Correlated evolution of sex and reproductive mode in corals (Anthozoa: Scleractinia)

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Sexuality and reproductive mode are two fundamental life-history traits that exhibit largely unexplained macroevolutionary patterns among the major groups of multicellular organisms. For example, the cnidarian class Anthozoa (corals and anemones) is mainly comprised of gonochoric (separate sex) brooders or spawners, while one order, Scleractinia (skeleton-forming corals), appears to be mostly hermaphroditic spawners. Here, using the most complete phylogeny of scleractinians, we reconstruct how evolutionary transitions between sexual systems (gonochorism versus hermaphroditism) and reproductive modes (brooding versus spawning) have generated large-scale taxonomic patterns in these characters. Hermaphrodites have independently evolved in three large, distantly related lineages consisting of mostly reef-building species. Reproductive mode in corals has evolved at twice the rate of sexuality, while the evolution of sexuality has been heavily biased: gonochorism is over 100 times more likely to be lost than gained, and can only be acquired by brooders. This circuitous evolutionary pathway accounts for the prevalence of hermaphroditic spawners among reef-forming scleractinians, despite their ancient gonochoric heritage.

Keywords: coral reef; evolution; life history; phylogeny; reproduction

1. INTRODUCTION

Sexuality refers to the degree and manner of sexual allocation, i.e. it describes whether and how investment in sex function is partitioned within an organism or colony. Reproductive mode concerns the manner in which reproduction or mating occurs, such as via internal fertilization, broadcast spawning or brooding. Population and quantitative genetic approaches to understanding the evolution of sexuality and reproductive mode have focused on the conditions under which selection on these traits can occur. Experimental tests in these fields take advantage of intraspecific variation in responses of an organism to the putative ecological factors mediating selection on these traits (e.g. [1,2]).

The macroevolutionary patterns and consequences of sexuality and reproductive mode, as well as those of many other life-history traits, have been much less explored. The simplest model of the evolution of two traits is one ascribing equal and independent rates of state change. However, this straightforward explanation of macroevolutionary patterns in sex and mode appears uncertain in light of the correlation between these characters as sometimes seen in species tallies of higher Linnean ranks [3]. Hence, correlations in rates of evolution between sexuality and reproductive mode may influence the marked and unexplained variation between higher level taxonomic units in the state frequencies of these traits. Explaining broad-scale taxonomic patterns of sex and mode is also complicated by the fact that there exist

numerous possible combinations of transition rates between the states of each trait that can generate a given set of state frequencies in a taxon, but these rates remain essentially unknown.

Using scleractinian corals as a model, we explore several issues concerning sexuality and reproductive mode from a macroevolutionary perspective. First, we ask to what extent does the state of an organism's reproductive mode influence the evolution of its sexual system and vice versa? For example, studies have often found that hermaphroditism is associated with brooding, and several ideas have been put forth to account for this pattern [4,5]. Second, what accounts for large-scale phylogenetic patterns in reproductive characters? In particular, why are so many species of scleractinian corals broadcast-spawning hermaphrodites? Over two-thirds of coral species tallied to date [6] possess this type of mating system. This pattern stands in contrast to that of non-scleractinian anthozoans, which are more often gonochoric and about equally brooding or spawning [5,7,8]. Finally, we ask what is the evolutionary history of sexual system and reproductive mode? Unlike some other groups of marine invertebrates with good fossil records (echinoids: [9]; gastropods: [10]), coral skeletons do not unequivocally record reproductive or developmental characteristics. As an alternative, several authors [11–14] have used the frequency of reproductive states of extant species within higher level taxonomic groups to make tentative, but conflicting inferences about the ancestral condition of sexual system and reproductive mode. However, this approach fails to account for variation owing to phylogenetic relatedness, which can inflate perceived associations between traits [15]. Hence, to address the above questions, we used the phylogenetic comparative method of evolutionary biology.

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With maximum-parsimony and maximum-likelihood methods, we reconstruct character states onto a previously published coral supertree, and estimate rates of evolutionary transitions among and between reproductive modes and sexuality.

2. MATERIAL AND METHODS

(a) Reproductive data

We defined sexuality as a binary character (*sensu* [16]) with 'hermaphroditic' signifying that every polyp throughout the species is alike in this trait and 'gonochoric' signifying that polyps are not alike in sexuality. Population-level studies of gonochoric species often reveal a low incidence of hermaphroditism [13]. Consequently, species with mixed sexuality are here considered as 'stable' gonochores following Giese and Pearse [17]. Similarly, mode of development is also treated as a binary character with species categorized as either brooders or broadcast spawners. Mixed reproductive mode in *Pocillopora damicornis* and *Goniastrea aspera* was represented on the phylogeny as sister branches with brooding and spawning states. We found information on sexuality and reproductive mode for 368 species (28% of extant Scleractinia), 108 genera (48%) and 20 families (80%) from all seven suborders (electronic supplementary material, table S1). Of these species, 187 or 50.8% are reported here for the first time to our knowledge, and 349 or 94.8% have data on both sex and mode.

