

1 **Evolution and dynamics of branching colonial form in marine modular**
2 **cnidarians: gorgonian octocorals**

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9 **Abstract**

10 Multi-branched arborescent networks are common patterns for many sessile marine modular organisms
11 but no clear understanding of their development is yet available. This paper reviews new findings in the
12 theoretical and comparative biology of branching modular organisms (e.g. Octocorallia: Cnidaria) and new
13 hypotheses on the evolution of form are discussed. A particular characteristic of branching Caribbean
14 gorgonian octocorals is a morphologic integration at two levels of colonial organization based on whether
15 the traits are at the module or colony level. This revealed an emergent level of integration and modularity
16 produced by the branching process itself and not entirely by the module replication. In essence, not just a
17 few changes at the module level could generate changes in colony architecture, suggesting uncoupled
18 developmental patterning for the polyp and branch level traits. Therefore, the evolution of colony form in
19 octocorals seems to be related to the changes affecting the process of branching. Branching in these
20 organisms is sub-apical, coming from mother branches, and the highly self-organized form is the product of
21 a dynamic process maintaining a constant ratio between mother and daughter branches. Colony growth
22 preserves shape but is a logistic growth-like event due to branch interference and/or allometry. The
23 qualitative branching patterns in octocorals (e.g. sea feathers, fans, sausages, and candelabra) occurred
24 multiple times when compared with recent molecular phylogenies, suggesting independence of common
25 ancestry to achieve these forms. A number of species with different colony forms, particularly alternate
26 species (e.g. sea candelabrum), shared the same value for an important branching parameter (the ratio of
27 mother to total branches). According to the way gorgonians branch and achieve form, it is hypothesized
28 that the diversity of alternate species sharing the same narrow variance in that critical parameter for growth
29 might be the product of canalization (or a developmental constraint), where uniform change in growth rates
30 and maximum colony size might explain colony differences among species. If the parameter preserving
31 shape in the colonies is fixed but colonies differ in their growth rates and maximum sizes, heterochrony
could be responsible for the evolution among some gorgonian corals with alternate branching.

34 **Introduction**

35 Branching patterns, or tree-like forms, are every-
36 where in nature: river basins, organ vessels, trees,
37 fungi, algae, hydroids, and corals, just to mention
38 some. Most organisms on earth contain branching
39 networks. Still, regardless of the recurrence of this
40 pattern in multiple species and levels of organiza-

tion, we do not clearly know how this pattern 41
forms or evolves (see reviews in Buss, 2001; Lasker 42
& Sánchez, 2002; Rinkevich, 2002). This is of great 43
significance for the understanding of marine sessile 44
modular organisms such as algae, sponges, hy- 45
droids, bryozoans, and corals because growth and 46

47 form are their main means of interaction with the
 48 environment (e.g. Jackson, 1977; Hughes, 1983).
 49 Although modular organisms seem physiologically
 50 simple and repetitive, development and branching
 51 in these systems is evidently complex and dynamic
 52 (e.g. Kaandorp & Kübler, 2001).

53 The greatest difficulty in understanding the
 54 growth and form of colonial organisms is the ab-
 55 sence of an obvious causal mechanism producing
 56 form, which overall is a general problem in evo-
 57 lutionary developmental biology. In-depth devel-
 58 opmental studies have unavoidably revealed
 59 mechanisms concerning cell division, migration,
 60 and differentiation. Certainly, many genes play an
 61 important role in pattern differentiation, and for
 62 individual organisms (or individual modules).
 63 Homeobox genes, for example, play an important
 64 role in pattern formation and cell fate during
 65 development (see reviews in Popadic et al., 1998;
 66 Purugganan, 1999). It is important to note that
 67 these genes can act only after several other genes
 68 and maternal factors are expressed. Therefore, the
 69 process is complex enough to not be controlled by
 70 single molecules. Nonetheless, both individual and
 71 colonial forms of cnidarians exhibit most Hox/
 72 Parahox gene families present in higher metazoans
 73 (e.g. Finnerty & Martindale, 1997; Kuhn et al.,
 74 1999). These genes have been used as 'bottom-up'
 75 exemplars to understand the development of the
 76 individual polyps as well as during the polyp-me-
 77 dusa metamorphosis in hydroids (e.g. Aerne et al.,
 78 1996; Cartwright et al., 1999) and are promising
 79 for understanding the expansion of connecting
 80 colonial networks (e.g. Cartwright & Buss, 1999).
 81 Nonetheless, branching patterns seem to be an
 82 emergent property of modular replication in colo-
 83 nial organisms, which is not entirely understood.
 84 This paper reviews and summarizes recent results in
 85 the theoretical and comparative biology of modular
 86 organisms, which are 'top-down' approaches to
 87 understanding the problem of patterning and
 88 development of modular colonial organisms.

