frontiers | Frontiers in Marine Science

TYPE Original Research
PUBLISHED 10 January 2023
DOI 10.3389/fmars.2022.1068391

Sexual dimorphism in corallite size and modularity of a broadcast spawning coral, *Porites lobata*

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SPECIALTY SECTION
This article was submitted to Coral Reef Research, a section of the journal Frontiers in Marine Science

RECEIVED 12 October 2022
ACCEPTED 20 December 2022
PUBLISHED 10 January 2023

CITATION
Pedraza-Pohlenz RM, Balart EF, Tortolero-Langarica JJA, Rodríguez-Troncoso AP, Hellberg ME, Norzagaray-López O, Cabral-Tena RA, Cupul-Magaña AL and Paz-García DA (2023) Sexual dimorphism in corallite size and modularity of a broadcast spawning coral, *Porites lobata*. *Front. Mar. Sci.* 9:1068391. doi: 10.3389/fmars.2022.1068391

Differences in selective pressures and the energetic cost of gametes in gonochoristic corals should vary with the sex of the colony, which may lead to sexual dimorphism. Coral colonies are composed of subunits (corallites) that create a complex morphological architecture. If corallite features are distinct between sexes, then the degree of coordinated change among these subunits may also vary (phenotypic modularity). This study tested for sexual dimorphism in the corallites of the reef-building coral *Porites lobata*, a gonochoric broadcast spawner, and compared this with previously demonstrated sexual dimorphism in its congener *P. panamensis*, a gonochoric brooder. Corallite area in *P. lobata* was 17% larger for males than for females ($p < 0.05$). Phenotypic modularity analysis showed that the integration of skeletal traits differs between sexes in both *P. lobata* and in *P. panamensis*. In *P. lobata*, females showed a higher trait integration than males, while the opposite pattern was observed in *P. panamensis*. Our results demonstrate corallite traits differentiate between sexes and suggest that between-sex differences in the degree of corallite integration may vary with reproductive mode.

KEYWORDS

reproduction, morphometrics, *Porites*, corallite, Eastern Tropical Pacific (ETP), phenotypic modularity

1 Introduction

Sexual dimorphism is widespread among animals but has been considered rare in colonial marine taxa (Levitan, 2010). Recent studies on scleractinian corals, however, have found sexual dimorphism in size (Kramarsky-Winter and Loya, 1998; Loya and Sakai, 2008), calcification rates (Cabral-Tena et al., 2013; Tortolero-Langarica et al., 2016; Tortolero-Langarica et al., 2017; Mozqueda-Torres et al., 2018; Cruz-Ortega et al., 2020), skeletal isotopic signals (Cabral-Tena et al., 2013), and corallite morphologies (González-Espinosa et al., 2018). From these studies (Table 1), corallite differences have been found for only one species (González-Espinosa et al., 2018), leading us to ask whether the dimorphism previously observed (primarily in growth) could be seen in corallite's traits.

While inter-sexual differences may be more subtle in marine invertebrates (both clonal and unitary) than the conspicuous sexual dimorphism seen in many terrestrial animals (Berns, 2013), differences in mating strategies and the energetic cost of gametes (Parker, 1979) remain and should select for different trait optima between sexes (Parker, 1979; Levitan, 2008). In brooding gonochoristic corals, females both capture sperm for internal fertilization and, critically, brood larvae within their polyps, while males merely release sperm (Baird et al., 2009; Harrison, 2011). These differences may explain the divergent morphologies of their corallites (González-Espinosa et al., 2018). Meanwhile, in gonochoristic broadcast spawning corals, both sexes release their gametes and fertilization occurs externally (Baird et al., 2009; Harrison, 2011), with females freed of any larval care beyond provisioning eggs. This dissimilarity between reproductive mode could lead to different levels of sexual dimorphism in the corallites of reef-building species.

