

Evolutionary determinants of morphological polymorphism in colonial animals

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Abstract: Colonial animals commonly exhibit morphologically polymorphic modular units that are phenotypically distinct and specialize in specific functional tasks. But how and why these polymorphic modules have evolved is poorly understood. Across colonial invertebrates there is wide variation in the degree of polymorphism from none in colonial ascidians, to extreme polymorphism in siphonophores such as the Portuguese Man of War. Bryozoa are a phylum of exclusively colonial invertebrates that uniquely exhibit almost the entire range of polymorphism from monomorphic species to others that rival siphonophores in their polymorphic complexity. Previous approaches to understanding the evolution of polymorphism have been based upon analyses of (1) the functional role of polymorphs or (2) presumed evolutionary costs and benefits based upon evolutionary theory that postulates polymorphism should only be evolutionarily sustainable in more “stable” environments because polymorphism commonly leads to the loss of feeding and sexual competence. Here we use bryozoans from opposite shores of the Isthmus of Panama to revisit the environmental hypothesis by comparison of faunas from distinct oceanographic provinces that differ greatly in environmental variability and we then examine the correlations between the extent of polymorphism in relation to patterns of ecological succession and variation in life histories. We find no support for the environmental hypothesis. Distributions of the incidence of polymorphism in the oceanographically unstable Eastern Pacific are indistinguishable from those in the more stable Caribbean. In contrast, the temporal position of species in a successional sequence is collinear with the degree of polymorphism because species with fewer types of polymorphs are competitively replaced by species with higher numbers of polymorphs on the same substrata. Competitively dominant species also exhibit patterns of growth that increase their competitive ability. The association between degrees of polymorphism and variations in life histories is fundamental to understanding of the macroevolution of polymorphism.

Introduction

42 Modules of colonial organisms originate asexually as clones and typically remain physically and
44 physiologically connected (Beklemishev 1969; Jackson 1979a). Colonies reproduce sexually
46 although clonal reproduction of new colonies is common (Hughes and Cancino 1986; Jackson
48 1986; Jackson and Coates 1986). Some, but not all, colonial organisms evolve phenotypic
50 variation among their clonal members that ranges from simple shape differences of component
52 modules (Cheetham 1973) to profoundly disparate polymorphic forms (McKinney and Jackson
54 1991; Ryland 1970). Bryozoan species exhibit a remarkable range of modular polymorphism,
56 from uniform colonies within which every member is identical to colonies so polymorphic
58 they rival even siphonophores in the large numbers of distinct modular types they contain. In
60 highly polymorphic bryozoans, phenotypic differences among modules are accompanied by the
functional loss of many organ systems, including feeding and sexual competency (Ryland 1970;
Carter et al. 2010; Ostrovsky 2013). Darwin, in the sixth edition of the *Origin* (Darwin 1872),
recognized the difficulty inherent in understanding the evolutionary differentiation of bryozoan
polymorphs. Even now, there is no definitive understanding of the problem.

56 The evolutionary problem of polymorphism is related to the evolution of sex in that there
is an inevitable cost of differentiation caused by loss of feeding and sexual competency. These
58 costs must be recouped by the particular adaptive benefit associated with differentiating poly-
morphs. Any general understanding of the evolution of polymorphism must take this cost and
60 its balancing benefits into account.

62 Ever since Darwin, scientists have explored two explanations for the evolution of poly-
morphism. The first, similar to that advocated by Darwin, tries to understand the evolution of
different types of polymorphs by understanding the functions each type performs in a colony.
64 Unfortunately, except in rare cases such as the worm and leg pinching ability of the bird's-head
avicularia of *Bugula* (Ryland 1970), the functions of bryozoan polymorphic types are too poorly
66 understood for meaningful analysis. The second explanation for the evolution of polymorphism
is as a response to the stability of the external environment (Hughes and Jackson 1990; Schopf
68 1973). Unstable environments limit the number of different polymorph types and more stable
environments relax those limits. For bryozoans, this way of understanding was inspired by the
70 ergonomic theory of caste differentiation in social insects (Oster and Wilson 1979).

72 Neither approach has yielded a general understanding of the problem of modular polymor-
phism. Instead we have only incomplete snippets of functional information and phenomenolog-
ical descriptions. We addressed this problem in two ways. First, we revisit the environmental
74 hypothesis at an intermediate oceanographic spatial scale more appropriate to directly testing
the hypothesis. Second, we investigated the functional hypothesis by exploring correlations
76 between polymorphism and patterns of ecological succession and variation in life histories.
Patterns of succession provide good summaries of the adaptive benefits of polymorphism be-
78 cause they are the result of successful adaptive strategies. Furthermore, life-history strategies
show, in a broad sense, how the fitness benefits of those adaptive strategies are achieved.

80 **The nature of bryozoan polymorphism**

82 Bryozoans are colonial animals that grow by budding modules termed zooids, each of which is
84 homologous to a single solitary animal such as an ant or snail (McKinney and Jackson 1991;
86 Ryland 1970). Colonies are tessellated by generic feeding zooids termed autozooids. Scattered
88 among the autozooids are polymorphic zooids that are commonly discrete in shape and function
90 (Fig. 1). Autozooids feed by protrusion of a tentacular polypide animal through the orifice of
92 the zooid that is protected by a hinged flap called an operculum. Autozooids can also produce
gametes as well as perform all of the basic tasks required for survival, and are considered the
evolutionarily primitive condition (Banta 1973; Cheetham 1973; Cheetham et al. 2006; Silén
1977). Polymorphic zooids within a single colony may differ more from each other than even
the most extreme members of discrete social insect castes (Wilson 1975). Moreover, the number
and frequency of different types of polymorphs can vary from colony to colony both within and
among species.

94 The various types of polymorphs differ from autozooids by giving up one or more basic
96 tasks to specialize in particular functions. Avicularia are the most common polymorphs and
98 come in many forms and sizes, but they all share some basic attributes. Their hinged operculum
100 is modified so that, like a person waving a flag, it can be moved about across the surface of the
102 colony. Avicularia reduce or lose other body parts, such as the polypide with its tentacle crown
104 and major organs, though a vestigial polypide can provide a sensory function within many
106 types of avicularia (Carter et al. 2010). Because avicularia are so reduced, they cannot feed or
108 contribute to reproduction, so they remain connected to other zooids and depend on them for
nutrition. The tasks that avicularia perform in the colony include cleaning, defense, hygiene,
and patterning the flow of water across the colony surface (Carter 2008; Winston 1984; Winston
2010), although the specific functions of the various types of avicularia are poorly understood.
Vicarious avicularia (Fig. 1) are budded with other zooids in the main colony plane, replacing
an autozooid without changing the mosaic pattern. Adventitious avicularia (Fig. 1) are budded
atop the plane of the colony where they may overgrow preexisting zooids, adding a second
level. Adventitious avicularia are commonly found adjacent to the orifice of autozooids (Fig.
1), scattered across their frontal walls (Fig. 1), or encrusting other parts of the colony like salt
on a pretzel (Fig. 1).

110 There are three other major types of polymorphs: spines, kenozooids, and ovicells (Fig. 1).
112 Spines, also known as spinozooids (Silén 1977), are zooids that have been reduced into small
114 spiny skeletal protrusions. Nevertheless, each spine is separated from the adjacent autozooid
116 by cuticular tissue (Silén 1977), just as autozooids themselves are separated from each other
118 (Ryland 1970). Kenozooids are diminutive zooids that fill gaps in the colony's mosaic where a
full autozooid or avicularium would be too large. Although it may seem trivial, filling space is
crucial for protection from competitive overgrowth by other organisms that have the potential
to get a foothold in empty areas (Jackson 1979b; McKinney and Jackson 1991; Palumbi and
Jackson 1982).

