

Patterns of morphological integration in marine modular organisms: supra-module organization in branching octocoral colonies

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Despite the relative simplicity of their modular growth, marine invertebrates such as arborescent gorgonian octocorals (Octocorallia: Cnidaria) generate complex colonial forms. Colony form in these taxa is a consequence of modular (polyp) replication, and if there is a tight integration among modular and supramodular traits (e.g. polyp aperture, inter-polyp spacing, branch thickness, internode and branch length), then changes at the module level may lead to changes in colony architecture. Alternatively, different groups of traits may evolve semi-independently (or conditionally independent). To examine the patterns of integration among morphological traits in Caribbean octocorals, we compared five morphological traits across 21 species, correcting for the effects of phylogenetic relationships among the taxa. Graphical modelling and phylogenetic independence contrasts among the five morphological characters indicate two groups of integrated traits based on whether they were polyp- or colony-level traits. Although all characters exhibited bivariate associations, multivariate analyses (partial correlation coefficients) showed the strongest integration among the colony-level characters (internode distance and branch length). It is a quantitative demonstration that branching characters within the octocorals studied are independent of characters of the polyps. Despite the universally recognized modularity of octocorals at the level of polyps, branching during colony development may represent an emergent level of integration and modularity.

Keywords: modularity; phenotypic integration; branching colonies; octocoral; phylogeny; comparative analysis

1. INTRODUCTION

A common feature of virtually all organisms is phenotypic variation among individuals across populations and species. This variation is both the product of natural selection and the raw material upon which it operates. An important question in the study of phenotypic evolution is whether characters are independent of each other or behave and evolve as integrated modules or systems (Pigliucci 2002). Correlations among morphological traits across species depict patterns of integration during the evolutionary process (Olson & Miller 1958; Cheverud 1996; Marroig & Cheverud 2001). Such integration can be the product of common inheritance due to pleiotropy or linkage disequilibrium, or the result of the concerted evolution of morphological elements that operate together to perform a specific function (Cheverud 1996). The formation of these evolutionary modules or systems increases the organism's potential to evolve ('evolvability'; Wagner & Aitenberg 1996). The amount of morphological or molecular diversity/complexity among taxa is usually correlated to the amount of modularity at several magnitudes of characters ranging from proteins to bone complexes (e.g. Lipson *et al.* 2002). Consequently, the formation of modules can be considered a trend as organismal integration and complexity increases.

Questions concerning integration are particularly interesting for modular organisms (*sensu* Harper & White 1974) such as colonial marine invertebrates, which develop from the replication of morphological units such as polyps or zooids. Modular replication generates emergent properties such as the complex branching patterns of colonial bryozoans, hydroids and gorgonian octocorals (McKinney & Jackson 1989; Lasker & Sánchez 2002). What correlations exist within and between module and colony-level traits? Are colony-level traits simple products of the traits of the modules or are there suites of traits that vary independently of the module? This paper examines several aspects of the integration and evolution of traits at multiple levels of organization among Caribbean octocorals.

Modular organisms such as Caribbean branching octocorals are organized into colonial structures that are usually unconventional complex networks (Lasker & Sánchez 2002; Sánchez *et al.* 2003a). We will refer to the polyp as the module *sensu stricto* because it is the minimum unit of organization that a colony can be divided into that can live and function independently. In most cases individuals comprising a single polyp can only be found at the start of the colony's astogeny, but there are some octocorals comprising only one solitary polyp (Bayer & Muzik 1976). Octocoral polyps, in gorgonian species, have eight pinnate tentacles, and they are monomorphic, each capable of all physiological functions, for example, reproduction, feeding, excretion, defence, etc. Among branching octocorals polyps are connected to each other by hollow axial vessels (solenia; Bayer 1973), which continue along the branch axis, forming a branching tree-like structure that parallels the overall colony form.

