RESEARCH ARTICLE

An ecological driver for the macroevolution of morphological polymorphism within colonial invertebrates

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Abstract

Colonial marine invertebrates, such as corals and bryozoans, have modular growth. Individual modules within a colony are homologous to an individual solitary animal body. But in contrast to the predominately sexual origin of solitary animal bodies, modules within a colony are always produced asexually. The repetition of modules and the indeterminism of their organization gives colonies the ability to grow in ways solitary animals cannot. Colonial invertebrates consequently grow in such a way as to resemble weeds, bushes, or trees. The multitude of growth forms of colonial invertebrates arise from differences how individual colonies within a species tend to invest their energy into modular growth, persistence, asexual propagation, and sexual reproduction. Moreover, many colonial invertebrates possess several body types, morphological polymorphism among modules, where modules qualitatively differ in shape, size, and function. In this paper, I propose a mechanism that links the origin of novel body types to the evolution of life-history strategies among species. When colonies first evolve from solitary ancestors, the life-history strategy of the colony remains constrained by the life-history strategies of the individual modules within the colony until a new polymorph type evolves. The addition of novel body types within a colony introduces potential variation in life-history strategies. Colonies can then change strategies by regulating the frequencies of body types within the colony. This, along with the ability of body types to simplify their structure permits colonies to evolve more complex life-histories. Each new polymorph type that evolves permits more variation in colonial life-histories to exist.

KEYWORDS
coloniality, individuality, life-history evolution, major transitions, polymorphism

1 | INTRODUCTION

When bryozoans or other colonial organisms first evolved, they inherited all of their features from their solitary ancestors. The animals that form basal colonial species are homogeneous in most every way because they consist of clonal copies of the founding animal, and consequently do not have a wide variety of life histories (McKinney & Jackson, 1991). Over macroevolutionary time, new attributes evolved in the context of the colonial way of life. For example, many bryozoans, cnidarians, and some urochordates evolved multiple body types within a single colony. Each taxon has its own terminology for describing their various body types, but in general a colony with many body types is said to possess morphological polymorphism (Harvell, 1994; Simpson, 2012). With polymorphic body types,

animals within a colony specialize on tasks, such as reproduction, feeding, and defense (Beklemishev, 1969; Lidgard, Carter, Dick, Gordon, & Ostrovsky, 2012; Ryland, 1970; Schack, Gordon, & Ryan, 2018; Simpson, Jackson, & Herrera-Cubilla, 2017; Wilson, 1975). The ability to have diverse body types within a colony may be why species of colonial invertebrates exhibit a surprisingly wide variety of life-history strategies (Jackson, 1986a; McKinney & Jackson, 1991).

Polymorphism has evolved independently in many groups of colonial marine invertebrates, including bryozoans, hydrozoans, octocorals, graptolites, and thaliaceans (Harvell, 1994; Simpson, 2012; Wilson, 1975). Additionally, polymorphism has evolved within eusocial insects, including ants, bees, and termites, all of which have queens and workers that are phenotypically distinct (Harvell, 1994; Wilson, 1975). Observations of polymorphism in eusocial insects suggest that increased genetic relatedness aids in the evolution of phenotypic polymorphism (Abbot et al., 2011; Queller & Strassmann, 1998), so that the ease that distinct queen and worker castes in ant colonies evolve improves with increased relatedness among members (Abbot et al., 2011; Hamilton, 1964; Williams, 1966).

If our understanding of social insects applied to colonial animals, we would expect that they would all be polymorphic because colonial marine invertebrates are all clonal, and therefore are maximally related to each other. However, polymorphism is not ubiquitous across colonial animals (Harvell, 1994; Simpson, 2012; Wilson, 1975). Genetic homogeneity is one reason it is surprising that corals and ascidians, for example, have never evolved polymorphism (Harvell, 1994; Simpson, 2012) despite hundreds of millions of years of evolutionary history and extensive polymorphism in other members of their phyla. Therefore, some mechanism other than relatedness is necessary to understand the evolution of polymorphism.