Ovicells are dome-shaped polymorphs whose sole function is to brood larvae (Fig. 1). Ovi-

120 cells are budded from the distal end of a parental autozoid, placing the orifice of an ovicell
121 within reach of the parental autozoid polypide's tentacle crown. Ovicells vary among species
122 in their position relative to the surface of the colony. In some species they remain submerged
123 below the colony surface within the parental autozoid, but in others the ovicells stand in stark
124 relief above the frontal surfaces of nearby autozooids. Unfertilized eggs or embryos (the site of
125 fertilization is unknown) are passed from the tentacles of the adjacent zoid to the ovicell where
126 they are brooded until ready to disperse (Ostrovsky 2013). Ovicells are uncommon and are usu-
127 ally one or more orders of magnitude less frequent than autozooids within a colony (Simpson
128 2012).

Two Hypotheses

130 Polymorphic differences among constituent animals (or modules of a colony) are often func-
131 tional. Each distinct animal form within a society or a colony divides up the labor by special-
132 izing on a specific task, such as feeding, defense, or reproduction (Beklemishev 1969; Harvell
133 1994; Lidgard et al. 2012; Mackie 1986; Wilson 1975; Winston 1984). The division of la-
134 bor among specialist forms is thought to dramatically increase efficiency over generalist forms,
135 in which individual members are capable of doing everything alone (Beklemishev 1969; Hux-
136 ley 1912). However, the efficiency gained by evolving polymorphism can be structured over
137 macroevolutionary time in two ways. It can be structured environmentally or functionally.
138 These two hypotheses roughly map onto how the distribution of species of particular degrees
139 of polymorphism tend to be spatially structured. With the environmental hypothesis species
140 with similar degrees of polymorphism will track similar environments. With the functional hy-
141 pothesis, species with different degrees of polymorphism can co-occur as long as they differ in
142 adaptive strategy.

143 According to the environmental hypothesis, polymorphism is both costly and beneficial.
144 The costs come directly from reduction in the numbers of individuals or modules involved in
145 feeding or sexual reproduction. Polymorphism should increase only if the colonies or soci-
146 eties persist long enough for the evolutionary benefits of specialization to outweigh the costs
147 of decreased feeding or reproduction overall. Average longevity should in turn increase pro-
148 portionally with increased environmental stability. Conversely, colonies living in unstable en-
149 vironments will, on average, die before the benefit of polymorphism is accrued. Therefore,
150 the environmental hypothesis predicts that highly polymorphic colonies will be absent from
151 unstable environments.

152 This hypothesis is also known as the ergonomic hypothesis because the number of poly-
153 morph types evolves to fit the stability of the environment (Schopf 1973; Oster and Wilson
154 1979). In social insects, the ergonomic hypothesis has largely fallen out of favor as the cause
155 of caste type diversity (Bourke 2011). However, in sessile clonal organisms, the environmental
156 hypothesis takes on added strength because success or death is directly linked to the stability
of the substrates they grow upon and prefer (Jackson 1977; Jackson 1979b). Thus the environ-

158 mental hypothesis has the potential to be a valid for sessile colonial organisms even though it is
not supported in social insects. To evaluate this we examined the occurrence of polymorphism
160 in species occurring in the strikingly different oceanographic regimes on opposite sides of the
Isthmus of Panama.

162 Alternatively, the benefits of polymorphism may accrue through increased efficiency asso-
ciated with the proliferation of specialized functions. To evaluate this, we observed how species
164 with varying degrees of polymorphism sort themselves out along a successional sequence. Al-
though an indirect measure of the payoff of possessing polymorphs, this approach provides a
166 direct measure of the presence of those benefits exceeding the costs.

Methods

168 Environmental stability varies over a wide array of spatial and temporal scales. Stability can
range from very local—such as the ephemeral stability of a shell on the seafloor compared to a
170 large boulder or coral—to larger scale differences in prevailing climactic or oceanographic con-
ditions, such as the broad patterns of hurricane frequency across the tropics or along the eastern
172 and western borders of continents (Jackson 1991; McKinney and Jackson 1991; Jackson and
D’Croz 1997). All scales of environmental stability are important for the environmental hy-
174 pothesis for polymorphism because the costs and benefits of polymorphism need to be balanced
locally, within an individual colony, and also at larger scales as polymorphism evolves within a
176 population and among species. At the smallest scale, the maximum lifetime of a sessile colony
cannot exceed that of its substrate, as it cannot move. Similarly, at the largest scale, popula-
178 tions can persist only as long as their environments persist, unless they can tolerate a highly variable
environment—in which case the costs and benefits of polymorphism must be accounted for in
180 every environmental state. The costs in each state are important, because they are dominated by
maintaining non-feeding and non-reproducing members. Moreover, costs and benefits in each
182 environment may be at odds with each other, making an optimized strategy more difficult to
evolve.

184 The environmental hypothesis has been tested in bryozoans twice at the two extremes of
spatial scale. Schopf (1973) compared the incidence of polymorphism on a global scale between
186 shallow, supposedly unstable tropical seas versus supposedly more stable, high-latitude and
deep-sea environments. However, Schopf’s assumptions about oceanographic stability were
188 incorrect, since highly stable and unstable environments exist in all three regions. In the second
test, Hughes and Jackson (1990) compared levels of polymorphism along a narrow stretch of
190 the Caribbean coast of Panama in relation to the size and physical stability of different sized
substrata. They compared substrates ranging from small shells and pebbles that are easily buried
192 and rolled about on the sea floor, up to large, firmly attached and long-lived corals and reef
framework. They found no difference in the number of types of polymorphs in relation to the
194 substrate stability at this small spatial scale.

Nevertheless, the environmental hypothesis remains untested by comparison of the levels

196 of polymorphism from different oceanographic regimes. We therefore compared the incidence
of polymorphism between the strikingly different shallow-water coastal environments on op-
198 posite sides of the Isthmus of Panama (D’Croz and O’Dea 2007; Jackson and D’Croz 1997;
Lessios 2008; O’Dea and Jackson 2009; O’Dea et al. 2007). Eastern Pacific coastal environ-
200 ments exhibit strong seasonal upwelling with large fluctuations in temperature and planktonic
productivity, as well as considerable interannual variation in oceanographic conditions that di-
202 rectly impact marine faunas (Baker et al. 2004; Colgan 1990; Glynn and Colgan 1992; Glynn
et al. 2001). Development of coral reefs is meager and seagrass beds are absent. In contrast,
204 Caribbean coastal environments exhibit low seasonality and planktonic productivity, and coral
reefs and seagrass beds are extensive (Jackson and D’Croz 1997; O’Dea et al. 2007).

206 These environmental differences arose over the past 5 million years as the shallow seaways
connecting the two oceans gradually closed, resulting in considerable evolutionary divergence
208 in faunas (Lessios 2008; O’Dea et al. 2007; O’Dea et al. 2016). Consequently, bryozoans on
either side of the Isthmus have had sufficient time to evolve a largely independent set of species,
210 which have evolutionarily divergent differences in many aspects of their morphology (Jackson
and Herrera-Cubilla 2000). Thus, if the environmental hypothesis applies at this intermediate
212 scale, species of Caribbean bryozoans should have more types of polymorphs and the frequency
distribution of the number of types of polymorphs should be shifted upward in the Caribbean
214 relative to the Eastern Pacific.

Settling experiments using artificial substrates placed in the environment over varying lengths
216 of time have been used to observe the successional sequence of species occurrence in the devel-
opment of bryozoan communities (McKinney and Jackson 1991; Winston and Jackson 1984;
218 Barnes and Sanderson 2000). We exploited Winston and Jackson’s results to record the num-
ber of different types of polymorphic zooids characteristic of the bryozoan species observed to
220 be growing on these panels. Two sets of six replicate 15x15 cm square panels were set out in
shallow water off of Jamaica in 1977. Each plate was observed 7 times over 3 years to map
222 the occurrence, position, and percent cover of each of the ten species that varyingly settled and
grew on the panels. We transformed the percentage cover data to calculate proportional cover
224 over the course of the experiment for each species. We calculated the average the number of
types of polymorphs across species by weighting each species by its relative proportional cover.