89 **Modular and colonial traits in octocorals**

90 Colonial organization in gorgonian octocorals
 91 presents high complexity at several levels. Octo-
 92 coral polyps (modules) always have eight pinnate
 93 tentacles, and they are monomorphic, each capa-

ble of all physiological functions, i.e. reproduction, 94
 feeding, excretion, defense, etc. (e.g. solitary oc- 95
 tocorals: Bayer & Muzik, 1976). The polyps are 96
 immersed in coenenchyme, a mesoglear layer mix 97
 of calcareous sclerites and the non-cellular portion 98
 of the middle layer. The distribution of polyps on 99
 the branches varies between species, ranging from 100
 bilateral series of polyps along the edges of com- 101
 pressed branches to a random or uniform distri- 102
 bution over a cylindrical branch. Nonetheless, the 103
 highest complexity is observed in the process of 104
 branching; over 20 qualitative branching patterns 105
 have been identified by taxonomists (Bayer et al., 106
 1983). The polyps are connected to each other by a 107
 network of stem canals (Bayer, 1973). The connec- 108
 tions among polyps continue along the branch 109
 axis and form a branching tree-like structure 110
 (Sánchez & Lasker, in press). 111

112 In the study of form evolution, it is important
 113 to know if characters producing the form are
 114 independent of each other or evolve as integrated
 115 sets. In modular colonial organisms, which form
 116 by the repetition of identical units, the emergent
 117 forms are usually multi-branched complex net-
 118 works. To examine the patterns of integration
 119 among morphologic traits in Caribbean octoco-
 120 rals, Sánchez & Lasker (2003) compared five
 121 morphologic traits across 21 species, correcting for
 122 the effects of phylogenetic relationships using
 123 molecular phylogenies (Sánchez et al., 2003b).
 124 Although all characters exhibit associations with
 125 each other, a multivariate analysis, correcting for
 126 conditional independence (e.g. partial correlation
 127 coefficients), showed the strongest integration
 128 among the colony level (network) characters. This
 129 is a quantitative and comparative demonstration
 130 that branching characters within colonial organ-
 131 isms are independent of characters of the modules,
 132 which has also been observed in experimental
 133 studies of hydroid colony growth (e.g. Müller
 134 et al., 1987; Kossevitch et al., 2001).

135 Other marine branching invertebrates such as
 136 colonial bryozoans present such integration be-
 137 tween the different branching angles that their
 138 correlation generates a morphospace of realistic
 139 colonies (McKinney & Raup, 1982). In trees,
 140 interspecific comparisons among multiple traits
 141 such as twig, leaf, seed, and branches have exhib-
 142 ited correlated evolution (Ackerly & Donoghue,
 143 1998). Plasticity in plant populations also shows

144 morphologic integration (e.g. Waite & Levin, 1993;
 145 Pigliucci & Marlow, 2001). The co-evolution of
 146 modules of characters within the structure appears
 147 to be a common feature of species exhibiting
 148 multi-branched tree-like networks.