(b) Phylogeny and taxonomy

We used the largest available phylogeny of Scleractinia [18]. Large phylogenies possess more detailed character information and the statistical power to consider more complex patterns of character evolution [19]. To explicitly incorporate phylogenetic uncertainty, we performed our study using a subset of 25 randomly selected optimal trees from the analysis by Kerr [18]. Additional species were grafted post hoc onto the nodes subtending the relevant inclusive Linnean taxon when the grafted species' membership in the taxon cum clade was uncontroversial (*sensu* [20,21]). This resulted in a final confidence set of trees that were pruned to only include the 242 species for which we also possessed data on both sex and reproductive mode. Multifurcations were randomly resolved in an Adams consensus context. The taxonomy followed Cairns *et al.* [22] for azooxanthellate species and Veron [23] among zooxanthellate and apozooxanthellate forms, except for *Acropora*, which followed Wallace [24].

(c) Ancestral state reconstruction

To estimate the number of times that sexuality and reproductive mode evolved, as well as the rates of gains and losses of these characters over the trees, we mapped ancestral states using maximum-parsimony and maximum-likelihood methods. Sensitivity of parsimonious optimizations of reproductive characters on the shortest trees was assessed by comparing both accelerated- and delayed-state transformations [25] as implemented in MACCLADE 4.03 [26]. Parsimony mappings were the same whether unrooted or employing a corallimorpharian outgroup [27] using reproductive data from Daly *et al.* [28]. We also used maximum-likelihood model selection (the 'local' method of Pagel [29]) at the three most basal nodes: the root and those subtending the two basal subclades, Robusta and Complexa (*sensu* [30] *via* [18]) as implemented in DISCRETE 4.0 [29,31,32]. The probability p of a state at a node was calculated as its relative likelihood summed over all trees.

(d) Transition rates

To estimate transition rates, a simple four-parameter model $M(\alpha_1, \beta_1, \alpha_2, \beta_2)$ was initially considered in which sexuality and reproductive mode each evolve with independent forward and reverse transition rates. This model's fit to the data was tested via likelihood ratio tests in DISCRETE 4.0 by comparing the maximum-likelihood value with that of a full, eight-parameter model $M(q_{12}, q_{13}, \dots, q_{44})$ in which all state transitions covaried between characters. In the latter model, a rate parameter's subscripted indices record, respectively, the initial and final ordered pair of states for both characters: 1 $\equiv$ {gonochorism, brooding}, 2 $\equiv$ {gonochorism, spawning}, 3 $\equiv$ {hermaphroditism, brooding} and 4 $\equiv$ {hermaphroditism, spawning}. Parameter values estimated in the full model that were approximately equal suggested further tests to reduce model complexity.

(e) Handling phylogenetic uncertainty

The likelihood approach additionally permitted us to assess uncertainties in the parameter estimates owing to phylogeny reconstruction and branch lengths. Uncertainties in branch lengths were handled by maximum-likelihood estimation of the most complex model of transition rates over a range of monotonic transformations of initial branch lengths [31]. Trees were entered as ultrametric and then, using the branch-transformation parameter κ in DISCRETE (see [31]), compared using likelihood-ratio tests with that in which branches were of unit length, which approximates cladogenic evolution in a character, as when state change occurs solely at or near speciation events. We similarly tested for the possibility of rate heterogeneity in transitions across a tree by separately fitting the parameter from a four-category, discrete gamma distribution of rates [31]. To explicitly incorporate phylogenetic uncertainty into all analyses, the summed likelihoods of ancestral states or transition rates from each sampled tree was considered unweighted, approximating a uniform prior over the most probable trees [33].

To deal with taxon-sampling effects [34], we used the taxonomically most comprehensive analysis possible, one of the largest yet attempted. Nevertheless, shallow-water species were sampled 12 times more often than were their equally diverse deepwater forms [22], which are more likely to be gonochoric brooders. Thus, under-sampling of deepwater corals should have biased against our main findings of a more slowly evolving sexuality and an ancestral gonochorism recovered over all trees, branch-length sets and reconstruction methods. Finally, our conclusions are also insensitive to the placements of several taxa differing from those in more recent phylogenies [27,35]. For example, if the gonochoric Euphyllidae lies outside the large clades of hermaphrodites *sensu* [27], maximum likelihood would estimate an even lower rate of evolution in sexual system and in transition rates to gonochorism than those reported here.