226 Data

We estimated the total diversity of polymorphs among 79 species of ascophoran cheilostome
228 bryozoans in Smithsonian collections obtained from shallow-water coastal environments on
either side of the Isthmus of Panama (Jackson and Herrera-Cubilla 2000) (Table 1). All species
230 are encrusting and are found on many substrates, from shells and pebbles, to coral rubble and
reef-framework. Not all colonies express or preserve all of the polymorphs they are capable
232 of producing, so whenever possible we tallied the mean and maximum number of polymorphic
types observed from 1-28 colonies per species. We have counts for 40 species from 25 localities

234 in the Eastern Pacific and 39 species from 10 localities in the Caribbean.

235 We recognized eight basic types of polymorphs that differ qualitatively in body plan and
236 in the direction of budding from parent zooids (Fig. 1). These include: ovicells, kenozooids,
237 spines, vicarious avicularia that occur inline with autozooids, and adventitious avicularia (which
238 are frontally budded and can vary in shape and position). At least four different types of ad-
239 ventitious avicularia can be identified by their position on the zooidal or colony surface. Oral
240 adventitious avicularia occur adjacent to the autozooid's orifice. A second type of adventitious
241 avicularium occurs on the zooidal frontal wall. A third type occurs on the ovicell in some
242 species. The fourth type includes large adventitious avicularia that overgrow multiple zooids.

243 The total number of possible types of polymorphs exceeds the number actually observed
244 in any species. Moreover, the eight polymorph types that we recognize here are a subset of
245 the total number of possible polymorphs that occur in cheilostome bryozoans as a whole (Silén
246 1977). We lumped other named polymorph types together into one of the eight categories.
247 However, we distinguished between polymorphs beyond our eight named types if they differed
248 in shape from other polymorphs in the same positional category. For example, we considered
249 vibricalae to be a bristly type of avicularium. Thus, if a species expressed both bristly and
250 flap-like avicularia, we would count these as two different types of polymorphs.

Results

252 The frequency distributions of numbers of types of polymorphs per species are statistically
253 indistinguishable between the Eastern Pacific and the Caribbean (Fig. 2). An average bryozoan
254 species in both the Eastern Pacific and the Caribbean has an ovicell, spines or a kenozooid,
255 and one type of avicularium, or perhaps an ovicell and two types of avicularia. Eleven genera
256 occur on both sides of the isthmus, yet the distributions of their polymorphs are not statistically
257 distinct between the oceans based on a comparison of the maximum incidence of polymorphic
258 zooid types (Wilcoxon $W = 49$, $P = 0.45$). The mean of the maximum observed number of
259 polymorphs observed in each species is 2.79 in the eastern Pacific and 2.38 in the Caribbean
260 (Wilcoxon $W = 1039.5$, $P = 0.12$). The median number of polymorphs for species is 2 in the
261 Pacific and 3 in the Caribbean. If we incorporate the variation in expressed polymorphism from
262 colony to colony within species by calculating the mean observed, we still find no difference
263 between distributions (average for Eastern Pacific species = 2.2; average for Caribbean species
264 = 2.03; Wilcoxon $W = 961$, $P = 0.48$). Our results are consistent with the pattern Hughes
265 and Jackson (1990) found at much smaller spatial scales. The incidence of polymorphism in
266 ascophoran bryozoans is not optimized ergonomically between the strikingly different coastal
267 environmental conditions on opposite sides of the Isthmus of Panama.

268 Nevertheless, there are important differences between the oceans in the extremes of the
269 distributions of polymorphism (Fig. 2). For example, there are 17 Caribbean species with 4 or
270 more types of polymorphs versus only five such species in the Eastern Pacific. We find strong
statistical support for an excess of highly polymorphic species in the Caribbean relative to the

272 Eastern Pacific ($\chi^2 = 7.45$, $df = 1$, $P = 0.006$). Moreover, these highly polymorphic species
increasingly dominated the fouling panels as ecological succession occurred over three years of
274 the experiment (Fig. 3, Fig. 4; Spearman's $\rho = 0.64$, $P = 0.014$).

Discussion and Conclusion

276 The stability of the physical environment plays no direct role in the evolution of bryozoan poly-
morphism as postulated on the basis of environmental theory. In contrast, the incidence of
278 polymorphism is strongly correlated with variations in ecological dominance and life-history
as observed from both the increase in polymorphism generally as well as the increased domi-
280 nance of exceptionally polymorphic species during ecological succession on the panels. This
result is further borne out by an analysis of polymorphism of 20 ascophoran species ranked in
282 terms of modes of budding that confer exceptional competitive ability and persistence in bio-
logical interactions (Table 7.2 in McKinney and Jackson 1991). The score is given by the sum
284 of the presence or absence of multizoidal budding, self-overgrowth, and frontal budding. Only
species with all three budding characteristics associated with dominance in competitive interac-
286 tions have exceptionally high degrees of polymorphism (Table 2, Fig. 5). Conversely, species
that lack one or more of these budding characteristic also lack diverse polymorph types (Fig. 5).

288 Opportunistic, early successional species tend to have lower levels of polymorphism than
late successional species regardless of the overall oceanographic stability of their habitat. Rather
290 than providing the time to accrue the benefits of expensive polymorphs, as expected by evolu-
tionary theory, the stability of the coral habitats provides the time for ecological succession of
292 different species to play out through a dense set of competitive ecological interactions. By spe-
cializing in particular life-history strategies, more bryozoan species, each with a different level
294 of polymorphism, can coexist and interact.

Many rounds of succession can occur on the same substrate. Species with low levels of
296 polymorphism are succeeded by species with higher levels so long as their substrate persists.
However, physical disturbance or predation resulting in the death of an extremely polymorphic
298 colony, such as many species of *Stylopoma* (Herrera et al. 1996; McKinney and Jackson 1991),
permits the establishment of pioneering species with generally fewer polymorphic types. And so
300 just as the death of a canopy tree in a tropical forest sets off a scramble among early successional
species of trees (Connell 1978), the competitive cycle among bryozoans begins again.

302 How different types of modular polymorphs are developmentally specified still remains un-
known. Within a single colony, all the diverse types of polymorphs are genetic clones. And so
304 in some sense, the set of polymorphic types are each a part of a phenotypic reaction norm that
the bryozoan genome is capable of. Yet the reaction norm perspective is an over simplification
306 because of the discrete nature of modular polymorphic phenotypes and because not all types of
polymorphs are derived from autozooids. Ovicells are derived from spines (Ostrovsky and Tay-
308 lor 2004; Taylor and McKinney 2001) whereas avicularia are derived from autozooids (Banta
1973; Cheetham 1973). Thus, the modular form of a mother zooid may set limits on which

310 types of polymorphs she and her descendants can produce.

312 There are hints that the evolution of polymorphism is linked to the evolution of life history
314 strategies because species with more types of polymorphs tend to have less frequent reproduc-
316 tive specialists (Simpson 2012). Over macroevolutionary time there are two pathways to de-
318 crease that frequency that are contingent on the starting size of the most primitive colony. From
originally small colonies, there must be a higher rate of increase in the number of “worker”
or “soma” members relative to reproductives as the colony grows in size. Alternatively, when
colonies are primitively large, colony members tend to loose reproductive competency even if
the colony size remains largely the same.

320 In bryozoans, and perhaps other colonial and social animals, colonies with a single type
322 of zooid will presumably have a life-history strategy that is tightly linked to the reproductive
324 capabilities of its constituent zooids. If true, this implies that primitive colonies along both
pathways inherit their life-histories from their members. From this perspective, understanding
the macroevolution of polymorphism is critical to understanding the macroevolutionary prolifer-
ation of life history strategies.

