

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

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8 *Key words:* colonial organisms, heterochrony, Cnidaria

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. Waitt & 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-

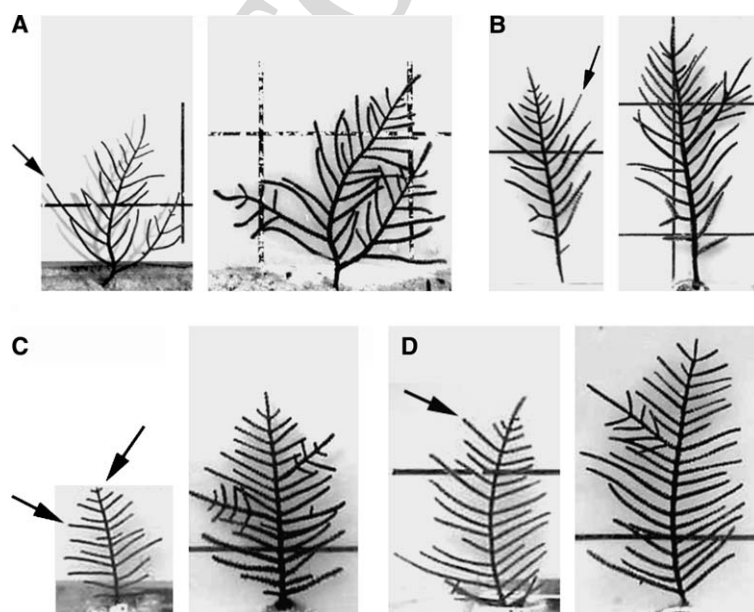


Figure 1. Sequential images (Dec-1999 and Dec-2000) of several Caribbean gorgonian octocorals (Riding rock reef, 15 m, San Salvador, Bahamas). (A) *Pseudopterogorgia americana*. (B) *P. elisabethae*. (C) *P. bipinnata*. Arrows show the daughter branches that developed into mother branches after a 6 month 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 corals
 223 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