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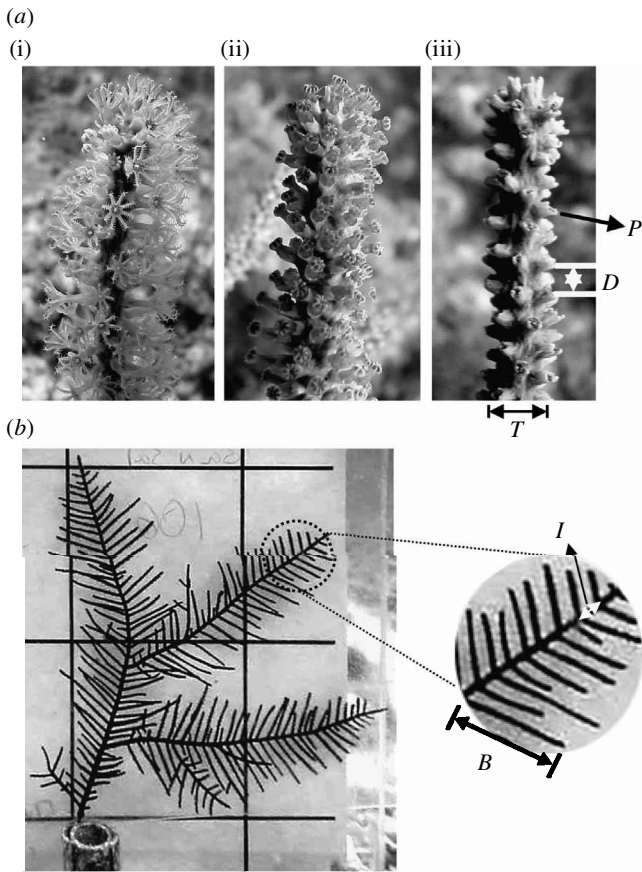


Figure 1. (a) Some traits related to polyps in a colony of *Eunicea* sp. The photographs show the branch with the polyps extended (i), partly retracting (ii) and fully retracted into the calyx (iii). *P*, polyp aperture; *D*, inter-polyp distance; *T*, branch thickness. (b) Macroscopic colonial traits in a colony of *Pseudopterogorgia bipinnata* (grid 10 cm × 10 cm). *B*, daughter branch length; *I*, internode length. Images were taken against a background grid with a Sony Mavica FD-81 camera, corrected for distortion using PHOTOSHOP (Adobe) as in Sánchez *et al.* (2003a), and measurements were made with the software program IMAGEJ (Java version of NIH Image, National Institutes of Health, USA).

The networks produced by colonial growth exhibit a great deal of complexity. Phylogenetic analyses suggest multiple origins of branching structures and axial materials (Sánchez *et al.* 2003b,c). Colonies generally have highly individual growth histories and, with the exception of the youngest colonies, are never identical to each other (Bayer 1973). Consequently, it is difficult to identify landmarks that can be used to compare the form of colonies, even colonies from the same species. The morphological characters of colonies can be divided into groups distinguished by their organization and magnitude. Features of branching colonies can be decomposed into characters of individual polyps, individual branches and the whole colony. Polyp characters are microscopic (*ca.* 0.1–2 mm) and include traits such as the polyp aperture, the structure into which the polyp retracts often forming a calyx (figure 1). Characters of the branches range in scale from 0.1 to 30 mm and reflect patterns of polyp replication such as the distance or spacing between polyps and the branch thickness (figure 1). All the branches in a colony are structurally similar to each other, but there are size and

positional differences among them. Branching in holaxonian octocorals (which are gorgonian corals) is a subapical process where branches, ‘mother branches’, produce new branches, ‘daughter branches’, at roughly fixed distances or internodes (Sánchez *et al.* 2003d). The process of branching can be described by an array of colony-level traits such as the length of a daughter branch and the length of internodes (the distance between daughter branch points; figure 1). Although these characters are ultimately products of the replication of modules, they reflect an emergent property, the organization of branching (Lasker & Sánchez 2002; Sánchez *et al.* 2003d). However, the evolution of these traits and their relationship to module (polyp) evolution is unknown.