References

- 326 Baker, A. C., C. J. Starger, T. R. McClanahan, and P. W. Glynn. 2004. Coral reefs: corals’
adaptive response to climate change. *Nature* 430:741-741.
- 328 Banta, W. C. 1973. Evolution of avicularia in cheilostome Bryozoa, Pages 295-303 in R. S.
Boardman, A. H. Cheetham, and W. A. Oliver Jr, eds. *Degrees of colony dominance in*
330 *stenolaemate and gymnolaemate Bryozoa*. Pennsylvania, Dowden, Hutchinson & Ross.
- Barnes, D.K.A., and Sanderson, W.G. 2000. Latitudinal patterns in the colonization of marine
332 debris. In: *Proceedings of the 11th International Bryozoology Association Conference*
(Herrera-Cubilla, A. and Jackson, J.B.C., editors), Smithsonian Tropical Research Insti-
334 tute, Balboa, R.P, pp. 154-160.
- Beklemishev, W. 1969, *Principles Of Comparative Anatomy of Invertebrates 1: Promorphol-*
336 *ogy*. Chicago, Illinois, University of Chicago Press.
- Bourke, A.F., 2011. *Principles of social evolution*. Oxford: Oxford University Press.
- 338 Carter, M., D. Gordon, and J. A. Gardner. 2010. Polymorphism and vestigiality: comparative
anatomy and morphology of bryozoan avicularia. *Zoomorphology* 129:195-211.
- 340 Carter, M. C. 2008. *The functional morphology of avicularia in cheilostome bryozoans*, Vic-
toria University of Wellington, Wellington.

- 342 Cheetham, A. H. 1973. Study of cheilostome polymorphism using principal components anal-
344 ysis, Pages 385-409 in G. P. Larwood, ed. Living and Fossil Bryozoa. London, Aca-
ademic Press.
- Cheetham, A. H., J. Sanner, P. D. Taylor, and A. N. Ostrovsky. 2006. Morphological differ-
346 entiation of avicularia and the proliferation of species in mid-Cretaceous *Wilbertopora*
(Bryozoa: Cheilostomata). *Journal of Paleontology* 80:49-71.
- 348 Colgan, M. W. 1990. El Niño and the history of eastern Pacific reef building, Pages 183-232
350 in P. W. Glynn, ed. Global Ecological Consequences of the 1982-83 El Niño-Southern
Oscillation.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302-1310.
- 352 D’Croz, L., and A. O’Dea. 2007. Variability in upwelling along the Pacific shelf of Panama
and implications for the distribution of nutrients and chlorophyll. *Estuarine, Coastal and*
354 *Shelf Science* 73:325-340.
- Darwin, C. 1872. *On the origin of species*, Macmillan.
- 356 Glynn, P. W., and M. W. Colgan. 1992. Sporadic disturbances in fluctuating coral reef environ-
ments: El Niño and coral reef development in the eastern Pacific. *American Zoologist*
358 32:707-718.
- Glynn, P. W., J. L. Mat, A. C. Baker, and M. O. Caldern. 2001. Coral bleaching and mortality
360 in Panama and Ecuador during the 1997–1998 El Niño-Southern Oscillation event: spa-
tial/temporal patterns and comparisons with the 1982–1983 event. *Bulletin of Marine*
362 *Science* 69:79-109.
- Harvell, C. D. 1994. The evolution of polymorphism in colonial invertebrates and social
364 insects. *Quarterly Review of Biology* 69:155-185.
- Herrera, A., J. Jackson, D. Hughes, J. Jara, and H. Ramos. 1996. Life-history variation
366 in three coexisting cheilostome bryozoan species of the genus *Stylopoma* in Panama.
Marine Biology 126:461-469.
- 368 Hughes, D. J., and J. B. C. Jackson. 1990. Do Constant Environments Promote Complexity of
Form?: The Distribution of Bryozoan Polymorphism as a Test of Hypotheses. *Evolution*
370 44:889-905.
- Hughes, R. N., and J. M. Cancino. 1986. An ecological overview of cloning in Metazoa,
372 Pages 297-356 in J. B. C. Jackson, L. W. Buss, and R. E. Cook, eds. *Population Biology*
and Evolution of Clonal Organisms. New Haven, Yale University Press.

- 374 Huxley, J. 1912, *The Individual In The Animal Kingdom*. New York, Cambridge University
Press.
- 376 Jackson, J. B. C. 1977. Competition on marine hard substrata: the adaptive significance of
solitary and colonial strategies. *American Naturalist* 111:743-767.
- 378 —. 1979a. Morphological Strategies of Sessile Animals, Pages 499-555 in G. Larwood, and
B. R. Rosen, eds. *Biology and Systematics of Colonial Organisms*. London and New
380 York, Academic Press.
- . 1979b. Overgrowth competition between encrusting cheilostome ectoprocts in a Jamaican
382 cryptic reef environment. *The Journal of Animal Ecology*:805-823.
- . 1986. Distribution and ecology of clonal and aclonal benthic invertebrates, Pages 297-356
384 in J. B. C. Jackson, L. W. Buss, and R. E. Cook, eds. *Population Biology and Evolution
of Clonal Organisms*. New Haven, Yale University Press.
- 386 —. 1991. Adaptation and diversity of reef corals. *BioScience* 41:475-482.
- Jackson, J. B. C. and Cheetham, A.H., 1994. Phylogeny reconstruction and the tempo of
388 speciation in cheilostome Bryozoa. *Paleobiology*, 20(4), pp.407-423.
- Jackson, J. B. C., and A. G. Coates. 1986. Life cycles and evolution of clonal (modular) ani-
390 mals. *Philosophical Transactions of the Royal Society of London. Series B, Biological
Sciences* 313:7-22.
- 392 Jackson, J. B. C., and L. D'Croz. 1997. The ocean divided, Pages 38-71 in A. G. Coates, ed.
Central America: A Natural and Cultural History. New Haven, Yale University Press.
- 394 Jackson, J. B. C., and A. Herrera-Cubilla. 2000, Adaptation and constraint as determinants of
zooid and ovicell size among encrusting ascophoran cheilostome Bryozoa from opposite
396 sides of the Isthmus of Panama. In: *Proceedings of the 11th International Bryozoology
Association Conference* (Herrera- Cubilla, A. and Jackson, J.B.C., editors), Smithsonian
398 Tropical Research Institute, Balboa, R.P, pp. 249-258
- Lessios, H. A. 2008. The great American schism: divergence of marine organisms after the
400 rise of the Central American Isthmus. *Annual Review of Ecology, Evolution, and Sys-
tematics* 39:63-91.
- 402 Lidgard, S., M. C. Carter, M. H. Dick, D. P. Gordon, and A. N. Ostrovsky. 2012. Division of
labor and recurrent evolution of polymorphisms in a group of colonial animals. *Evolu-
404 tionary Ecology*:1-25.
- Mackie, G. O. 1986. From aggregates to integrates: physiological aspects of modularity in
406 colonial animals. *Philosophical Transactions of the Royal Society of London. B, Bio-
logical Sciences* 313:175-196.