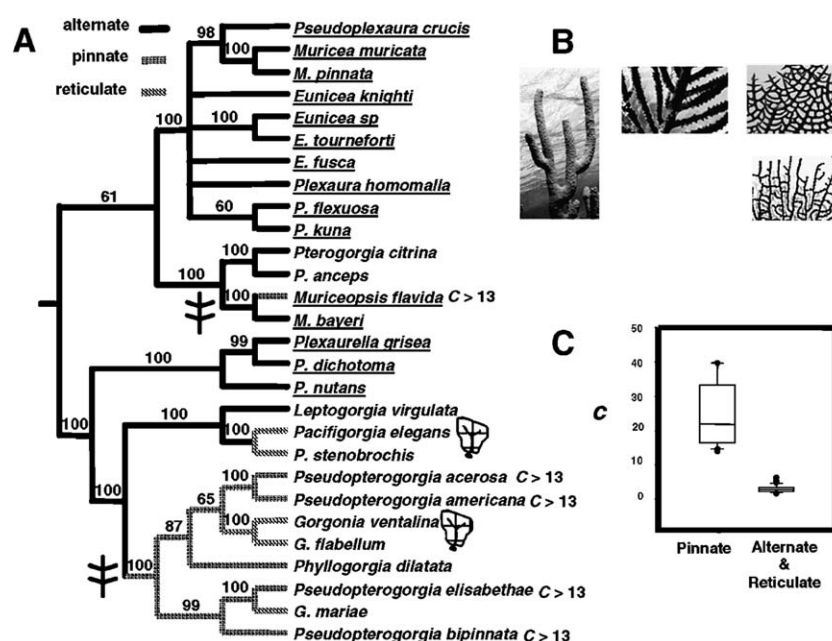


Figure 2. (A) Bayesian-estimated Likelihood tree (HKY) using nucleotide partition by positions (NADH-dehydrogenase subunits 2 and 6, and mutS homolog [msh1], 1633 bp); above node support is the 50%-majority rule consensus from 10,001 sampled trees generated by PAUP* (see details in Sánchez et al., 2003b). 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- 309
 289 ances in c , whereas pinnate forms had high values 310
 290 of c (Fig. 2B). C is an indicator of the form or the 311
 291 relationship between form and growth. If different 312
 292 colonies have the same c values, the topological 313
 293 relationships among branches will be nearly iden- 314
 294 tical, differing only in the branching (=growth) 315
 295 rate and the maximum colony and module sizes. 316
 296 This seems to occur among gorgonians with 317
 297 alternate branching. Among these species some 318
 298 colony forms are augmented versions of a small 319
 299 segment of a few branches of small highly bran- 320
 300 ched species (e.g. Fig. 3). The notable conservation 321
 301 in this trait suggests some canalization (see review 322
 302 in Debat & David, 2001) in many species by 323
 303 maintaining the same developmental outcome de- 324
 304 spite the change in the traits involved. Alterna- 325
 305 tively, the presence of physical developmental 326
 306 constraints (see review in Resnik, 1995) acting on 327
 307 branching properties could keep certain param- 328
 308 eters constant across species. In contrast, pinnate 329

branching species exhibit a wide range of c values, 309
 suggesting an absence of constraining and cana- 310
 lizing factors from one end or just a difference in 311
 relative variability because they have more bran- 312
 ches (e.g. Lewontin, 1966). Due to the low number 313
 of sea fans included, it was not possible to see if 314
 there is a link between fixed c values across species 315
 and the reticulate form. 316

Differences in colony size and the similarities 317
 among alternate species could be the product of 318
 heterochrony. As in individual organisms (e.g. 319
 Gould, 1977; McNamara, 1995), the timing and 320
 rate of colony development in marine invertebrates 321
 can be studied in the context of heterochrony 322
 (Pandolfi, 1988). Alteration of the timing of dif- 323
 ferent aspects of colony development may result in 324
 adult organisms that are similar to juveniles of 325
 other species or vice versa (McKinney, 1988). In 326
 addition, the germ line may mature early or late 327
 during development as another outcome of evo- 328
 lution through heterochrony. Changes in colony 329



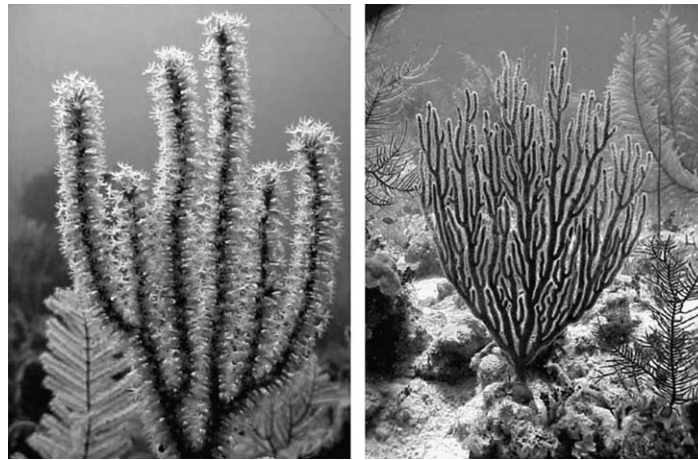


Figure 3. Adult colonies of alternate branched sea candelabrum octocorals from the Caribbean Sea. Left, colony of *Eunicea laxispica*, 30 cm height, Carrie Bow Cay, Belize; Right, colony of *Plexaura flexuosa*, 120 cm height, San Salvador, Bahamas.

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 hetero-
 355 chrony 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

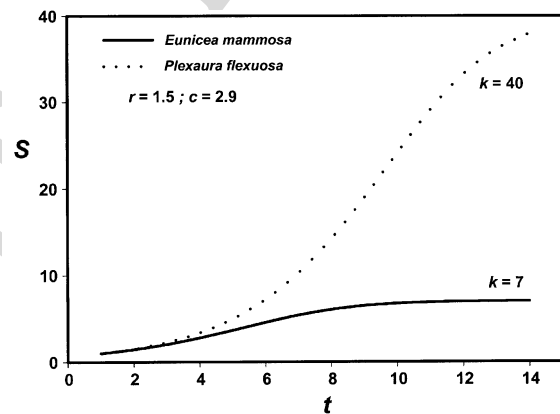


Figure 4. Results from the iteration (14 times) of the model (2) using different values of k corresponding to the species from Figure 3.