149 Colonial growth in gorgonian octocorals: branching

150 The usage of ordering schemes, assuming growth
 151 of the network through bifurcation, does not
 152 realistically explain the branching and/or growth
 153 of modular marine organisms such as Caribbean
 154 octocorals (Sánchez et al., 2003c). Branching in
 155 gorgonian octocorals is a subapical process where
 156 all the branches are structurally the same but some
 157 branches, 'mother branches', produce new branches,
 158 'daughter branches', at roughly fixed distances or
 159 internodes (Fig. 1). Branching does not
 160 follow a bifurcation-based process but a dynamic
 161 production of daughter branches from established
 162 mother branches. According to Sánchez (2002)
 163 and Sánchez et al. (2004), branching starts at a
 164 constant rate, r (daughter branches year⁻¹), at the
 165 first primordial mother branch. As the colony
 166 grows, a few daughter branches turn into mother

branches (Fig. 1) and start branching at a rate that
 maintains a fixed ratio between the total number
 of branches and the number of mother branches, c .
 This parameter is critical for the process of
 branching since octocoral colonies grow in a self-
 organized dynamic process maintaining as constant
 as possible the ratio of mother to daughter
 branches. Colony growth proceeds in this manner,
 but slows asymptotically as the colony reaches a
 maximum number of mother branches, k , which
 seems to be related to branch interference and
 allometry (Sánchez et al., in press). Branching can
 be modeled with the simple parameters r , c , and k
 with this recurrence expression (1):

$$S_{t+1} = S_t + \frac{S_t r}{c} \left(1 - \frac{S_t}{k}\right) \quad (1)$$

where S is the number of mother branches. This
 expression predicts sigmoid- or logistic-like accu-
 mulation of branches through time, which meets
 the predictions from empirical observations from
 multiple growth studies found in the hydroid and
 octocoral literature (e.g. Kauffmann, 1981; Steb-
 bing, 1981; Coma et al., 1998). This approach to
 branching explains how modular colonial organ-
 isms preserve form during development, indepen-

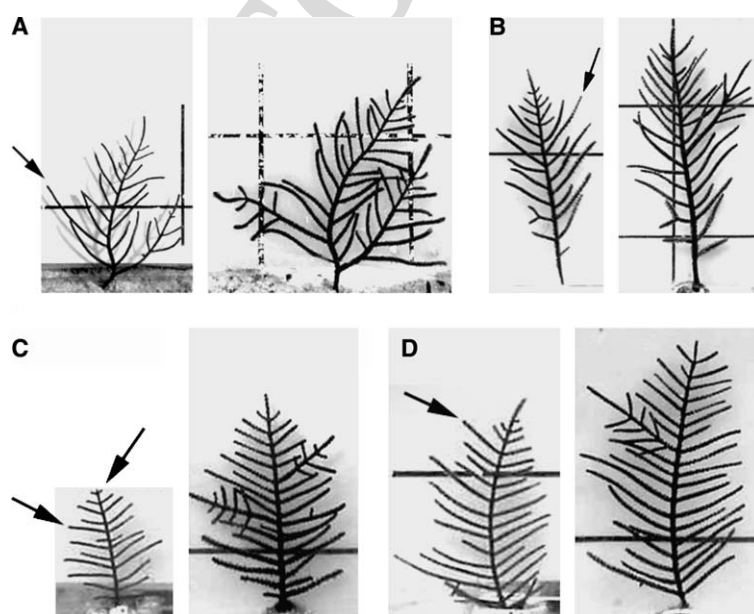


Figure 1. Sequential images (Dec-1999 and Dec-2000) of several Caribbean gorgonian octocorals (Riding rock reef, 15 m, San Salvador, Bahamas). (A) *Pseudopterogorgia americana*. (B) *P. elisabethae*. (C) *P. bipinnata*. Arrows show the daughter branches that developed into mother branches after a 6 month period.



191 dently of the maximum size allowed by ecological/
 192 physiological constraints. This understanding of
 193 branching suggests a new perspective on the
 194 functional and evolutionary biology of these
 195 colonial organisms.