Colony development, or astogeny, is controlled by some combination of a genetically mediated developmental programme and plastic responses to the environment. At the genetic level, changes in the number and function of developmental genes are believed to have resulted in the evolution of the body plan in individual organisms (e.g. derived metazoans; De Rosa *et al.* 1999), and modular body plans such as the patterning of cnidarian polyps may also be related to developmental genes. Modular cnidarians, for instance, harbour most of the *Hox* gene families present in upper metazoans (see Aerne *et al.* 1995; Cartwright & Buss 1999; Cartwright *et al.* 1999; Kuhn *et al.* 1999). If colony form is the product of aggregated effects acting on the different levels and scales of modular replication, hypothetically, just a few changes at the module level could generate changes in colony architecture suggesting a saturated (e.g. all traits strongly correlated) and thus integrated evolution of the phenotype (e.g. Gould 1977; Cheverud 1982).

Branching and module replication seem to be affected by ecological/physiological effects/constraints acting on different scales and levels of organization (Kim & Lasker 1997; Lasker & Sánchez 2002). For instance, selection on the size of the module to optimize prey capture or defence against predators might (or might not) necessitate a change in the branch size or internode distance. By contrast, decreased branch size among species that enabled them to survive in wave-swept environments, might not require a change in the calyx or distance among calyces, and in both examples there might not be any concomitant change in branching patterns. Hypothetically, some traits could be more integrated than others because of common genetic control, developmental interactions, mechanical constraints or functional effects. The integration of different components of the phenotype/genotype into groups of covarying traits can be detected as patterns of conditional dependence and independence among traits. In the case of polyp- and colony-level traits the question is whether the traits, many of which are correlated, still have strong correlations after controlling for the effects of other characters.

An application of graph theory called graphical modelling provides a method to examine hypotheses of morphological integration. The technique plots and tests the level of association among phenotypic characters (figure 2; see review in Magwene 2001). The rationale of the approach is to delineate sets of strong interactions by removing interactions for which there is compelling evidence of conditional independence, consequently delineating

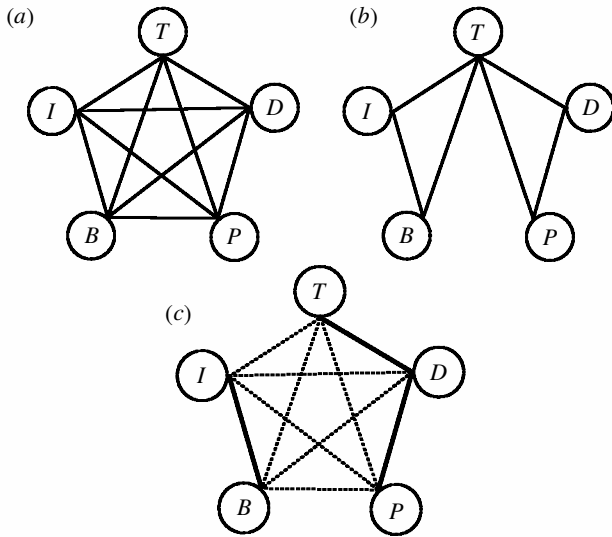


Figure 2. Graphical models among the traits studied. (a) Saturated model of correlation, no conditional independence is found, all characters are dependent each other. (b) Model showing morphological integration. Only strong, significant edges are shown. (c) Graphical model for the morphological integration among supra-modular traits. Bold edges show strong bonds after using third-order PCC and the edge thickness corresponds to edge strength values (see electronic Appendix C), dashed lines depict only background zero-order bivariate correlations existing among all contrast variates (table 1). *P*, polyp aperture; *D*, inter-polyp distance; *T*, branch thickness; *B*, daughter branch length; *I*, internode length.