3. RESULTS

(a) Ancestral-state reconstruction

Considering first sexual system, maximum-parsimony reconstruction indicated three major derived clades of mostly hermaphrodites, shown in green in figure 1. The first is comprised of numerous families from the suborder Faviina (from *Mycedium robokaki* to *Acanthastrea* spp. in figure 1). The second major clade is comprised mostly of Pocilloporidae and *Madracis* spp. (from *Pocillopora*

Figure 1. Ancestral reconstructions of sexual system and reproductive mode on one of 25 randomly bifurcated optimal trees with the 242 species used in the analyses. Colours on branches indicate maximum-parsimony mappings using an accelerated transformation (red, gonochorism; green, hermaphroditism; blue, brooding; orange, broadcast spawning). Relative maximum likelihoods of states are shown at the three basal-most nodes and based on the best-fit, four-rate model of state change. The basal subclades Robusta and Complexa (*sensu* [18,30]) extend above and below the root, respectively. When sex and mode are both invariant in a taxon cum clade, that group is shown as a single branch for economy of presentation.

damicornis to *Madracis* spp.). The third clade of hermaphrodites consists of members of Acroporidae, plus the poritids *Alveopora* spp. and others (from *Alveopora tizardi* to *Pseudosiderastrea tayamai*). Within these clades, there appear a few scattered reversions to gonochorism. By contrast, when considering reproductive mode, there are no large mono- to paraphyletic groups of either brooders or spawners and state transitions are much more frequent.

Parsimony under both delayed and accelerated transformations reconstructed the ancestral state of the root as a gonochoric spawner for all 25 randomly dichotomized most parsimonious trees with or without the addition of a corallimorpharian outgroup. However, the equivocal maximum-likelihood estimate for spawning indicates that, unlike sex, reproductive mode evolves too quickly to be accurately reconstructed via maximum parsimony: using the maximum-likelihood estimated values for the transition rate parameters (via the 'local' estimator of Pagel [29]), the root state was also overwhelmingly preferred as being gonochoric ($p = 0.850$; hermaphroditism: $p = 0.150$). Conversely, maximum likelihood was ambiguous as to reproductive mode for the root (brooding: $p = 0.565$; spawning: $p = 0.435$), the subclades Complexa (brooding: $p = 0.561$; spawning: $p = 0.439$) and Robusta (brooding: $p = 0.412$; spawning: $p = 0.588$).

(b) Transition rates

A likelihood ratio test found that the model $M(\alpha_1, \beta_1, \alpha_2, \beta_2)$ in which each character evolved independently was a significantly worse fit to the data (d.f. = 100; $\ln L = -3359.24$; $\chi^2 = 529.86$; $p < 0.0001$) than was the maximally complex version $M(q_{12}, q_{13}, \dots, q_{44})$ with eight parameters in which state transitions covaried between characters ($\ln L = -3094.31$). Model complexity was subsequently reduced by first testing the fit of promising seven-parameter forms, that is, by sequentially equating pairs of parameters as indicated by any approximately equal parameter values in the full, unconstrained model (electronic supplementary material, table S2). This suggested the final preferred model with four rate parameters (d.f. = 100; $\ln L = -3103.89$; $\chi^2 = 19.16$; $p > 0.9999$). Parameters in the reduced set were significantly greater than zero and the final model equated to a full version in which $q_{12} = q_{34}$, $q_{13} = q_{21}$ and $q_{24} = q_{31} = q_{42}$ (figure 2). Relaxing branch-scaling and rate-heterogeneity parameters during model selection did not result in significantly better fits than the preferred model above in which branches were of equal length and had identical transition rates (d.f. = 175; $\ln L = -3050.16$; $\chi^2 = 88.30$; $p > 0.9999$). Hence, we cannot reject that branch lengths are of unit length (i.e. sex and mode evolve in cladogenic or punctuated fashion) and that transition rates of each character are equal across the tree.