Cheilostome bryozoans provide the best opportunity to understand the evolution of polymorphism because they span the known range of polymorphism in colonial animals (Simpson, 2012). Some species are monomorphic, many species have one or two types, while others have a dozen (or more) polymorph types (Silén, 1977; Simpson et al., 2017). Furthermore, cheilostome bryozoans are particularly interesting because of the diversity of growth forms. For example, some cheilostome bryozoans colonies can be small, with few widely spaced members. These species tend to find and settle on unoccupied seafloor. Their colonies extend out in a diffuse but wide form and reaching sexual maturity as soon as possible. Other cheilostome species only settle on already occupied space. They then proceed to out compete species already present, and eventually build robust and long-lived colonies with billions of members. Many other growth forms occur (McKinney & Jackson, 1991). The variety of growth forms and life-history strategies that cheilostome bryozoans have would not be possible with the typical morphological constraints of solitary animals.

Wilson (1968) proposed that the number and frequency of polymorph types within ant colonies is optimized to the environment, a hypothesis that he termed the ergonomic hypothesis. Starting with Schopf (1973), the ergonomic hypothesis was tested with bryozoan

colonies and yet was never observed (Hughes & Jackson, 1990; Schopf, 1973; Simpson et al., 2017). Instead, species with all degrees of polymorphism tend to coexist but that those species with more polymorph types tend to be ecologically dominant (Simpson et al., 2017). Moreover, when polymorphism first evolves in a taxon, the first morphologically distinct polymorph type to evolve is always a reproductive specialist—one polymorph type becomes responsible for the production of new colonies by sexual reproduction (Simpson, 2012). As additional polymorph types evolve, the relative frequency of reproductive specialists declines (Simpson, 2012).

In this paper, I explore the connection between polymorphism and life-history to understand the ecological and evolutionary mechanisms involved in the macroevolution of polymorphism. I present a hypothesis, termed the "life-history ratchet," that links the origin of novel life-history strategies to the origin of novel polymorph types. I show that new polymorph types differ from others in their individual strategy of energy investment, and that by varying the frequencies of polymorph types within a colony, the colony can form new life-history strategies. If the novel life-history strategies are ecologically advantageous then the novel polymorph type will likely become fixed. Over macroevolutionary time, this ratcheting leads to an increase in the number of polymorph types and life-history strategies within evolutionary lineages.

2 | COLONIAL LIFE-HISTORY STRATEGIES

If organisms (solitary or colonial) can only control a limited amount of energy, then they must evolve a strategy of investing that energy into growth, maintenance, asexual propagation, and sexual reproduction in such as way as to match their ecological needs. A species' life-history strategy refers to the pattern of investment that its constituent organisms tend to have. Strategies may differ among species because of energetic tradeoffs and the needs of their particular ecologies. For example, it is not possible to have a large number of offspring where each is large and costly to produce, as numerous expensive offspring would likely exceed the parent's energy budget. Rather, organisms evolve to have numerous small and inexpensive larvae or few large expensive ones. Likewise, organisms can brood larvae, investing in caring until they are ready to survive on their own, or organisms can let their larvae disperse early to fend for themselves. Whatever life history strategy that evolves within an individual species emerges as a consequence of that species' specific ecological needs.

Within an animal phylum, the bodyplan of the phylum restricts species to a narrow range of life-history strategies even if the phylum lives in many different environments. For example, the life-history strategy of a basal animal, like a sponge, involves having the ability to grow indeterminately, withstand partial death to regrow, and asexually propagate. In contrast, the life history strategy of a more derived animal, such as a snail, lacks most of the life-history attributes of the sponge, and instead the snail spends all its energy on making numerous offspring. Life-histories can vary within phyla,

but depending on the developmental constraints the phyla has, the variation is limited. Snails can vary the number and size of their offspring, limit or increase the yolk they provide. But their variation in life history is limited; the snail's developmental constraints prevent them from asexually propagating for example. And even parthenogenic snails achieve asexual reproduction by utilizing unfertilized embryos rather than clonal budding.