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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References 424

- Ackerly, D. D. & M. J. Donoghue, 1998. Leaf size, sapling 425
 allometry, and Corner's rules: phylogeny and correlated evo- 426
 lution in Maples (*Acer*). *American Naturalist* 752: 767–791. 427
 Aerne, B. L., H. Groger, P. Schuchert, J. Spring & V. Schmid, 428
 1996. The polyp and its medusa: a molecular approach. 429
Scientia Marina 60: 7–16. 430
 Bayer, F. M., 1953. Zoogeography and evolution in the octo- 431
 corallian family Gorgoniidae. *Bulletin of Marine Science of* 432
the Gulf and Caribbean 3: 100–119. 433
 Bayer, F. M., 1973. Colonial organization in Octocorals. In 434
 Boardman, R. S., A. H. Cheetham & W.A. Oliver (eds), 435
Animal Colonies, Development and Function through Time. 436
 Dowden, Hutchinson & Ross, Stroudsburg: 69–93. 437
 Bayer, F. M. & K. M. Muzik, 1976. A new solitary octocoral, 438
Taiaroa tauhou gen. et sp. nov. (Coelenterata: Protoalcyo- 439
 naria) from New Zealand. *Journal of the Royal Society of* 440
New Zealand 6: 499–515. 441
 Bayer, F. M., M. Grasshoff & J. Verseveldt, 1983. An Illus- 442
 trated Trilingual Glossary of Morphological and Anatomical 443
 Terms Applied to Octocorallia. E. J. Brill, Leiden, The 444
 Netherlands. 445
 Berntson, E. A., F. M. Bayer, A. G. McArthur & S. C. France, 446
 2001. Phylogenetic relationships within the Octocorallia 447
 (Cnidaria: Anthozoa) based on nuclear 18S rRNA se- 448
 quences. *Marine Biology* 138: 235–246. 449
 Blackstone, N. W., 1999. Redox control in development and 450
 evolution: evidence from colonial hydroids. *Journal of* 451
Experimental Biology 202: 3541–3553. 452
 Blackstone, N. W., 2000. Redox control and the evolution of 453
 multicellularity. *BioEssays* 22: 947–953. 454
 Blackstone, N. W. & L. Buss, 1993. Experimental heterochrony 455
 in hydractinid hydroids: why mechanisms matter. *Journal of* 456
Evolutionary Biology 6: 307–327. 457
 Buss, L. W., 2001. Growth by intussusception in Hydractiniid 458
 hydroids. In Jackson, J. B. C., S. Lidgard & F. K. McKinney 459
 (eds), *Evolutionary Patterns: Growth, Form, and Tempo in* 460
the Fossil Record. University of Chicago Press, Chicago: 3– 461
 26. 462
 Cartwright, P. & L. W. Buss, 1999. Colony integration and the 463
 expression of the Hox gene, *Cnox-2*, in *Hydractinia symbi-* 464
ologicarpus (Cnidaria: Hydrozoa). *Journal of Experimental* 465
Zoology 285: 57–62. 466
 Cartwright, P., J. Bowsher & L. W. Buss, 1999. Expression of a 467
 Hox gene, *Cnox-2*, and the division of labor in a colonial 468
 hydroid. *Proceedings of the National Academy of Sciences* 469
of the USA 96: 2183–2186. 470
 Coma, R., M. Ribes, M. Zabala & J. -M. Gili, 1998. Growth in 471
 a modular colonial marine invertebrate. *Estuarine and* 472
Coastal Shelf Science 47: 459–470. 473