- 408 McKinney, F. K., and J. B. C. Jackson. 1991, *Bryozoan evolution*, University of Chicago Press.
- 410 O’Dea, A., and J. Jackson. 2009. Environmental change drove macroevolution in cupuladriid bryozoans. *Proceedings of the Royal Society B: Biological Sciences* 276:3629.
- 412 O’Dea, A., J. B. C. Jackson, H. Fortunato, J. T. Smith, L. D’Croze, K. G. Johnson, and J. A. Todd. 2007. Environmental change preceded Caribbean extinction by 2 million years. *Proceedings of the National Academy of Sciences* 104:5501-5506.
- 414
- O’Dea, A., H. A. Lessios, A. G. Coates, R. I. Eytan, S. A. Restrepo-Moreno, A. L. Cione, L. S. Collins et al. Formation of the Isthmus of Panama. *Science Advances* 2, no. 8 (2016): e1600883.
- 416
- 418 Oster, G. F., and E. O. Wilson. 1979, *Caste And Ecology In The Social Insects*. Princeton, Princeton University Press.
- 420 Ostrovsky, A. N. 2013, *Evolution of Sexual Reproduction in Marine Invertebrates: Example of Gymnolaemate Bryozoans*, Springer.
- 422 Ostrovsky, A. N., and P. D. Taylor. 2004. Systematics of Upper Cretaceous calloporid bryozoans with primitive spinose ovicells. *Palaeontology* 47:775-793.
- 424 Palumbi, S. R., and J. Jackson. 1982. Ecology of cryptic coral reef communities. II. Recovery from small disturbance events by encrusting bryozoa: the influence of “host” species and lesion size. *Journal of experimental marine Biology and Ecology* 64:103-115.
- 426
- Ryland, J. S. 1970, *Bryozoans*, Hutchinson & Co.
- 428 Schopf, T. J. M. 1973. Ergonomics of polymorphism: Its relation to the colony as the unit of natural selection in species of the phylum Ectoprocta, Pages 247–294 in R. S. Boardman, A. H. Cheetham, and W. A. Oliver, eds. *Animal Colonies: Development and Function Through Time*. Stroudsburg, Pennsylvania, Dowden, Hutchinson, and Ross.
- 430
- 432 Silén, L. 1977. Polymorphism, Pages 184-232 in R. Woollacott, and R. Zimmer, eds. *Biology of Bryozoans*. New York, Academic Press.
- 434 Simpson, C. 2012. The evolutionary history of division of labour. *Proceedings of the Royal Society B: Biological Sciences* 279:116-121.
- 436 Taylor, P. D., and F. K. McKinney. 2001. Brooding in the Cretaceous bryozoan *Stichomicropora* and the origin of ovicells in cheilostomes. *Bryozoan studies*:307-314.
- 438 Wilson, E. O. 1975, *Sociobiology: The New Synthesis*. Cambridge, Mass., Belknap Press of Harvard University Press.

- 440 Winston, J. E. 1984. Why bryozoans have avicularia: a review of the evidence. *American*
Museum Novitates 2789:1-26.
- 442 —. 2010. Life in the colonies: learning the alien ways of colonial organisms. *Integrative and*
comparative biology 50:919-933.
- 444 Winston, J. E., and J. B. Jackson. 1984. Ecology of cryptic coral reef communities. IV.
446 Community development and life histories of encrusting cheilostome Bryozoa. *Journal*
of experimental marine biology and ecology 76:1-21.

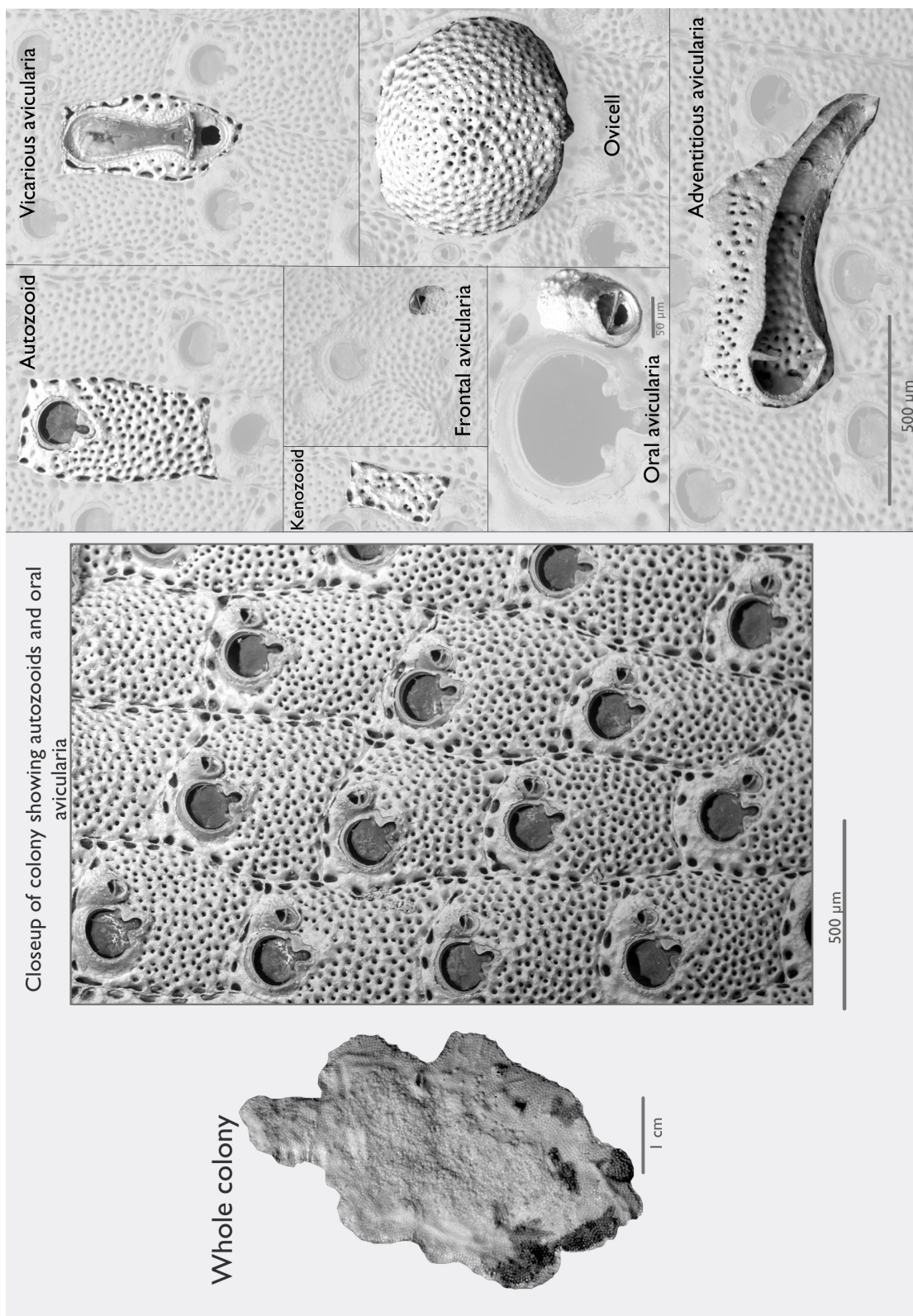


Figure 1: The zooids that constitute a bryozoan colony can be highly polymorphic. Whole colonies can be many tens to hundreds of square centimeters in area, but the thousands of zooids that make the colony are small, most commonly less than a millimeter in length. Zooids in encrusting species like this *Stylopoma* new species 3 (Jackson and Cheetham 1994) form a mosaic across their substratum. As the colonies grow, they radiate out from the oldest part of the colony, which is often near the center, as seen in the left image of a whole *Stylopoma* colony. Zooming into the colony shows zooid-level detail. Each repeated structure in the central image consists of two animals, an autozooid with an oral adventitious avicularium. *Stylopoma* autozooids protrude their tentacle crowns through a hatched orifice that is about 100 µm wide. Scattered across this colony (right panel) are six polymorph types. This colony has a single type of vicarious avicularium that replaces an autozooid inline. There is a type of kenozooid, which fills space. This species has ovicells, which commonly occur in a band halfway between the edge and the center of the colony, and three types of adventitious avicularia: an oral, frontal, and a large type that overgrows many zooids.