196 Evolution of branching in gorgonian octocorals

197 The recent molecular phylogenies of octocorals
 198 show how branching could evolve independently
 199 multiple times from non-branching hypothetical
 200 ancestors. Analyses of ribosomal DNA sequences,
 201 from either mitochondrial *lsu-rRNA* (16S) or nu-
 202 clear *ssu-rRNA* (18S), have revealed similar phy-
 203 logenetic relationships supporting two main
 204 groups of branching gorgonian corals: suborders
 205 *Calcaxonia* and *Alcyoniina-Holaxonia* (Sánchez
 206 et al., 2003a). This molecular evidence corrobo-
 207 rated results uncovering the evolution of two
 208 independent and convergent groups of branching
 209 octocorals, which have analogous rigid axial
 210 structures. These octocoral clades were also found
 211 in both France et al. (1996) and Berntson et al.
 212 (2001) with low statistical support. In addition, the
 213 two clades have qualitative differences in their
 214 predicted RNA secondary structures (Sánchez
 215 et al., 2003a). Likewise, comparing major mor-
 216 phological characters revealed that morphological
 217 complexity in both axial structures and sclerites
 218 developed in parallel in both *Calcaxonia* and *Al-*
 219 *cyoniina-Holaxonia* clades. Convergence of
 220 branching patterns among octocorals has also
 221 been observed in closely related species.

222 Modular colonies of Caribbean gorgonian cor-
 223 als are organized into unconventional branching
 224 networks (e.g. Fig. 1). There are three basic
 225 branching patterns among gorgonians: sea fans
 226 (reticulate), sea feathers (pinnate), and alternate
 227 (sea candelabra/sausages). These branching pat-
 228 terns occurred multiple times in a gorgonian
 229 molecular phylogeny (NADH dehydrogenase
 230 subunits 2 and 6 [*ND2*, *ND6*] and *mutS* homolog
 231 [*msh1*]; Sánchez et al., 2003b), suggesting that these
 232 forms can arise independently of common ancestry
 233 (Fig. 2A). Reticulate species could have both pin-
 234 nate and reticulate relatives, whereas pinnate forms
 235 only alternate ancestors (Fig. 2A). Changes in
 236 colonial form among modular organisms can re-
 237 flect genetic differences, the product of plastic

developmental responses to particular environ- 238
 ments, and there is the possibility of genotype-by- 239
 environment interactions as well. All paths can lead 240
 to the association of particular branching strategies 241
 with specific environments. Similarly, forms such 242
 as the reticulate fans found across octocoral genera 243
 are the result of convergent evolution. Bayer (1953) 244
 first proposed convergent evolution for gorgonian 245
 colony architectures such as sea fans (*Pacifigorgia* 246
spp. and *Gorgonia spp.*) and sea leaves (*Phycogor-* 247
gia spp. and *Phyllogorgia spp.*). Bayer's hypothesis 248
 is corroborated by a gorgonian molecular phylog- 249
 eny (Sánchez et al., 2003b). The differences within 250
 each particular branching pattern, on the other 251
 hand, can be explained as differences in the 252
 branching dynamics. 253

254 The ratio between total and mother branches or 254
c, an indicator of branching form and critical value 255
 for branching, presents an interesting correspon- 256
 dence according to the branching pattern. Carib- 257
 bean gorgonian corals with alternate or reticulate 258
 branching exhibited low values of *c* ranging from 2 259
 to 5 (Fig. 2C). The six species with pinnate 260
 branching all had *c* values higher than 13. Mapping 261
 these two characters on the phylogenetic hypothe- 262
 sis, it was clear that pinnate branching is associated 263
 with high *c* values (Fig. 2A). This association ap- 264
 pears to be independent of phylogeny since *Mu-* 265
riceopsis flavida and *Pseudopterogorgia spp.* both 266
 arose from different, presumably alternate, ances- 267
 tors. A number of reticulate sea fan species could 268
 have pinnate ancestor. The one exception to the 269
 pattern was the reticulate sea fans *Pacifigorgia ele-* 270
gans and *P. stenobrochis*. *Pacifigorgia spp.* had a 271
 sister relationship (*Leptogorgia virgulata*) with 272
 alternate branches, and traces of alternate branch- 273
 ing are still visible in *Pacifigorgia spp.* branching 274
 patterns (Fig. 2A). *Gorgonia spp.* comprise analo- 275
 gous reticulate sea fans with both clear pinnate 276
 branching and pinnate ancestors, which is evident in 277
 their sister relationship with some pinnate gorgo- 278
 nians (*Pseudopterogorgia spp.*) and traces of pinnate 279
 branching in their networks (Fig. 2A and B). 280