Because energy is always limited but ecological success is paramount, new patterns of investment may lead to novel ecological opportunities. Coloniality is one example of this. The colony, formed by large numbers of asexually produced organisms, has the possibility to take on different patterns of energetic investment than individual members can which provides species that evolve colonial growth with potential new ecological opportunities (Buss, 1979). Colonial organisms occur in many phyla, and despite the differences in their phylum-specific body plans and inherent constraints of life-histories, as colonies, they share many major features of life-history and ecology (Buss, 1979; Jackson, 1986a; Jackson & Coates, 1986), including a tendency for colonial species of all phyla to brood larvae (Strathmann, 2020).

Many colonial invertebrates, such as cheilostome bryozoans, relax constraints on their body plans and evolve distinct polymorph types that are genetically identical and occur together within the same colony (Harvell, 1994; Ryland, 1970; Silén, 1977). Members sometimes evolve modified body plan that lack major parts of their ancestral bodies (Carter, Gordon, & Gardner, 2010), losing their ability to feed for example. This is possible because many modules are also physically and physiologically connected between members (Ryland, 1970). Those members that are unable to feed themselves due to their modified bodies are able to survive and function because they are nourished by resources shared with them by physiologically connected feeding members (Ryland, 1970). Once polymorphism evolves, further ecological benefits emerge.

3 | A MODEL OF COLONIAL LIFE-HISTORIES

To understand what polymorphism does for a colony, it is important to know what colonial features occur ancestrally, before the evolution of polymorphism. Uniform, homogeneous, monomorphic colonies are the most common type of colony and society (Simpson, 2012), but monomorphic colonies do not all have the same history. Many monomorphic colonies can be newly evolved from solitary ancestors. They can also be ancient and stable, as they are in ascidians (Zeng, Jacobs, & Swalla, 2006), and corals (Coates & Oliver, 1973). In colonial taxa that lack polymorphism, such as corals, coloniality may be lost (Barbeitos, Romano, & Lasker, 2010; Simpson, 2013). Despite many independent origins, monomorphic colonies share many similarities with each other, including constituent animals with large sizes, larger-scale colonies (not necessarily colonies with more members, but large absolute scale), and similar reproductive

strategies (Hughes & Cancino, 1986; Jackson, 1977; Jackson, 1986a; Jackson, 1986b; Jackson & Coates, 1986). These similarities among independent origins of coloniality arise because they are all inherited from solitary ancestors.

To see how basal colonial life-histories are inherited from solitary ancestors, let's use a simple model. Imagine a solitary polyp, similar to a sea anemone, living on the sea floor. It has a simple life-cycle starting as a larvae in the plankton before settling on a patch of seafloor and then growing larger. When it reproduces, it can do so sexually or asexually. It reproduces asexually by budding, then after physically separating, its daughter polyp moves off to live nearby. Otherwise it sexually produces a larvae that disperses further afield. After some time, and numerous reproductive events, both asexual and sexual, the polyp may die. Because this organism has a finite amount of energy, there are trade-offs between how much energy it can spend for each of its life-history attributes.

The total life-history budget of this polyp is partitioned between growth (g), persistence (p), asexual (a), and sexual (s) reproduction. For this polyp, or any other, this partitioned life-history budget can be expressed as a vector where each element is the investment in a life-history attribute:

$$b = \begin{bmatrix} g \\ p \\ a \\ s \end{bmatrix}.$$

Particular life-history strategies are expressed by the values of the elements in the vector b and that different strategies will differ in the values in the elements of b.

The ability for solitary species to transition from one life-history strategy to another (from b to b') tends to be constrained by details of development. To consider why this is the case, consider, for example, two related snail species. Due to their shared bodyplan, they will both lack the ability to reproduce clonally and have determinant growth. Both species will therefore have zeros in those two elements of their b vectors. The b vector for two related solitary snail species cannot be that different from each other:

$$b_{snail1} = \begin{bmatrix} 0 \\ p_{snail1} \\ 0 \\ s_{snail1} \end{bmatrix} \quad \text{and} \quad b_{snail2} = \begin{bmatrix} 0 \\ p_{snail2} \\ 0 \\ s_{snail2} \end{bmatrix}.$$

Moreover, the persistence (p) and sexual reproduction (s) elements for both snail species may in fact be similar in magnitude, such that the difference between the two snail's life-history strategies will be small.