integrated modules by identifying traits that are not integrated. In cases of conditional independence, two characters that are correlated become statistically independent after using partial correlation coefficients to include the effect of a third character (or set of characters) that is positioned between the two in a graph model (Stirzaker 1994; Magwene 2001). Linked characters, however, maintain a strong association after controlling for other characters (or sets of characters). Potential outcomes of such an analysis are depicted in figure 2. In the case of an analysis of five characters, when all of the traits of a colony are correlated, even after third-order partial effects are removed (i.e. each two-character interaction is significant after controlling for three characters), then the whole phenotype can be characterized as completely integrated (or saturated). In such a case there are no cases of conditional independence and no patterns of morphological modularization (*sensu lato*) (figure 2a). Such a case would suggest that controls affecting polyp formation (i.e. module *sensu stricto*) also affect aspects of the phenotype at other levels such as branch length or internode. In figure 2b conditional independence, for example trait integration, is illustrated by the presence of traits that are only correlated with each other through a third variable. For instance, the variables associated with branch length (*B*) are conditionally independent of the variables from the polyp aperture (*P*) because of the interaction with variables from the internode (*I*) and so on (figure 2b). Groups of traits that are conditionally dependent act as integrated modular units (*sensu lato*, e.g. Magwene 2001). In that case, following Magwene's notation, $\{I, B\}$ ($I|B$,

or, *I* dependent on *B*) would comprise a morphological module conditionally independent of the module $\{D, P\}$ due to *T*, which can be expressed as $\{I, B\} \perp \{D, P\} | T$ or $\{I, B\}$ conditionally independent of $\{D, P\}$ due or depending on *T*. The main purpose of this study is to investigate the evolution and morphological integration of traits among 21 species of branching octocorals. We aim to determine if there are patterns of integration between and within polyp and colony-level traits.

2. MATERIAL AND METHODS

To study interspecific integration among traits, we measured polyp-, branch- and colony-level traits from three replicate colonies of each of 21 Caribbean octocoral species. All parameters were measured for each of the colonies and means for the species determined from the pooled samples. A complete list of the species and the sources of the specimens are presented in figure 3. Many of the specimens were collected in the field with colony-level traits determined from digital images of the *in situ* colonies. Some specimens were obtained from the US National Museum (NMNH, Smithsonian Institution, Washington, DC), in which case colony-level traits were measured directly from the specimen.

Polyp aperture (*P*) (figure 1a) was measured between the external edges of the longest portion of the calyx wall. Distance to the nearest polyp (*D*) was measured between the external walls of calices if present or the polyp aperture. The nearest module was chosen in the ascending branch direction. Owing to the three-dimensionality of the branch surface, measurements were taken with a caliper that was positioned using a dissecting microscope. For the polyp aperture and nearest module distance 10 measurements per colony were recorded (30 per species). Branch thickness (*T*; figure 1) was measured with vernier calipers 3 cm below the branch tip from three haphazardly chosen different branches per colony (nine measurements per species). Macroscopic branch and colony-scale parameters were obtained directly from the collected specimens, the museum specimens or from *in situ* digital images of the same colonies used above. Whole adult colonies were photographed *in situ* or from the museum specimens delineated above. Daughter branch length (*B*) and internode distance (*I*; figure 1b) were measured from the digital images. The number of branch length and internode distance measurements per colony varied from 5 to 15 depending on the specimens (some specimens did not have more than five daughter branches or internodes).

Resolved phylogenetic relationships and species phylogenetic distances for the comparative analyses were reconstructed from coding mitochondrial DNA (mtDNA) sequences (Sánchez *et al.* 2003b; see also figure 3 and electronic Appendix A, available on The Royal Society's Publications Web site). For continuous quantitative traits, the method of independent contrasts (Felsenstein 1985, 1988), using species means, was applied to each parameter using the Contrast routine in PHYLIP v. 3.6 (Felsenstein 1989). This program standardizes all contrasts by the square roots of tree branch lengths, using the phylogenetic distance among species to also assess phylogenetic independence (e.g. Harvey & Pagel 1991). Using contrasts, third-order partial correlation coefficients (PCCs) were determined among the variables studied (SPSS 10.1). A single third-order PCC was estimated for each set of two variables controlling for the remaining three variables. Patterns of morphological integration