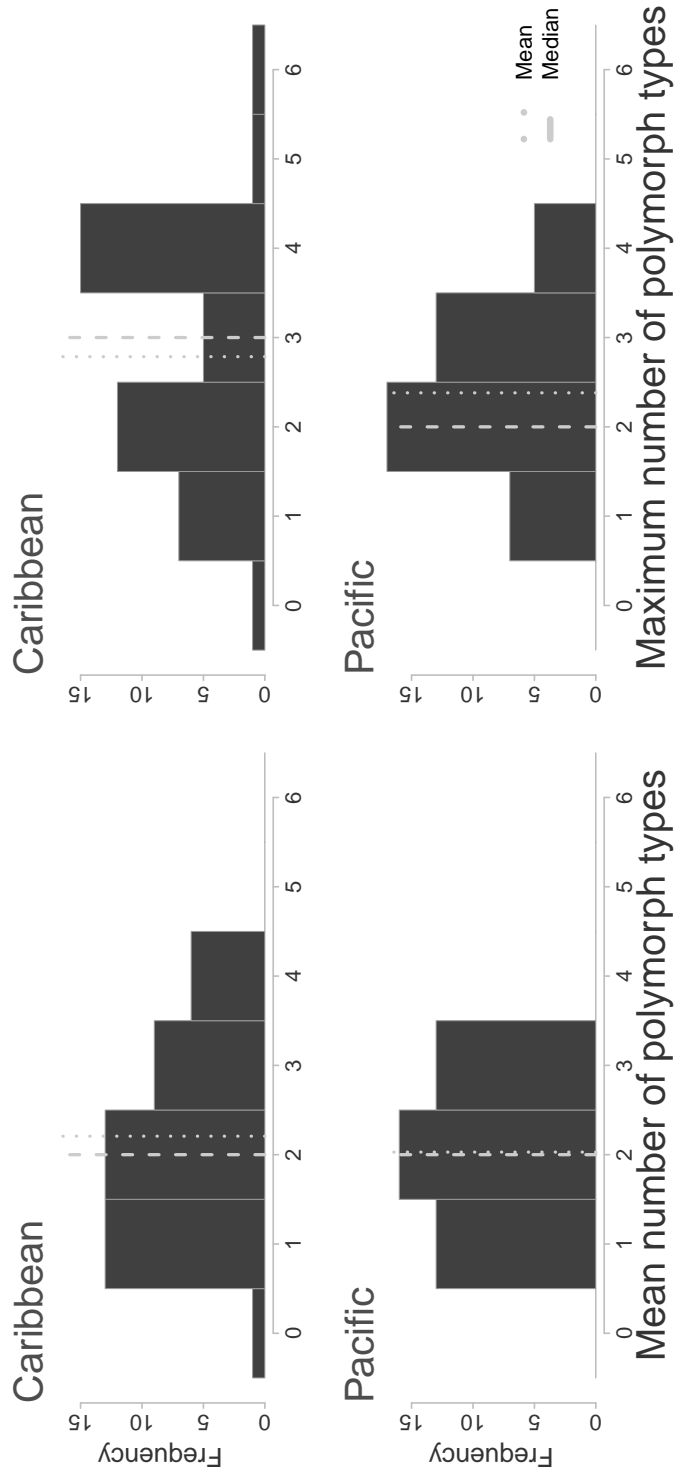


Figure 2: The frequency distributions of maximum and mean numbers of polymorph types observed in colonies of each species are compared between the shallow-water coastal bryozoans in the Caribbean and the East Pacific. We took the maximum and the mean numbers of polymorph types for 1-28 colonies per species. We compare 39 species in the Eastern Pacific to 40 species in the Caribbean.

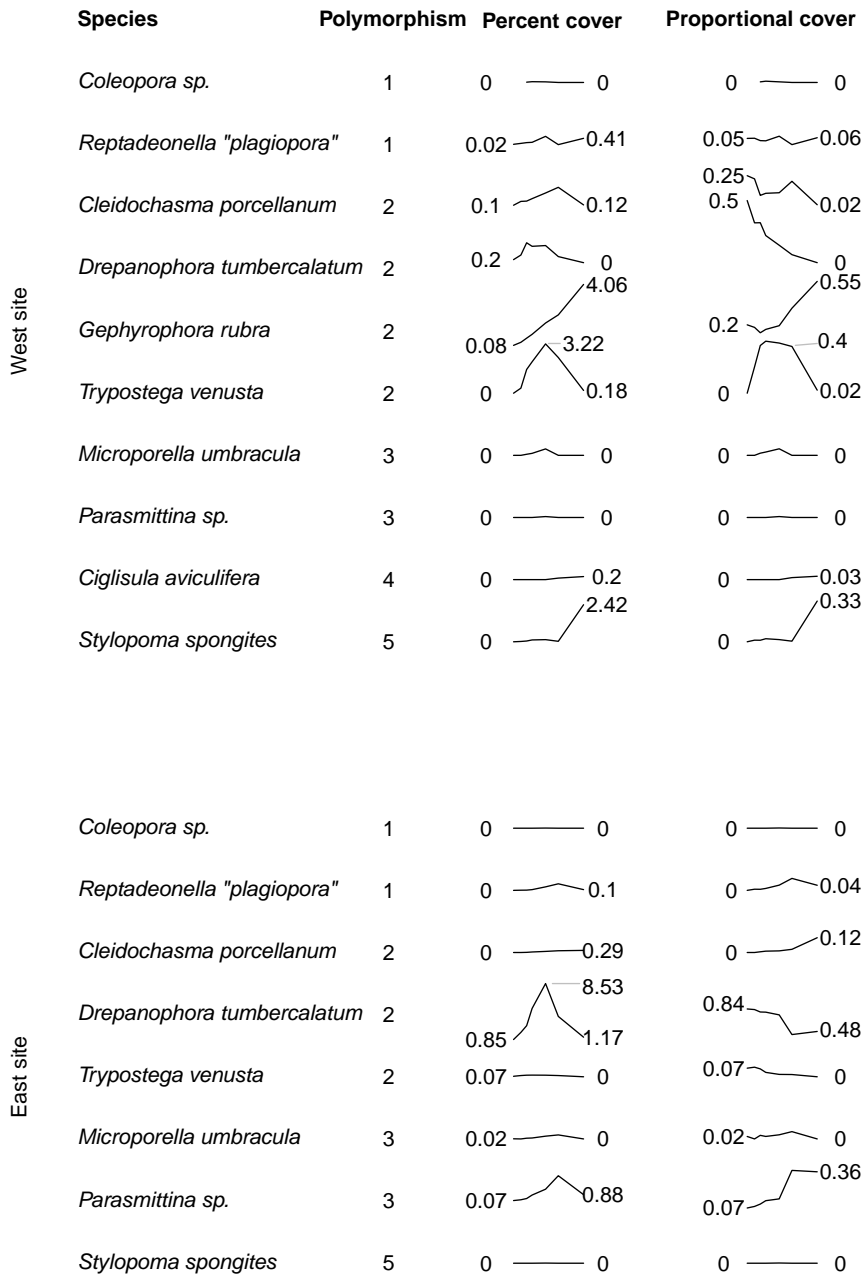


Figure 3: We used the results of a settling experiment that tracked the recruitment, growth, and mortality of encrusting bryozoans onto clean “fouling” panels (data from Table 2 in Winston and Jackson 1984). Two sets of six 15 cm square panels were set out approximately 100 m apart in 12-13 m water depth along the fringing coral reef on the west side of the embayment at Rio Brueno, Jamaica. A census was conducted for each plate 7 times over 3 years. During each census, 10 species of ascophoran bryozoans were evaluated for the percentage of the plate that their colonies covered. This set of 10 species happens to be a subset of the ones we surveyed in Table 1 and we pulled the observed degree of polymorphism from our Table 1. Here we show the incidence of polymorphism for each species, the percentage of the fouling plate covered by each species, and the proportional cover to show the relative dominance of each species over time. The percent and proportional cover are shown as sparkline timeseries that span the three year experiment. Each time series is scaled to others in its site and row. Start and ending percentages are shown and if the time series is strongly peaked the maximum percentage is also shown. The percent cover is the average replicate samples and are highly variable. The standard deviations can be found Table 2 in Winston and Jackson (1984).