Major changes in life-history strategy require shifting the magnitude and direction of this b vector. Solitary organisms that lack an ability to clone and possess determinate growth cannot easily change their bodyplans, and so they occupy constrained life-history strategies.

Now consider a colony of polyps. Each member polyp has its own life-history strategy, b. The colony, as a whole has a life history strategy (E) that is the average of its constituent's life-histories:

$$E = \frac{1}{n}\sum_{i=1}^{n}b_i$$

Where n is the number of polyps in the colony and b_i is the investment strategy of the ith polyp. Due to developmental constraints, polyps in the colony may not vary much at all, and so E is likely to equal b.

With the evolution of a new polymorph type there is the possibility for them to dramatically differ in life history strategies. One example of a dramatic change in the life history in a new polymorph type are the adventitious avicularia of bryozoans which lack the ability to feed and lose their asexual and sexual abilities. This magnitude of shift in life history is possible because the bryozoan animal is drastically reduced in adventitious avicularia (Carter et al., 2010). The loss of body parts is not common in solitary animals (with the exception of some parasites), but is common in colonial animals (McShea & Changizi, 2003) and also within cells during the transition to multicellularity (McShea, 2002), because simplified body types can be nourished by other members of the colony.

A new vector (b_2) can therefore be written summarizing the life-history strategy of the polymorph type:

$$b_2 = \begin{bmatrix} g_2 \\ p_2 \\ a_2 \\ s_2 \end{bmatrix}.$$

Through the loss of body parts, any of the elements in vector b_2 can change. When colonies have two or more body types, its overall life-history strategy is a function of the relative frequencies of body types (w_i). If each of n body types with different strategies (b_i) within a colony and the frequencies of body types within a colony (w_i), the overall life-history strategy of the colony is:

$$E = \sum_{i=1}^{n}w_i b_i.$$

The colony's life-history is a function of the differences in life-histories of its constituent body types and their frequency. This allows colonies to easily change life-histories by changing the frequency of body types it has.

We can quantify how the number body types a colony has influences the number of possible life histories by computing the total number of possible colony compositions for a colony with given number of body types (n) and a size (k). The exact number of colony compositions for a colony with k members and n body types can be calculated using n multichoose k from combinatorics:

$$\left(\!\!\binom{n}{k}\!\!\right) = \binom{n+k-1}{k} = \frac{(n+k-1)!}{k!(n-1)!},$$

which grows quickly as the number of body types increases. As expected, monomorphic colonies, those with only one polymorph type, have a fixed life history, identical to the life-history of its members regardless of colony size. Colonies with two body types have many possible life-histories: 10,001 possible strategies for colonies of 10,000, 11 possible strategies for colonies of 10 members. Increasing the number of body types to 3 or more leads to a wide range of possible body types.

It is important to note that some combinations of body types cannot survive, especially ones where only non-feeding members are present, for example. Consequently, the total number of combinations maybe slightly smaller than this calculation. However, the timing of differentiation between body types within a colony may vary also between species. If this occurs, it serves to further increase the number of possible strategies.

In bryozoans, each polymorph type differs dramatically from others in terms of its investment strategy (b_i). Autozooids are large, asexual, and in some species sexual. Kenozoids are small and asexual. Spines in bryozoans have a diversity of forms, and lack sexual and asexual abilities. The various types of avicularia have different sizes, some are small others large, some are asexual and some lack any ability to propagate. With body types as distinctive as they are in bryozoans, the number of life-history strategies that a colony with a given set may take will be close to that given by the multichoose calculation. If, however, body types are similar to each other, then the colony's possible available life-history strategies (E) produced by adding novel body types with modified life-histories (b_i) can be estimated by varying the frequencies of each polymorph type throughout the full range possible. The scale of E is quantifiable in by taking its norm, $\|E\|$. The variation among possible life-history strategies can be described by taking the difference from the average life history of colonies with all relative frequencies, $\|E\| - \overline{\|E\|}$, and is a function of the number of body types and their differences.