- 474 Debat, V. & P. David, 2001. Mapping phenotypes: canaliza- 532
475 tion, plasticity and developmental stability. *Trends in Ecol- 533*
476 ogy and Evolution 16: 555–561. 534
477 Finnerty, J. R. & M. Q. Martindale, 1997. Homeoboxes in sea 535
478 anemones (Cnidaria: Anthozoa): a PCR-based survey of 536
479 *Nematostella vectensis* and *Metridium senile*. *Biological 537*
480 Bulletin 193: 62–76. 538
481 France, S. C., P. E. Rosel, J. E. Agenbroad, L. S. Mullineaux & 539
482 T. D. Kocher, 1996. DNA sequence variation of mitochon- 540
483 drial large-subunit rRNA provides support for a two-sub- 541
484 class organization of the Anthozoa (Cnidaria). *Molecular 542*
485 Marine Biology and Biotechnology 5: 15–28. 543
486 Gould, S. J., 1977. *Ontogeny and Phylogeny*. Belknap Press, 544
487 Cambridge. 545
488 Hughes, R. N., 1983. Evolutionary ecology of colonial reef- 546
489 organisms, with particular reference to corals. *Biological 547*
490 Journal of the Linnaean Society 20: 39–58. 548
491 Jackson, J. B. C., 1977. Competition on marine hard substrata: 549
492 the adaptive significance of solitary and colonial strategies. 550
493 *American Naturalist* 111: 743–767. 551
494 Kaandorp, J. A. & J. Kübler, 2001. *The Algorithmic Beauty of 552*
495 Seaweeds, Sponges and Corals. Springer-Verlag, Amsterdam. 553
496 Kapela, W. & H. R. Lasker, 1999. Size-dependent reproduction 554
497 in the Caribbean gorgonian *Pseudoplexaura porosa*. *Marine 555*
498 Biology 135: 107–114. 556
499 Kaufmann, K. W., 1981. Fitting and using growth curves. 557
500 *Oecologia* 49: 293–299. 558
501 Kossevitch, I. A., K. Herrmann & S. Berking, 2001. Shaping of 559
502 colony elements in *Laomedea flexuosa* Hinks (Hydrozoa, 560
503 Thecaphora) includes a temporal and spatial control of 561
504 skeleton hardening. *Biological Bulletin* 201: 417–423. 562
505 Kuhn, K., B. Streit & B. Schierwater, 1999. Isolation of Hox 563
506 genes from the Scyphozoan *Cassiopeia xamachana*: implica- 564
507 tions for the early evolution of Hox genes. *Journal of 565*
508 Experimental Zoology 285: 63–75. 566
509 Lasker, H. R. & J. A. Sánchez, 2002. Allometry and Astogeny 567
510 of modular organisms. In Hughes, R. N. (ed.), *Reproductive 568*
511 Biology of Invertebrates, Vol. XI. Progress in Asexual 569
512 Reproduction. John Wiley, New York: 207–253. 570
513 Lasker, H. R., M. L. Boller, J. Castanaro & J. A. Sánchez, in 571
514 press. Modularity and determinate growth in a gorgonian 572
515 coral. *Biological Bulletin*. 573
516 Lewontin, R. C., 1966. On the measurement of relative vari- 574
517 ability. *Systematic Zoology* 15: 141–142. 575
518 McKinney, F. K. & D. M. Raup, 1982. A turn in the right 576
519 direction: simulation of erect spiral growth in the bryozoans 577
520 *Arquimedes* and *Bugula*. *Paleobiology* 8: 101–112. 578
521 McKinney, M. L., 1988. Classifying heterochrony allometry, 579
522 size, and time. In McKinney, M. L. (ed.), *Heterochrony in 580*
523 Evolution. A Multidisciplinary Approach. Plenum Press, 581
524 New York: 17–34. 582
525 McNamara, K. J. (ed.), 1995. *Evolutionary Change and Hetero- 583*
526 chrony. John Wiley & Sons, New York. 584
527 Müller, W. A., A. Hauch & G. Plickert, 1987. Morphogenetic 585
528 factors in hydroids. I. Stolon tip activation and inhibition. 586