281 Pinnate gorgonians were associated with 281
 changes in the branching parameter *c*, (the ratio of 282
 total branch to mother branch). Therefore, the 283
 change from alternate to pinnate could involve a 284
 duplication in the set point of branching that 285
 changed completely the branching function and 286
 growth/form relationship. Forms with alternate 287
 288

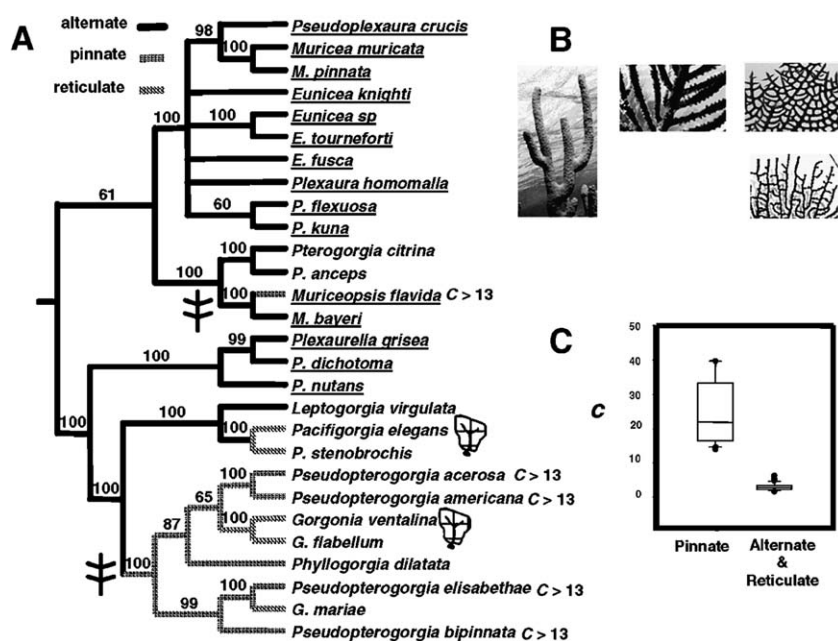


Figure 2. (A) Bayesian-estimated Likelihood tree (HKY) using nucleotide partition by positions (NADH-dehydrogenase subunits 2 and 6, and mutS homolog [msh1], 1633 bp); above node support is the 50%-majority rule consensus from 10,001 sampled trees generated by PAUP* (see details in Sánchez et al., 2003b). Branches are showing a parsimonious distribution of the character type of branching. The pinnate or fan sketches indicate the multiple origins of sea feathers and fans respectively. Underlined species names correspond to nominal plexaurid octocorals, otherwise they are Gorgoniidae. (B) Hypothetical trajectories among different branching types accordingly. Left, *Plexaura flexuosa*-alternate; middle, *Pseudopterogorgia americana*-pinnate; upper right, *Gorgonia ventalina*-reticulate-pinnate; lower right, *Pacifigorgia elegans*-reticulate-alternate. (C) Box plots from the distribution and variance of c values among the 24 studied species. The median line is inside the 25th and 75th percentiles with external error bars at the 10th and 90th percentiles.