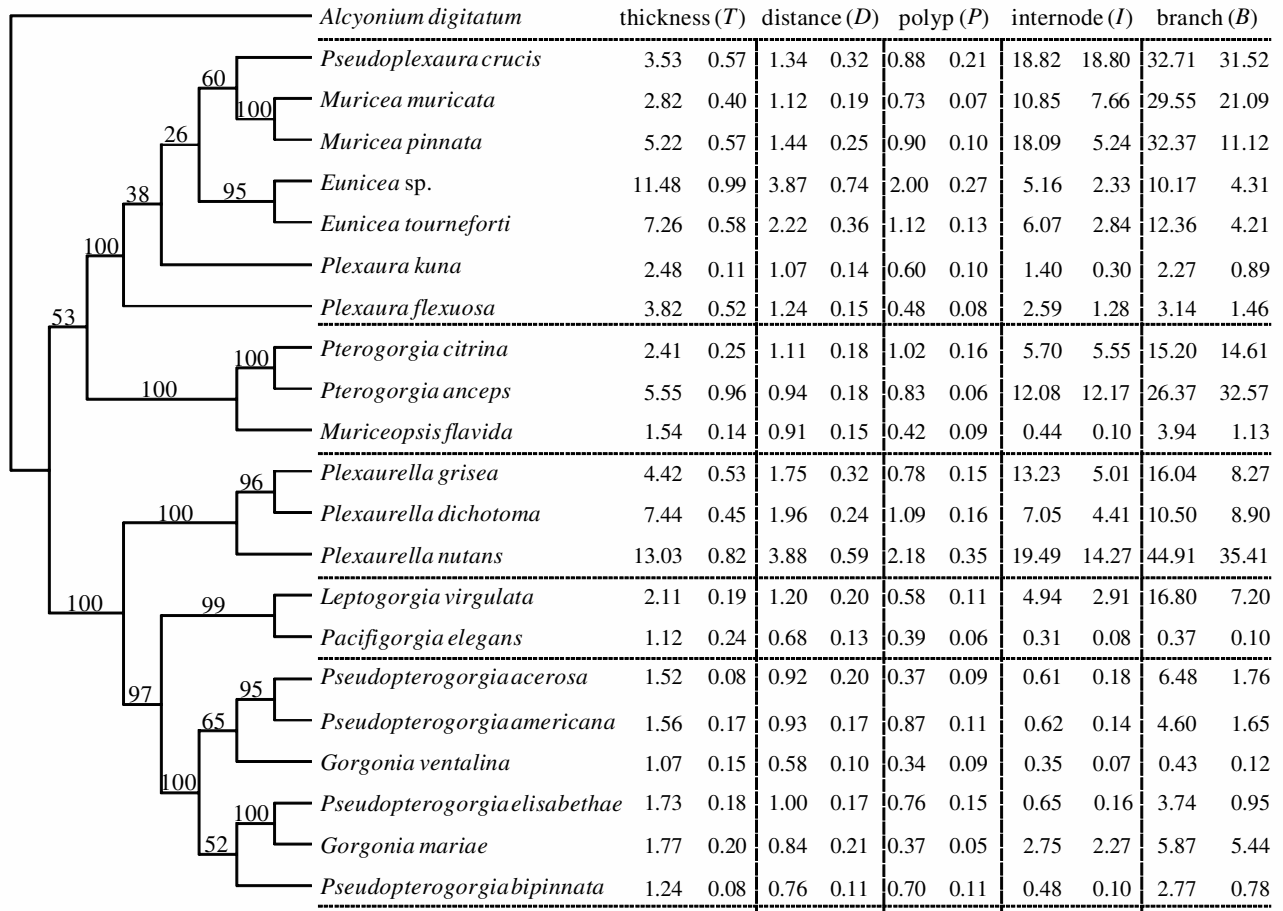


Figure 3. Bootstrap majority-rule consensus tree (1000 replicates) (one most parsimony tree, length of 514; CI of 0.79; RI of 0.88; outgroup: *Alcyonium digitatum*). Analyses following the methods and alignments from Sánchez *et al.* (2003b). There were no significant differences in topology and genetic distances when using maximum likelihood. At the right of the tree, mean and standard deviation values for the five morphological traits measured are presented. Most species collected at Lee Stocking island, Bahamas (2000). *Gorgonia mariae* (Cabo Lobo, Puerto Rico 1999), *Pacifigorgia elegans* (museum specimens NMNH, Smithsonian Institution, Washington, DC; from Trinidad: USNM 55684; and Suriname: USNM 50953), *Leptogorgia virgulata* (Florida: USNM 49690) and *Eunicea* sp. (Akumal, Mexico, 2002) were obtained from other locations (see details in Sánchez *et al.* 2003b).

were examined as proposed by Magwene (2001). PCCs were compared statistically for edge exclusion deviance and edge strength to determine which of the edges could be removed from the saturated graphical hypothesis (figure 2a). Edge strength was used to magnify the differences between strong and weak correlations. Two resampling strategies were applied to examine the robustness of the results, relative to the effects of particular species or contrasts in the PCC outcome (see details in electronic Appendices D–E).

3. RESULTS

Figure 3 presents the raw means and standard deviations without correcting for phylogenetic effects from the five morphological traits measured. Electronic Appendix B contains the phylogenetic independent contrasts from the five morphological traits. Multivariate correlation and normality was evident with the significant zero-order bivariate correlations among all the variables, which showed a great deal of colinearity (table 1). After controlling each bivariate case by the remaining variables, i.e. third-order PCCs, only a few associations remained that were both strong and significant (table 1). The association