Rejection of $M(\alpha_1, \beta_1, \alpha_2, \beta_2)$ implies rejection of subsumed, simpler (i.e. effectively fewer parameter) models such as $M(\alpha_1 = \beta_1, \alpha_2 = \beta_2)$ and $M(\alpha_1 = \beta_1 = \alpha_2 = \beta_2)$. This indicated that transition rates differed significantly between, as well as among, characters. Reproductive mode was over four times more likely to evolve than was sexuality ($q_{12} + q_{21} + q_{34} + q_{43}$ versus $q_{13} + q_{31} + q_{24} + q_{42}$ in figure 2). Forward and reverse transition rates for each character were also unequal. There was a

Figure 2. Flow diagram showing most probable paths of correlated evolution in sexuality and reproductive mode among scleractinian corals. Subscripts of rate parameter q_{ij} refer to state transitions listed in §2. Decreasing robustness of arrows (from thick, medium, thin, to dashed) indicates decreasing magnitude of transition rates that do not significantly differ from one another via likelihood ratio tests.

fourfold greater rate of transition from brooding to spawning ($q_{12} + q_{34}$) than vice versa ($q_{21} + q_{43}$). As well, gonochorism evolved to hermaphroditism at an order of magnitude greater rate than the reverse transition. Among the four joint character states, transition rates differed by over two orders of magnitude. Among spawners, gonochores were an order of magnitude more likely to evolve brooding than were hermaphrodites. Conversely, among brooders, the evolution of spawning appeared independent of sexual system. Among gonochores, brooders were an order of magnitude more likely to evolve hermaphroditism than were spawners, while the reverse transitions to gonochorism among hermaphrodites were rare and appeared independent of reproductive mode (figure 2).

4. DISCUSSION

(a) Ancestral-state reconstruction

Both parsimony- and likelihood-based methods of character reconstruction indicate that the ancestor of scleractinian corals was gonochoric (figure 1). These results are consistent with this feature being the prevalent and presumably ancestral state in the rest of Anthozoa [28]. Harrison [12] notes that sperm-head morphology in gonochoric scleractinians is identical to that of other cnidarians and suggested that gonochorism was likewise a retained ancestral feature. The author also indicates that reproductive mode was too variable between taxa to speculate on the identity of its ancestral state. Indeed, in this study, maximum-likelihood model selection, which incorporates branch-length information, was likewise equivocal as to the ancestral state of reproductive mode (figure 1) because of high transition rates, indicating that the parsimony-based inference, which requires low rates for accuracy, is inappropriate.

Maximum-parsimony reconstruction reveals that hermaphrodites have independently arisen in three large, distantly related lineages consisting of most reef-building corals (figure 1). The ages of the oldest scleractinian genera found in each of these lineages as based on fossil first occurrences extend to at least the Middle Eocene expansion of modern reefs, ca 45 Myr ago [36,37]. Hence, hermaphroditic spawning has been a stable, long-term life-history strategy for most reef corals, despite

several small lineages and single species that have reverted to other combinations of sex and mode.

Our analysis also shows a strikingly high acquisition of brooding by Atlantic species (48% of species for which we have records versus 10% of Indo-Pacific species). These brooders have numerous independent origins, among both gonochoric and hermaphroditic lineages, including small groups or single species of Caribbean and western Atlantic endemics (figure 1 and electronic supplementary material, table S1). The relative abundance of brooders in the Atlantic has previously been attributed to lower rates of extinction in the Oligocene when compared with that of spawners [38]. However, our analysis indicates that switches in mode of reproduction have been the major mechanism accounting for the prevalence of Atlantic brooders (e.g. *Agaricia* spp., *Eusmilia fastigiata*, *Scolymia wellsi*, *Favia fragum* in figure 1).

Alternatively, the reconstructed states may not indicate the original conditions of Scleractinia, but rather the extinction probabilities associated with different life-history states. Character reconstruction methods generally assume either minimal extinction or that extinction rates are equal across character states [39]. Information about state change is lost when taxa go extinct that might have otherwise given rise to a lineage retaining information about states deeper in the tree [40]. Therefore, our reconstructions may instead reflect the dominant states of the lineages that have best survived on average the tumultuous, ca 250 Myr history of Scleractinia [41]. If so, reconstructions at the lower nodes suggest that gonochores have fared better through the early history of corals than have hermaphroditic species, perhaps because these also tend to be deep-water forms. Similarly, the equivocal reconstruction via maximum likelihood of ancestral reproductive mode (figure 1) could indicate that spawners and brooders have fared about equally well over time.

(b) Transition rates

Sexual system and reproductive mode in scleractinian corals evolve in a correlated fashion. The simpler models that we considered, in which state transitions in these two characters occurred independently, were significantly less preferred over the one with marked biases in transition rates between joint states. This indicates, for example, that the probability of evolving reproductive mode, such as switching from spawning to brooding (or vice versa), depends on a coral's sexuality, i.e. whether it is gonochoric or hermaphroditic. This association of sexuality and reproductive mode has been suggested for several animal groups (e.g. scleractinian corals: [11]; alcyonacean anthozoans: [5]; unionioid bivalves: [42]; asterinid asteroids: [43]), but its rate and direction of change have not previously been determined.