288 branching always exhibited low values and vari-
 289 ances in c , whereas pinnate forms had high values
 290 of c (Fig. 2B). C is an indicator of the form or the
 291 relationship between form and growth. If different
 292 colonies have the same c values, the topological
 293 relationships among branches will be nearly iden-
 294 tical, differing only in the branching (=growth)
 295 rate and the maximum colony and module sizes.
 296 This seems to occur among gorgonians with
 297 alternate branching. Among these species some
 298 colony forms are augmented versions of a small
 299 segment of a few branches of small highly bran-
 300 ched species (e.g. Fig. 3). The notable conservation
 301 in this trait suggests some canalization (see review
 302 in Debat & David, 2001) in many species by
 303 maintaining the same developmental outcome de-
 304 spite the change in the traits involved. Alterna-
 305 tively, the presence of physical developmental
 306 constraints (see review in Resnik, 1995) acting on
 307 branching properties could keep certain param-
 308 eters constant across species. In contrast, pinnate

branching species exhibit a wide range of c values,
 suggesting an absence of constraining and cana-
 lizing factors from one end or just a difference in
 relative variability because they have more bran-
 ches (e.g. Lewontin, 1966). Due to the low number
 of sea fans included, it was not possible to see if
 there is a link between fixed c values across species
 and the reticulate form.

Differences in colony size and the similarities
 among alternate species could be the product of
 heterochrony. As in individual organisms (e.g.
 Gould, 1977; McNamara, 1995), the timing and
 rate of colony development in marine invertebrates
 can be studied in the context of heterochrony
 (Pandolfi, 1988). Alteration of the timing of dif-
 ferent aspects of colony development may result in
 adult organisms that are similar to juveniles of
 other species or vice versa (McKinney, 1988). In
 addition, the germ line may mature early or late
 during development as another outcome of evo-
 lution through heterochrony. Changes in colony



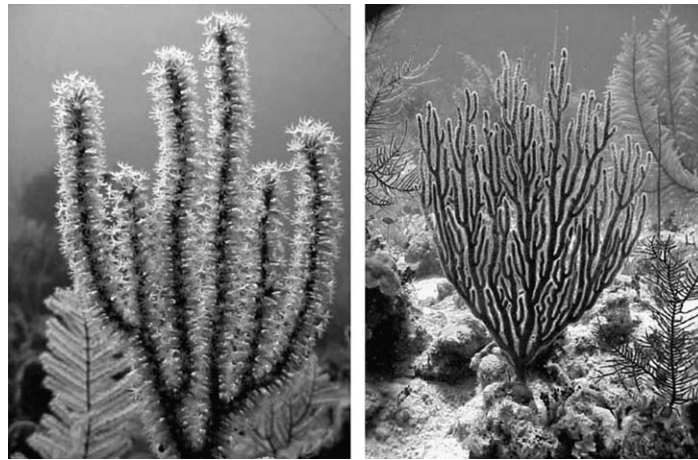


Figure 3. Adult colonies of alternate branched sea candelabrum octocorals from the Caribbean Sea. Left, colony of *Eunicea laxispica*, 30 cm height, Carrie Bow Cay, Belize; Right, colony of *Plexaura flexuosa*, 120 cm height, San Salvador, Bahamas.

330 architecture have been experimentally induced by
 331 accelerating and decelerating growth rates of col-
 332 onies from the same species (Blackstone & Buss,
 333 1993; Blackstone, 1999, 2000). Those experimental
 334 findings demonstrate that uniform change in the
 335 rate of colony development generates different
 336 colony forms though heterochrony. However, be-
 337 fore we can suggest that heterochrony has driven
 338 the process leading to the evolution of colony form
 339 among alternate gorgonians, we must demonstrate
 340 that the developmental trajectories follow the same
 341 growth function (Rice, 1997). Interestingly,
 342 growth of gorgonian corals with similar values of c
 343 (e.g. $c \sim 2.9$) would branch in a simpler manner (2):