From the perspective of linear algebra, the numbers of body types needed to fully span E is equal to the length of the E vector. I have quantified life-history strategy with four elements, growth, persistence, asexual reproduction, and sexual reproduction. With this set of elements, only four body types are needed to span E, if the relative frequencies of body types are unconstrained. But the frequencies of body types are constrained—they can only be positive, and the frequencies of body types with non-zero sexual investment are empirically observed to decline as the number of body types increases (Simpson, 2012). Moreover, the first polymorph type to evolve introduces a division of labor where sexual reproduction is restricted to a single polymorph type (Simpson, 2012). Together these limit the frequencies of body types and consequently permits the evolution of more body types than the minimum required to span a small number of life-history attributes.

4 | THE MACROEVOLUTION OF POLYMORPHISM BY LIFE-HISTORY RATCHET—A HYPOTHESIS

When colonial species originate from solitary species, they inherit many features and adaptations that evolved under the ancestral solitary condition. An inherited life-history that evolved in a solitary
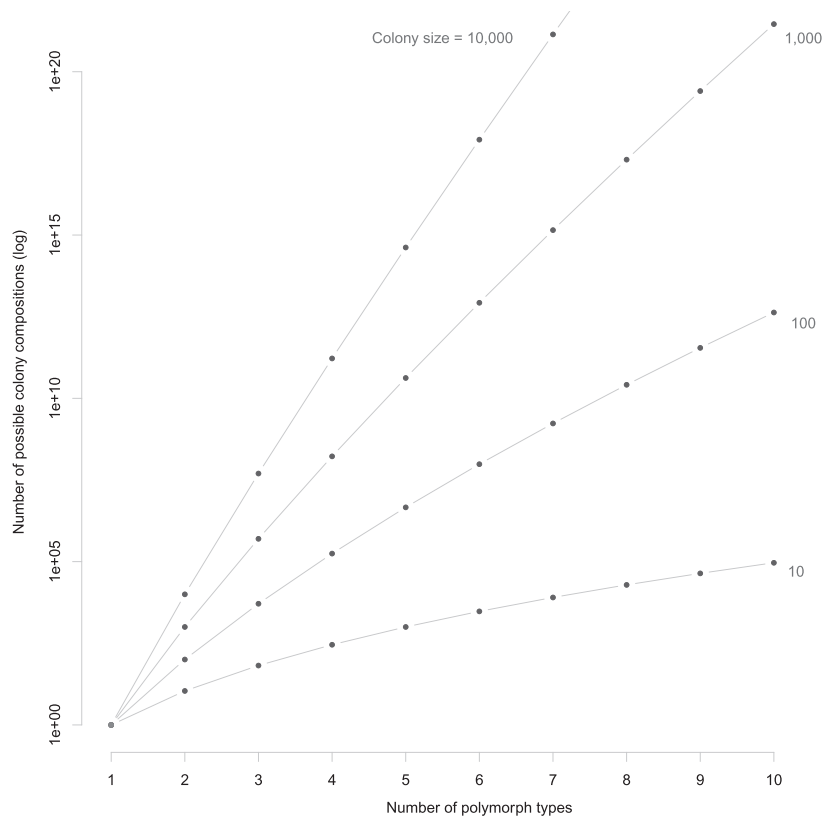
FIGURE 1 The variety of colony compositions available to a colony increases with the addition of body types (polymorphism), which consequently increases the potential variety of life-history strategies as measured by the number of possible colony compositions. Monomorphic colonies, those with only one polymorph type, have a fixed life history, identical to the life-history of its members regardless of colony size. As the number of body types within a colony increases, not only may the variation in life-history strategy among body types increase, but the frequency of each polymorph type with a colony can also vary. When more than one polymorph type occurs within a colony, the number of possible frequencies of body types within a colony of a given size is very large. The exact number of colony compositions for a colony with k members and n body types can be calculated using n multichoose k from combinatorics

organism may be very limiting in the new context of a colonial way of life. As shown in Figure 1 and the model of life-history variation within colonies presented above, evolving novel polymorphisms (new body types) can free a colony from a constraining life-history strategy. And changing the frequencies of the new body types allows colonies to further explore an ever-expanding array of life-history strategies.