529 *Journal of Experimental Zoology* 243: 111–124. 587
530 Pandolfi, J. M., 1988. Heterochrony in colonial marine animals. 588
531 In McKinney, M. L. (ed.), *Heterochrony in Evolution. A 589*
Multidisciplinary Approach. Plenum Press, New York: 135–
158. 532
Pigliucci, M. & E. T. Marlow, 2001. Differentiation for flower- 534
ing time and phenotypic integration in *Arabidopsis thaliana* 535
in response to season length and vernalization. *Oecologia* 536
127: 501–508. 537
Popadic, A., A. Abzhanov, D. Ruch & T. C. Kaufman, 1998. 538
Understanding the genetic basis of morphological evolution: 539
the role of homeotic genes in the diversification of the 540
arthropod bauplan. *International Journal of Developmental 541*
Biology 42: 453–461. 542
Purugganan, M. D., 1999. The molecular evolution of develop- 543
ment. *BioEssays* 29: 700–711. 544
Resnik, D., 1995. Developmental constraints and patterns: 545
some pertinent distinctions. *Journal of Theoretical Biology* 546
173: 231–240. 547
Rice, S. H., 1997. The analysis of ontogenetic trajectories: when 548
a change in size or shape is not heterochrony. *Proceedings of 549*
the National Academy of Sciences of the USA 94: 907–912. 550
Rinkevich, B., 2002. The branching coral *Stylophora pistillata*: 551
contribution of genetics in shaping colony landscape. *Israel 552*
Journal of Zoology 48: 71–82. 553
Sánchez, J. A., 2002. Dynamics and evolution of colony form 554
among branching modular organisms. Ph.D. Thesis, Uni- 555
versity at Buffalo (The State University of New York), 556
Buffalo (USA). 557
Sánchez, J. A. & H. R. Lasker, in press. Do multi-branched 558
colonial organisms exceed normal growth after partial 559
mortality? *Proceedings of the Royal Society of London series 560*
B-Biological Sciences (supplement). 561
Sánchez, J. A. & H. R. Lasker, 2003. Patterns of morphologic 562
integration in branching colonies of marine modular 563
organisms: supra-module organization in gorgonian corals. 564
Proceedings of the Royal Society of London series B-Bio- 565
logical Sciences 270: 2039–2044. 566
Sánchez, J. A., H. R. Lasker & D. J. Taylor, 2003a. Phyloge- 567
netic analyses among octocorals (Cnidaria) according to 568
mitochondrial and nuclear DNA sequences (*lsu-rRNA 16S*, 569
and *ssu-rRNA 18S*) support two convergent clades of 570
branching gorgonians. *Molecular Phylogenetics Evolution* 571
29: 31–42. 572
Sánchez, J. A., C. S. Mcfadden, S. C. France & R. Lasker, 573
2003b. Molecular phylogenetic analyses of shallow-water 574
Caribbean octocorals. *Marine Biology* 142: 975–987. 575
Sánchez, J. A., W. Zeng, V. R. Coluci, C. Simpson & R. Lasker, 576
2003c. How similar are branching networks in nature? A 577
view from the ocean: caribbean gorgonian corals. *Journal of 578*
Theoretical Biology 222: 135–138. 579
Sánchez, J. A., H. R. Lasker, E. G. Nepomuceno, J. D. Sánchez 580
& M. J. Woldenberg, in press. Branching and self-organi- 581
zation in marine modular colonial organisms: a model. 582
American Naturalist. 583
Stebbing, A. R. D., 1981. The kinetics of growth control in a 584
colonial hydroid. *Journal of the Marine Biological Associ- 585*
ation of the United Kingdom 61: 35–63. 586
Waitt, D. E. & D. A. Levin, 1993. Phenotypic integration and 587
plastic correlations in *Phlox drummondii* (Polomoniaceae). 588
American Journal of Botany 80: 1224–1233. 589