between internode (*I*) and branch (*B*) was only reduced from 0.918 to 0.873 when controlling for association with other variables. Strong associations prevailed between thickness (*T*) and inter-polyp distance (*D*), and the latter with polyp aperture (*P*) also remained. Conditional independence was evident between *T* and *P* given *D* (complex: $\{T \perp P | D\}$) but no partial association occurred between these integrated groups of traits, $\{I, B\}$ and $\{T \perp P | D\}$. PCC results were corroborated by edge exclusion deviance and strength analyses, which led to the exclusion of six edges from the saturated model proposed in figure 2a (electronic Appendix C).

The results from graphical modelling are summarized in figure 2c, where two apparent morphological modules (*sensu lato*) or complexes are shown (e.g. $\{I, B\}$ and $\{T \perp P | D\}$). It is worth noting that the strongest association occurred between *I* and *B*, which are products of branching and thus emergent colonial characters. The PCCs from the three edges depicting morphological integration were not greatly affected when recalculated using resampled species and/or contrasts, suggesting that the results are not attributable to the effects of a few species and/or contrasts (electronic Appendices D–E).

Table 1. Third-order partial correlation coefficients (PCCs) for the five supra-modular variables among contrasts (below the diagonal).

(Bivariate (zero-order) correlation coefficients (above the diagonal). *T*, thickness; *D*, inter-polyp distance; *P*, polyp aperture; *I*, internode length; *B*, daughter branch length.)

	<i>T</i>	<i>D</i>	<i>P</i>	<i>I</i>	<i>B</i>
<i>T</i>	1	0.963***	0.921****	0.565**	0.585**
<i>D</i>	0.756***	1	0.951***	0.463*	0.505*
<i>P</i>	-0.0152	0.626**	1	0.493*	0.572**
<i>I</i>	0.2767	-0.257	-0.257	1	0.918***
<i>B</i>	-0.411	-0.1614	0.388	0.873***	1