Among scleractinian corals, a 2×2 test of association between the binary states of sex and mode in the absence of phylogenetic information (table 1) is significant ($n = 349$; d.f. = 1; G -test with Williams' correction: $G_{adj} = 4.940$, $p = 0.0274$), suggesting correlated evolution of transition rates. However, this result is largely driven by the proportional increase in hermaphroditic spawners from speciose groups, such as the genus *Acropora*. Effectively, the putative high speciation rate of this genus [44]

Table 1. Number (and per cent) of species of scleractinian corals with different reproductive traits, excluding species with a pronounced mixed sexuality or reproductive mode, and those species for which only one of the two reproductive characters was known.

sexuality	reproductive mode		
	brooding	spawning	sum
gonochorism	19 (5.8)	80 (24.3)	=99 (30.1)
hermaphroditism	23 (7.0)	207 (62.9)	=230 (69.9)
summary	42 (12.8)	287 (87.2)	=349

inflates the apparent association between reproductive characters by 'pseudoreplicating' those species sharing hermaphroditic spawning by descent [15]. However, when considering the issue of character correlation by incorporating phylogenetic relationships into a large-scale analysis, here we show that the evolution of sexuality and reproductive mode across the Order Scleractinia is, in fact, unambiguously and highly correlated.

The correlated evolution of sex and mode is also consistent with the hitherto untested prediction, based on broad taxonomic trends, that reproductive mode evolves faster than sexual system among scleractinians. Harrison [45]; also [13] noted that hermaphroditism or gonochorism more often distinguish higher level taxa of scleractinians than does brooding or spawning, the latter two states often occurring in the same genus, or even species. In this study, reproductive mode was found to evolve at over four times the rate of sexual system. Interestingly, the predictions based on taxonomic tallies hold, despite the recently discovered and substantial conflict between Linnean and evolutionary units among corals [27,30,46,47], apparently because polyphyletic taxa almost always still occur within a clade monophyletic for their shared reproductive states.

Evolutionary transitions from planktonic development to brooding and back again might be expected to occur with equal ease in corals by a shift in the timing of release of propagules [13,48]. Since coral larvae are relatively unspecialized when compared with those of bilaterian invertebrates, there exist no known mechanical or developmental constraints to inhibit such transitions in either direction. Nonetheless, we find that scleractinian corals have a nearly fourfold higher transition rate from brooding to spawning compared with that of the reverse shift ($q_{12} + q_{34}$ versus $q_{21} + q_{43}$ in figure 2). Numerous evolutionary pressures could account for the evolutionary bias to spawning. For example, the average dispersal range of spawned larvae is larger than for brooders [13] and spawning reduces the potential for inbreeding [6]. Spawning also avoids the vertical transmission of algal symbionts that occurs in almost all brooded larvae [49], which could enable selection of locally appropriate symbionts when spawners colonize new habitat. Finally, only the reverse transition from spawning to brooding depends on sexuality, evolving at an order of magnitude higher rate among gonochores than among hermaphrodites (q_{21} versus q_{43}). Thus, the ease of an evolutionary shift from planktonic development to brooding suggests mediation by sexual selection, which can only operate among gonochores [1,2].

Our findings provide a robust evolutionary explanation for the prevalence of hermaphroditic spawning among scleractinian corals, revealing a complex evolutionary pathway with deep historical roots. Transition rates between states differed significantly and by as much as two orders of magnitude among, as well as within, characters. Gonochorism is over 100 times more likely to be lost than gained and then only among brooders (q_{21} versus q_{24} in figure 2), such that gonochoric spawners seldom, if ever, evolve hermaphroditism. Thus, the most probable pathways of state change (figure 2) indicate that a gonochoric spawner would preferentially shift to gonochoric brooding, then to hermaphroditic brooding before finally attaining hermaphroditic spawning—the dominant reproductive condition in shallow-water corals. This roundabout evolutionary journey is nevertheless twice as likely as a direct shift from gonochoric spawning to hermaphroditic spawning (figure 2). This bias accounts for the dominant reproductive condition among shallow-water scleractinians, hermaphroditic spawning. Further, in general, the reproductive traits generate the observed large-scale taxonomic and phylogenetic patterns of their joint character states through unanticipated and extended pathways of state change because the characters evolve in a correlated fashion.

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