I propose that the macroevolution of new body types is best understood in light of this link between their origin and the expansion in life-histories that they provide. Any successful novel life-history strategies associated with novel body types confers a fitness benefit to the colony containing the novel polymorph type and stabilizes and fixes polymorph type in the species. Moreover, because varying the frequency of that polymorph type within a colony permits the further exploration of life-history strategies, new species may originate through the adaptive exploration of strategies, increasing diversification rates. This process can repeat with the origin of each new polymorph type.

The end result of repeated rounds of new body types permitting new life-histories is a macroevolutionary ratcheting process, that I term the "life-history ratchet." Each lineage of species that evolves

under the life-history ratchet will have a diverse set of body types and a diversity of life-history strategies. Additionally, this process acts independently in each lineage and due to the undirected nature of evolutionary processes, will proceed along a different path in each lineage. Consequently, over time, each lineage will evolve a distinct sequence of body types. Yet, because it is the number of distinct the body types that influences life-history strategies and not the identity of those body types, different lineages will converge on similar life-history strategies.

5 | ALTERNATIVES, PREDICTIONS, AND TESTS OF THE LIFE-HISTORY RATCHET

The life-history ratchet is an ecological alternative to Wilson's ergonomic hypothesis. In ergonomic theory (Oster & Wilson, 1979; Wilson, 1968), colonial or social species tune the number of polymorph types (castes) and their frequencies, to balance the costs and benefits of polymorphism. Polymorph types are costly because many are non-feeding and require others in the colony to feed them. Moreover, many polymorphs are sterile and potentially lower the

reproductive capacity of the colony. The benefits of polymorphism arise from more efficient feeding and defense. The stability of the environment is thought to play an important role in ergonomic theory because it sets the timescale over which the optimization occurs (Simpson et al., 2017). But species can migrate into and out of stable environments over evolutionary timescales, and so ergonomic theory does not predict an increasing trend in the number of polymorph types over time. Rather, polymorph types can be lost when species that evolved in stable environments immigrate to less stable ones. Several studies have tested the ergonomic theory in bryozoans, but none have found the predicted correlation between environmental stability and the degree of polymorphism (Hughes & Jackson, 1990; Schopf, 1973; Simpson et al., 2017).

In contrast, the life-history ratchet hypothesis predicts that the macroevolution of polymorphism is cumulative, with lineages independently gaining novel polymorph types, and rarely if ever losing them due to the ecological advantages they confer. Because the origin of novel polymorph types are rare, and there are no optimal life-history strategies, polymorphism will not increase within all lineages. Moreover, the number of polymorph types is predicted to be associated with ecological dominance and an increase in the diversity of ecological strategies. There are empirical hints that higher levels of polymorphism are associated with ecological dominance—on settling plates, bryozoan species with more polymorph types increasingly dominate over ecological time, outcompeting species with fewer polymorph types in a pattern of succession (Simpson et al., 2017). Additionally, species with frontal budding, multizooidal growth, and the ability to self-overgrow, all correlates of ecological dominance (McKinney & Jackson, 1991), tend to occur in species with a wide array of polymorph types (Simpson et al., 2017).

However, some bryozoan polymorph types are expressed in a context dependent and inducible way (Harvell, 1991). In bryozoans, the majority of these types of inducible polymorphisms are of a single type, spines, and there is a diversity of forms spines may take on across species (Harvell, 1991, 1992, 1998). The presence of inducible polymorphs highlights the role of developmental control of polymorph expression. And to many, it suggests that the lack of a polymorph type in a species where related species possess it is due to developmental inhibition. Even in the 1920s, the question of whether or not inducible polymorphism indicated a macroevolutionary pattern from simple patterns of polymorphism to complex, or from low inhibition to highly regulated expression was a concern (Lang, 1921, pp. 34–35). And today it is an issue that we cannot resolve without a phylogenetic context and developmental data on how polymorph types are regulated within colonies. However, colony-level patterns involving the numbers, position, and orientations of several polymorph types within colonies are heritable at the colony level (Simpson, Herrera-Cubilla, & Jackson, 2020).