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

4. DISCUSSION

Colonies can be described based on characters of individual polyps, individual branches and the whole colony. However, among these 21 Caribbean octocorals some of these characters were interdependent. Using graphical modelling and phylogenetic independent contrasts among five morphological characters from 21 species of Caribbean octocorals, we found support for morphological integration among polyp-level traits and among colony-level traits. There was conditional independence after PCC analyses between branch thickness (*T*) and polyp aperture (*P*) given inter-polyp distance (*D*) $\{T \perp P | D\}$ but no association was found between the sets $\{I, B\}$ and $\{T \perp P | D\}$, suggesting the presence of at least two modular levels for morphological integrations in octocorals. Although all characters exhibited a certain level of association, the multivariate analyses showed the strongest interaction between colony-level characters. This suggests that whole-colony characters (internode and branch lengths) are a product of the emergent process of branching and may act as an integrated system or as a supra-polyp module.

Morphological integration, or the coevolution of subgroups of characters within the phenotype, appears to be a common feature of species exhibiting branching tree-like networks. In woody plants, for instance, interspecific comparisons of multiple traits such as twig, leaf, seed and branches have shown correlated evolution using phylogenetic independent contrasts (Ackerly & Donoghue 1998). Intraspecific plasticity in plants also exhibits a great deal of morphological integration (e.g. Waitt & Levin 1993; Pigliucci & Marlow 2001). Morphological integration in animals has been explained as a result of functional interactions during development (Zelditch 1988) and ecological adaptations (e.g. Marroig & Cheverud 2001), both of which generate a phenotype that evolves as an integrated entity (e.g. Gould 1977). In considering colonial bryozoans, McKinney & Raup (1982) suggested that colonial traits are integrated so that their interaction can generate different arrays of colony forms in a morphospace. Patterns of variation across species are always subject to spurious correlation based not on the ecological or ontogenetic controls on development, but rather from the common ancestry of some taxa. The results presented here identified integration within microscopic branch-polyp and macroscopic colonial traits by using the comparative method among species that were independent of phylogenetic effects.

Modular systems such as octocorals are seemingly simple systems in which the effects of pleiotropic genes that control module form are expected to have an effect on the whole colony. Nonetheless, polyp/branch- and colony-level traits were not associated after controlling for the effects of all characters (PCCs). The presence of two modular units (*sensu lato*) or trait complexes of morphological integration were evident: a branching complex $\{I, B\}$ and a polyp/branch complex $\{T \perp P | D\}$. This indicates that the proximate processes responsible for polyp size and arrangement do not account directly for the colony/branching scale traits of branch or internode size. This suggests the presence of different levels of integration (*sensu* Magwene 2001) that, although nested, owing to the modular nature of octocorals, could respond independently to environmental challenges (e.g. Pigliucci 2002). Similarly, evolutionary changes in the branching and polyp/branch complexes need not affect each other.

The philosopher Husserl referred to the parts of an object as distinguishable pieces that are relatively independent but always a part of something else (McCarthy 1992). Likewise, colonial traits such as daughter branches and internode distances, although made of polyps (or modules, *sensu stricto*), exhibited another category of phenotypic modularity (*sensu lato*). This emergent level of integration is produced by the branching process itself and is not a necessary outcome of the module replication process. Given the presence of these rather independent levels of integration among Caribbean octocorals, the question arises whether variation in these traits, either within or across species, can be related to environmental variation operating through either selection or phenotypic plasticity. At the intraspecific level, the different levels of modularity found here among species have also been noted in branching modular invertebrates (see Lasker & Sánchez 2002), and variation in growth of branches in the gorgonian octocoral *Pseudopterogorgia elisabethae* can be partitioned into effects of both the branch, as a module, and the colony (Lasker *et al.* 2003). In addition, observations of a population of *P. bipinnata* across different depths and wave exposures showed how both branch and internode lengths change and correlate whereas polyp aperture, inter-polyp distance and thickness did not have a significant change (J. A. Sánchez, in preparation), which supports the ideas suggested here. In some individual organisms, correlations between traits seem to respond differently depending on whether they are interspecific or intraspecific (e.g. Green *et al.* 2001). In modular colonial organisms, however, it is

possible that correlation among traits respond in the same manner despite the level of comparison.

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