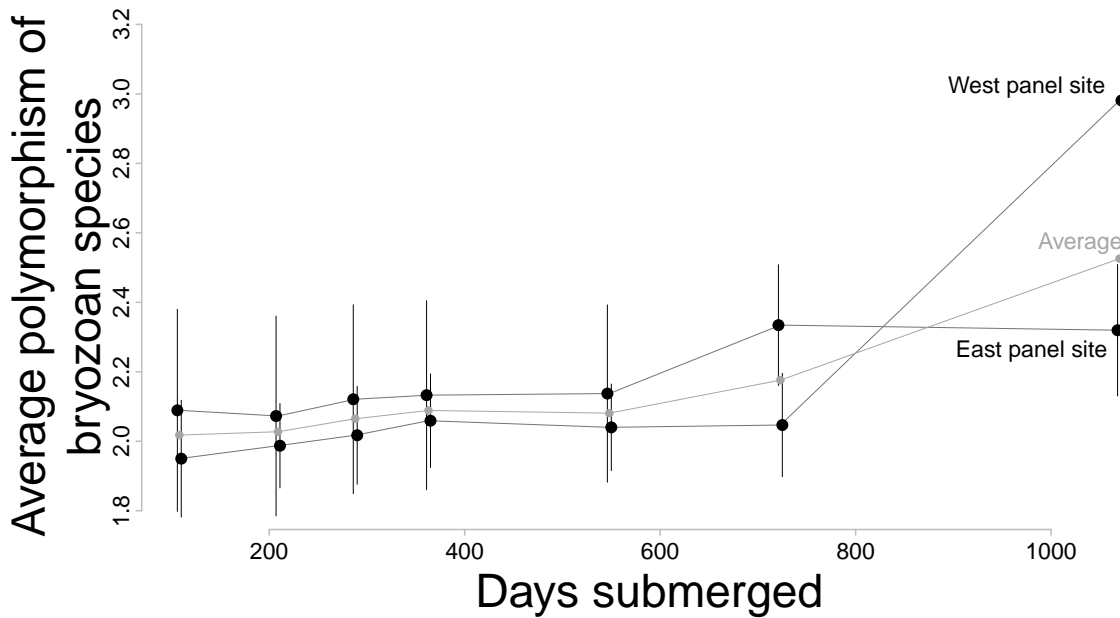


Figure 4: A direct comparison of competitive ability and polymorphism. Here we transform the percentage cover observed by Winston and Jackson (1984) to a relative proportion cover for each species to track the relative dominance of each species over time. We used the information in Fig. 3 to calculate the average number of polymorph types across species by weighting each species by its relative proportional cover. The average degree of polymorphism increases over three years despite the co-occurrence of species that differ in polymorphism. For both replicates pooled, the correlation of average polymorphism and time (Spearman's ρ) is equal to 0.64 ($P = 0.014$). Time and polymorphism are also correlated in both replicate panels considered separately (west panel: Spearman's $\rho = 0.89$, $P = 0.012$; east panel: Spearman's $\rho = 0.93$, $P = 0.008$). The error bars summarize the variation among plates at each site and show one standard deviation on either side of the mean. We also offset the census days for east and west sites by 2 days to avoid overplotting of the points and error bars.

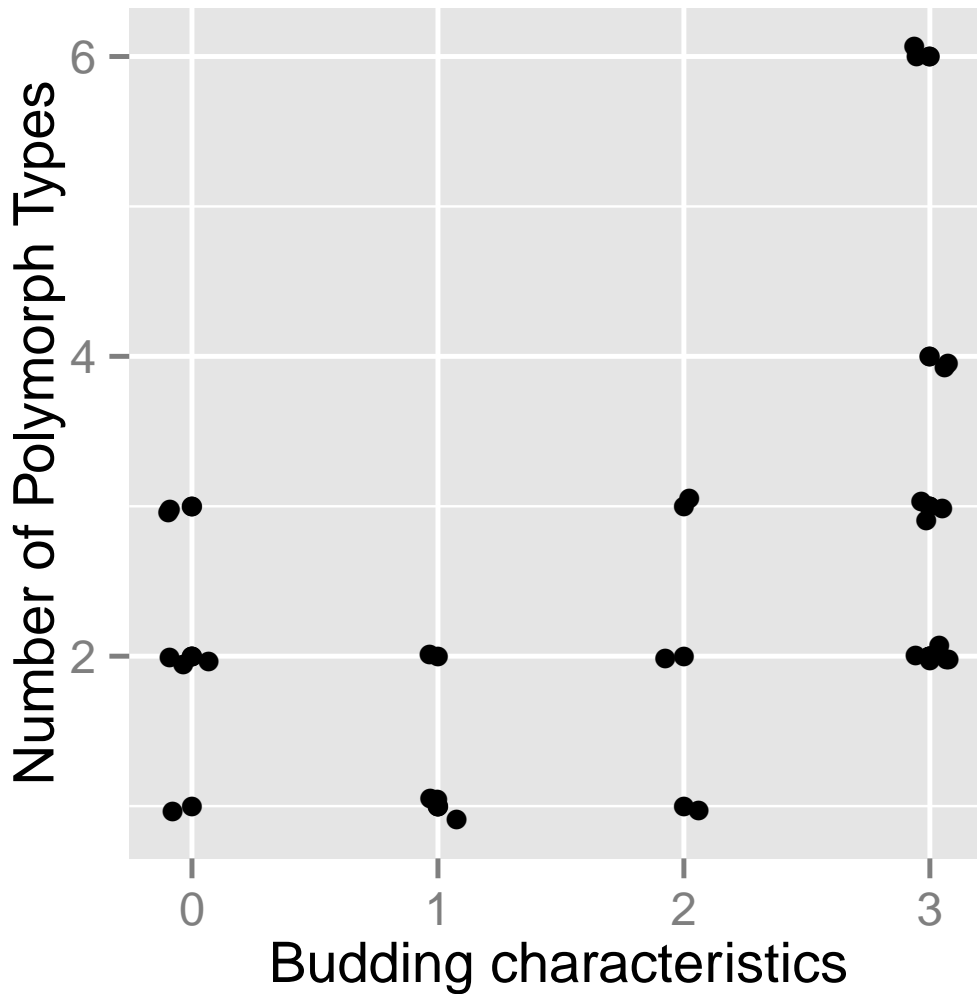


Figure 5: A comparison of budding characteristics and polymorphism of abundant encrusting ascophoran bryozoans. Bryozoans come from substrates that range in stability from algal fronds to corals and reef framework. Species are scored for the presence of three budding characteristics: multizoidal budding, self-overgrowth, and frontal budding. A species with all three budding characteristics will have a score of 3. Higher scores are correlated with an increased competitive ability. Data on budding characteristics is from McKinney and Jackson (1991), Table 7.2. and the species list, incidence of polymorphism and budding score used for this plot is shown in Table 2.

Table 1: Polymorph types for ascophoran cheilostome bryozoan species from shallow coastal waters of the East Pacific and Caribbean of Panama. We show the number of distinct polymorphs of each type observed in a species, which maybe more than the maximum observed in any single colony. N = number of sampled colonies; Ov. = Ovicell; Sp. = spines; Ad. Av. = Adventitious Avicularia; Vic. Av. = Vicarious Avicularia; K. = kenozooid.