$$S_{t+1} = S_t + \frac{S_t r}{2.9} \left(1 - \frac{S_t}{k}\right) \quad (2)$$

345 Different branching species that had similar values
 346 of c would, therefore, vary as a function of their
 347 growth rates or maximum sizes, which are exam-
 348 ples of heterochrony. Additionally, maximum size
 349 as well as the size of first reproduction in gorgo-
 350 nian corals seems to be very predictable and spe-
 351 cies-specific (e.g. Kalpela & Lasker, 1999).
 352 Variation in these traits could provide additional
 353 sources of heterochrony (e.g. progenesis). For in-
 354 stance, Figure 4 shows a hypothetical heterochrony
 355 example for the species of Figure 3, which
 356 both have an empirical value of $c = 2.9$, assuming
 357 equal branching rates, r , for the two species but
 358 different k values. The latter values seem to be
 359 affected and correlated to other parameters from

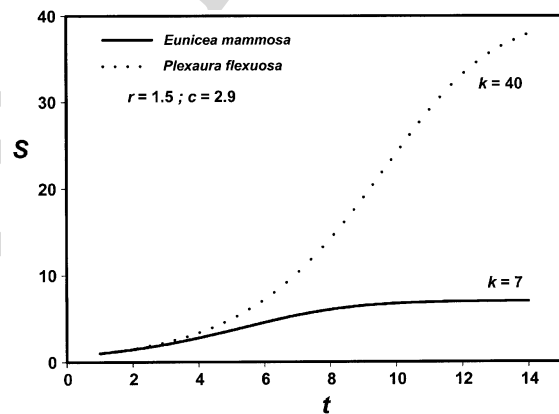


Figure 4. Results from the iteration (14 times) of the model (2) using different values of k corresponding to the species from Figure 3.

the modular construction of the colony (e.g. 360
 branch/polyp/internode size, axial material resis- 361
 tance, etc.), which are different between the two 362
 species. Further study on the maximum and 363
 reproductive colony/module sizes as well as on 364
 branching rates could provide an assessment on 365
 the occurrence of heterochrony for the evolution 366
 of colony form in modular organisms. 367

Branching in modular organisms: what is particular? 368

A feature that is characteristic of modular colonial 369
 organisms is the presence of supra-modular levels 370
 of organization creating new modular structures. 371



372 This emergent level of integration is produced by
 373 the branching process itself and is not a necessary
 374 outcome of the module replication process (Sánchez & Lasker, 2003b). The occurrence of these
 375 mostly independent levels of integration in
 376 branching Caribbean octocorals presents the
 377 question if variation in these traits, either within or
 378 among species, can be related to environmental
 379 variation operating *via* selection and/or morpho-
 380 logic plasticity. The different levels of modularity
 381 found across species have also been noted at the
 382 intraspecific level (Lasker & Sánchez, 2002). There
 383 is a partitioning in the levels of growth organiza-
 384 tion, in individual branches, and in the colony as a
 385 whole (Lasker et al., 2003). Therefore, not just a
 386 few changes at the module level could generate
 387 changes in colony architecture, suggesting an
 388 uncoupled developmental patterning for the polyp
 389 and branch level traits.

391 Colony growth and form in gorgonian oc-
 392 tocorals can be predicted by the dynamic interac-
 393 tion of a few parameters. The changes in these
 394 parameters show correspondence with changes in
 395 the branching pattern and colony form. The dy-
 396 namic interaction of some of the parameters sug-
 397 gests a great deal of heterochrony, explaining the
 398 evolution of forms that maintain the same
 399 branching hierarchy (e.g. ratio of mother to total
 400 branches). These parameters can be considered as
 401 intrinsic characterizations of the processes that
 402 control branching, and this intrinsic aspect of
 403 branching can be regarded as genetic in nature
 404 (Rinkevich, 2002). Nonetheless, extrinsic effects
 405 also have an important effect on colony form but
 406 should be constant for a given colony as part of its
 407 surrounding environment.

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