Because the sequence of gain of polymorph types among lineages are unlikely to be the same, it is likely that polymorph types that are similar among lineages are convergent. The patterns of acquisition, homology, and convergence among polymorph types observed among many lineages provides a strong test of the life-history ratchet. In previous work, I showed that there are relatively few bryozoan species

with a high diversity of polymorphism and that those species are likely to be phylogenetically independent (Simpson et al., 2017).

The life-history ratchet hypothesis predicts an increase in the possible life-history strategies associated with the origin of a novel polymorph type (Figure 1). In earlier work, I (Simpson, 2012) presented data that shows a positive association between the frequency of nonreproductive members and the number of polymorph types that is shared across all colonial and social groups. Using this dataset (Simpson, 2012), we can ask whether or not the variation in the frequency of nonreproductive members in bryozoans and colonial cnidarians species increases as the number of polymorphism increases from monomorphic, to dimorphic, and polymorphic with three or more polymorph types (Figure 2). Pooling together the frequencies of all nonreproductive polymorph types underestimates the variation possible in life-history strategies of species with polymorphic (three or more body types). Nevertheless, dimorphic bryozoan and cnidarian colonies both exhibit considerable variation in the frequencies of nonreproductive members. Polymorphic cnidarian species show an even greater range of variation in the frequency of nonreproductive members. Bryozoans with polymorphic colonies maintain a very high level of variation in the frequency of nonreproductive members. It is important to note that for all these species only one polymorph type is reproductive.

Another prediction of the life-history ratchet hypothesis is that clades with a constant number of polymorph types will diversify their frequencies of types over macroevolutionary time. This is difficult data to attain, as it requires a resolved phylogeny and detailed
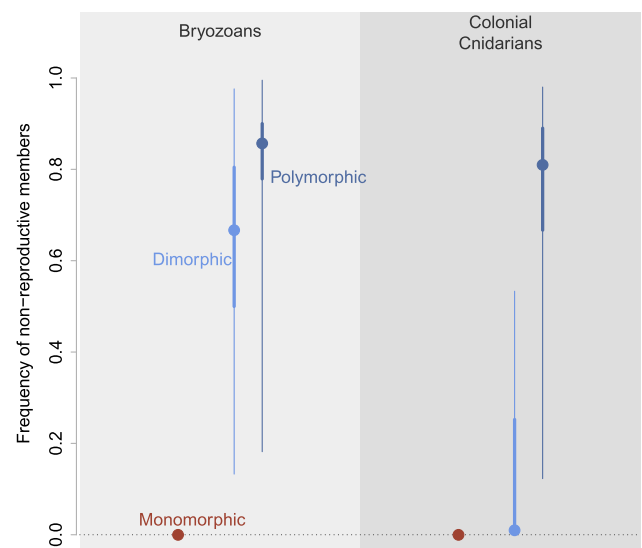

