			

Table S5. – Results of the emmean analysis in *Ptilella* and *Pennatula* colonies. Confidence level used 0.95. Standard error = 0.266, degrees of freedom= 252.

Species	Zone	Basal	Medial	Distal
	emmean	**5.25**	**5.10**	**6.22**
Ptilella grayi	Lower limit	4.73	4.58	5.69
	Upper limit	5.78	5.62	6.74
	emmean	**3.04**	**3.69**	**3.70**
Ptilella grandis	Lower limit	2.52	3.17	3.18
	Upper limit	3.56	4.22	4.22
	emmean	**2.92**	**3.24**	**4.22**
Ptilella inflata	Lower limit	2.40	2.72	3.70
	Upper limit	3.44	3.77	4.75
	emmean	**2.49**	**2.65**	**2.73**
Pennatula phosphorea	Lower limit	1.96	2.12	2.21
	Upper limit	3.01	3.17	3.26
	emmean	**2.87**	**3.10**	**3.09**
Pennatula sp.	Lower limit	2.34	2.58	2.57
	Upper limit	3.39	3.62	3.62
	emmean	**1.90**	**2.03**	**1.73**
Pennatula rubra	Lower limit	1.38	1.51	1.21
	Upper limit	2.43	2.55	2.25

Table S6. – Result of the mixed effects linear model in *Ptilella* and *Pennatula* species; ape, result of ape analysis; ME, Measurement error. Based on 540 observations. Approx. 95% confidence intervals.

Polyp size	$VAR_{between}$	VAR_{zone}	VAR_{within}
Variance	1.39	0.35	0.67
ape	0.5774	0.1455	0.2769
%VAR	**57%**	14%	**27%**
ME			<1% (0.00071)
Repeatability			≈99%