Species	N	Ocean	Ov.	Sp.	Ad. Av.	Vic. Av.	K.	Total
<i>?Coleopora corderoi</i>	2	Caribbean						0
<i>Coleopora americana</i>	4	Caribbean		1				1
<i>Escarina porosa?</i>	2	Caribbean	1					1
<i>Exechonella antillea</i>	14	Caribbean		1				1
<i>Hippopodina</i> sp. 2	2	Caribbean	1					1
<i>Reptadeonella bipartita</i>	3	Caribbean			1			1
<i>?Hippoporina</i> sp.	2	Caribbean	1		1			2
<i>Gephyrophora rubra</i>	6	Caribbean	1		1			2
<i>Hippopodina feegeensis</i>	18	Caribbean	1		1			2
<i>Hippopodina irregularis</i>	6	Caribbean	1		1			2
<i>Hippoporina</i> sp.	2	Caribbean	1		1			2
<i>Parasmittina</i> sp. 2?	15	Caribbean	1		1			2
<i>Schedocleidochasma porcellanum</i>	12	Caribbean	1		1			2
<i>Schizoporella cornuta</i>	1	Caribbean	1		1			2
<i>Smittoidea pacifica</i>	17	Caribbean	1		1			2
<i>Stylopoma spongites</i>	1	Caribbean	1			1		2
<i>Crepidacantha longiseta</i>	14	Caribbean	1	1	1			3
<i>Crepidacantha</i> sp. A	10	Caribbean	1	1	1			3
<i>Escharina porosa</i>	4	Caribbean	1		1	1		3
<i>Gemelliporidra multilamellosa</i>	19	Caribbean	1		2			3
<i>Rhynchozoon rostratum</i>	4	Caribbean	1	1	1			3
<i>Tremogasterina mucronata</i>	5	Caribbean	1	1	1			3
<i>Celleporaria mordax?</i>	18	Caribbean	1	1	1	1		4
<i>Celleporaria albirostris</i>	20	Caribbean	1	1	1	1		4
<i>Celleporaria mordax</i>	2	Caribbean	1	1	2			4
<i>Escharina porosa</i>	8	Caribbean	1	1	1	1		4
<i>Hippaliosina rostrigera</i>	8	Caribbean	1	1	2			4
<i>Hippopleurifera belizae</i>	10	Caribbean	1	1	2			4
<i>Hippopleurifera</i> sp.	2	Caribbean	1	1	2			4
<i>Parasmittina serrula</i>	26	Caribbean	1	1	2			4
<i>Parasmittina spathulata</i>	6	Caribbean		1	3			4
<i>Rhynchozoon solidum</i>	1	Caribbean	1	1	1	1		4
<i>Rhynchozoon spicatum</i>	6	Caribbean	1	1	2			4

continued ...

Table 1: Polymorph types for ascophoran cheilostome bryozoan species from shallow coastal waters of the East Pacific and Caribbean of Panama. We show the number of distinct polymorphs of each type observed in a species, which maybe more than the maximum observed in any single colony. N = number of sampled colonies; Ov. = Ovicell; Sp. = spines; Ad. Av. = Adventitious Avicularia; Vic. Av. = Vicarious Avicularia; K. = kenozooid.

Species	N	Ocean	Ov.	Sp.	Ad. Av.	Vic. Av.	K.	Total
<i>Stylopoma</i> n. sp. 15	1	Caribbean	1		3			4
<i>Stylopoma projecta</i>	1	Caribbean	1		2	1		4
<i>Trematooecia aviculifera</i>	3	Caribbean	1	1	1	1		4
<i>Trematooecia turrita</i>	3	Caribbean	1	1	2			4
<i>Gemelliporidra belikina</i>	8	Caribbean	1	1	2		1	5
<i>Stylopoma spongites</i> type 2	28	Caribbean	1		2	2		5
<i>Stylopoma spongites</i> type 3	22	Caribbean	1		4	1		6
Caribbean totals:	40							336
<i>A. clustracasa</i>	2	Pacific			1			1
<i>Hippaliosina</i> sp.	2	Pacific			1			1
<i>Phylactelipora</i> sp.	2	Pacific	1					1
<i>Reptadeonella bipartita</i>	13	Pacific			1			1
<i>Reptadeonella tubulata</i>	6	Pacific			1			1
<i>Reptadeonella tubulifera</i>	1	Pacific			1			1
<i>Tecatia sinaloensis</i>	1	Pacific			1			1
<i>Adeona tubulifera</i>	6	Pacific	1		1			2
<i>Calypthotheca</i> sp. 1	4	Pacific	1		1			2
<i>Celleporaria mordax</i>	1	Pacific		1	1			2
<i>Derpanophora tuberculatum</i>	2	Pacific	1		1			2
<i>Hippopetraliella dorsiporosa</i>	6	Pacific	1		1			2
<i>Hippoporella costulata</i>	1	Pacific	1		1			2
<i>Hippopetraliella japonica</i>	2	Pacific	1		1			2
<i>Lagenicella hippocrepis</i>	2	Pacific	1	1				2
<i>Parasmittina</i> sp. 2	6	Pacific	1		1			2
<i>Reptadeonella cf tubulifera</i>	2	Pacific	1		1			2
<i>Rhynchozoon tuberculatum</i>	8	Pacific	1		1			2
<i>Schedocleidochasma contractum</i>	1	Pacific		1	1			2
<i>Schedocleidochasma porcellanum</i>	14	Pacific	1		1			2
<i>Tremogasterina mucronata</i>	1	Pacific	1		1			2
<i>Trypostega venusta</i>	4	Pacific	1			1		2
<i>Celleporaria aperta</i>	2	Pacific	1		1	1		3

continued ...

Table 1: Polymorph types for ascophoran cheilostome bryozoan species from shallow coastal waters of the East Pacific and Caribbean of Panama. We show the number of distinct polymorphs of each type observed in a species, which maybe more than the maximum observed in any single colony. N = number of sampled colonies; Ov. = Ovicell; Sp. = spines; Ad. Av. = Adventitious Avicularia; Vic. Av. = Vicarious Avicularia; K. = kenozooid.

Species	N	Ocean	Ov.	Sp.	Ad. Av.	Vic. Av.	K.	Total
<i>Escharina pesanseris</i>	2	Pacific	1	1	1			3
<i>Escharina porosa</i>	2	Pacific	1	1	1			3
<i>Microporella marsupiata</i>	4	Pacific	1	1	1			3
<i>Microporella umbracula</i>	4	Pacific	1	1	1			3
<i>Parasmittina fraseri</i>	1	Pacific	1	1	1			3
<i>Rhynchozoon globosum</i>	6	Pacific	1		2			3
<i>Rhynchozoon verruculatum</i>	10	Pacific	1	1	1			3
<i>Schizoporella cornuta</i>	6	Pacific	1	1	1			3
<i>Stylopoma minuta</i>	2	Pacific	1		2			3
<i>Trematooecia hexagonalis</i>	6	Pacific	1	1	1			3
<i>Trematooecia turrata</i>	3	Pacific	1	1	1			3
<i>Celleporaria brunnea</i>	2	Pacific	1	1	1	1		4
<i>Hippoporella gorgonensis</i>	14	Pacific	1	1	2			4
<i>Parasmittina crosslandi</i>	22	Pacific	1	1	2			4
<i>Parasmittina sp.5</i>	2	Pacific	1	1	2			4
<i>Parasmittina hastingsae</i>	4	Pacific	1	1	2			4
Pacific totals:	39							179

Table 2: Budding characteristics and polymorphism for 20 ascophoran cheilostome bryozoan species. The score is determined by the presence multizoidal budding, self-overgrowth, and frontal budding. Data on budding characteristics is from McKinney and Jackson (1991), Table 7.2.

Species	Budding score	Polymorph types
<i>Celleporella hyalina</i>	1	1
<i>Reptadeonella biparta</i>	2	1
<i>Escharella immersa</i>	0	2
<i>Fenestrulina malusi</i>	0	2
<i>Microporella cribosa</i>	0	2
<i>Reptadeonella costulata</i>	2	2
<i>Schizoporella errata</i>	3	2
<i>Schizoporella sanguinea</i>	3	2
<i>Schizoporella schizostoma</i>	3	2
<i>Schizoporella unicornis</i>	3	2
<i>Thalamoporella californica</i>	1	2
<i>Celleporella fusca</i>	3	3
<i>Escharina hynmanni</i>	0	3
<i>Microporella ciliata</i>	0	3
<i>Parasmittina raigi</i>	3	3
<i>Petraliella bisinuata</i>	2	3
<i>Rhynchozoon llarreyi</i>	3	3
<i>Schizoporella auriculata</i>	3	4
<i>Trematooecia aviculifera</i>	3	4
<i>Stylopoma spongites</i>	3	6