FIGURE 2 Species with dimorphic or polymorphic colonies show an increased variety of colony compositions. Dimorphic and polymorphic species always have only one reproductive body type, yet the frequencies of the reproductive and nonreproductive members can vary. Points indicate the median across species. Thick lines show the interquartile range. And thin lines show the maximum and minimum of the range. Data from Simpson (2012) [Color figure can be viewed at wileyonlinelibrary.com]
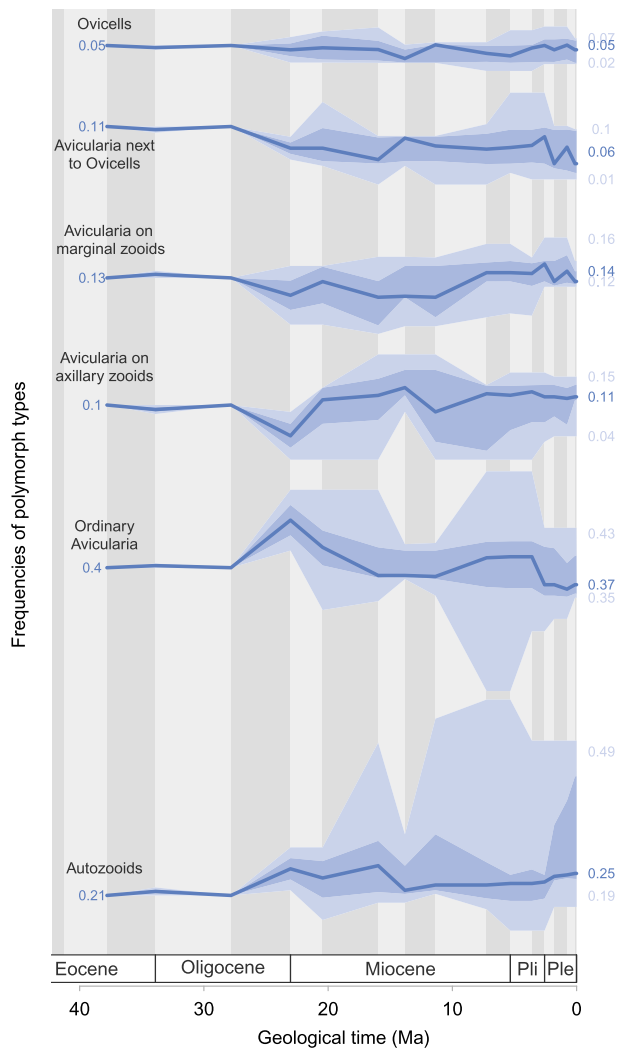
FIGURE 3 The macroevolution of colony composition among species of the bryozoan *Metrarabdotos*. Here, I track the distribution frequencies of specific polymorph types as *Metrarabdotos* species diversify and go extinct. Frequencies are constant within species but vary among species. As new species evolve, the distribution of colony frequencies increases. Contractions in this distribution come about by extinction. Median colony frequencies are tracked (indicated by numbers). And the interquartile range, maximum, and minimum frequencies are shown. Vertical gray bars denote geological stages. Data from Cheetham et al. (2007) [Color figure can be viewed at wileyonlinelibrary.com]

polymorph types and is only reduced by extinction (Figure 3). This result suggests that *Metrarabdotos* species tend to explore new variants of their ancestral life-history strategy, by evolving novel frequencies of each polymorph type, rather than species exploiting the same strategy over millions of years.

6 | CONCLUSIONS

The macroevolution of polymorphism in colonial animals remains a profound evolutionary problem. Attempts to understand the origin of polymorph types and division of labor have been dominated by work on social insects and therefore a focus on genetic relatedness as both necessary and sufficient for the evolution of body types that forego sexual reproduction and other general attributes that are important in evolutionary processes. However, colonial and clonal marine invertebrates demonstrate the insufficiency of genetic relatedness, because polymorphism is relatively rare. Here, I propose an alternative hypothesis. Rather than genetic relatedness acting to free colonial organisms to evolve complex features, it instead binds them to life-history strategies that evolved in different contexts and yet are difficult to modify. Relatedness, and the monomorphism it produces, is something that must be overcome for colonial animals to take full advantage of the modular way of life. Polymorphism acts to free colonies from the limits of monomorphic and uniform genetic identity. Through polymorphism, colonies can evolve new ecological strategies, rich ways of life, and profoundly complex morphologies.

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stratigraphic sampling for all species in a genus. The bryozoan genus *Metrarabdotos* has been sufficiently studied (Cheetham, 1986; Cheetham, Sanner, & Jackson, 2007; Jackson & Cheetham, 1994, 1999) to provide a quantitative estimate of any macroevolutionary changes in the frequencies of polymorph types. Figure 3 shows the how the distribution in frequencies of each polymorph type changes as new species evolve. *Metrarabdotos* species increase in diversity from two basal species to 28 over the Neogene, but only five of these species remain extant (Cheetham et al., 2007). While the median frequency of each polymorph type remains stable as species diversity increases, the range of frequencies increases for all

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