In modular plants, both morphology and integration of traits can differ between sexes (Barrett and Hough, 2013). As corals are modular organisms, sexual dimorphism could appear not only in the most fundamental unit of colony morphology (a single tentacled polyp and its underlying skeleton, the corallite) but also in the degree of integration among these units (Lasker et al., 2003; Shaish et al., 2007). The environment can induce morphological changes in colony architecture (phenotypic plasticity) (Todd, 2008) and in the integration between these traits (e.g., branch density and length, polyp aperture and distance between them), as seen in octocorals (Sánchez and Lasker, 2003; Sánchez et al., 2007) and scleractinian corals (Paz-García et al., 2015). Such integration of traits (modularity) has not been compared between sexes in corals.

Different reproductive modes carry different energetic costs among reef corals (Ward, 1995; Hall and Hughes, 1996), which in turn may lead to different levels of sexual dimorphism among reef-building species. In this study, we tested for sexual dimorphism in the corallite features and phenotypic modularity of two congeneric corals with separate sexes but different modes of reproduction: *Porites lobata* and *P. panamensis*. *P. lobata* is a broadcast spawner that shows sexual dimorphism in skeletal growth rates (Tortolero-Langarica et al., 2016; Table 1) but whose corallite morphology has not been previously tested for sexual dimorphism. Meanwhile, *P. panamensis* broods its larvae (Carpizo-Ituarte et al., 2011). Its corallites show sexual dimorphism in their diameter, density, and number of neighboring corallites (González-Espinosa et al., 2018) but the integration of these traits has not been analyzed before.

2 Materials and methods

2.1 Sample collection and sex identification

Porites lobata is one of the most abundant massive coral species in the eastern tropical Pacific (Glynn et al., 2017). We collected samples at Isla Isabel National Park in the central Mexican Pacific (Figure 1) in October 2013 (permission number: DGOPA.04552.040711.1798). All colonies (~70 cm in diameter size) were collected using a hammer and chisel from the same habitat at depths 3–5 m to minimize phenotypic differences caused by different light or flow microenvironments. We collected 18 colonies total: 12 males and 6 females. Species identification was based on visual taxonomical characteristics (Veron, 2000). *P. lobata* is a gonochoric broadcast spawner (Glynn et al., 1994; Neves, 2000) whose gametes mature throughout the year along the eastern Pacific (Glynn et al., 1994; Glynn et al., 2011). A small percentage of hermaphroditic colonies have been reported in Costa Rica (Glynn et al., 1994), although reproductive season and hermaphroditism have not been documented in Mexico.

Colony sex was determined using the histological procedure of Cabral-Tena et al., 2013 and Tortolero-Langarica et al (2016). Briefly, two subsamples were used from each colony (previously collected in Tortolero-Langarica et al., 2016). One (~ 5 x 5 cm) was decalcified to obtain tissue, dehydrated, and stained using Masson's trichrome protocol. Each colony was sexed by inspecting for the presence of oocytes or spermaries using a Zeiss AxioVision R1 microscope. The second fragment (~ 10 x 10 cm) was used for morphological analysis of the skeleton and its constituent corallites. Tissue was removed with 5% sodium hypochlorite to characterize their morphological traits.

TABLE 1 Evidence of sexual dimorphism in coral reef-building species. Males (m), hermaphrodites (h), females (f), Eastern Tropical Pacific (ETP).

Coral species	Type of Reproduction	Type of sexual dimorphism	Number and type of traits supporting sexual dimorphism	Study location	Reference
Fungia scutaria	Gonochoric spawner	Size dimorphism	**1 trait:** Diameter of the coral (f > m)	Eilat, Israel	(Kramarsky-Winter and Loya, 1998)
Ctenactis echinata	Gonochoric spawner*	Size dimorphism	**2 traits:** Length of coral (f > m) Wet weight of the coral (f > m)	Sesoko, Okinawa, Japan	(Loya and Sakai, 2008)
Porites panamensis	Gonochoric brooder	Skeleton growth	**2 traits:** Extension rate (m > f) Calcification rate (m > f)	Gulf of California (ETP)	(Cabral-Tena et al., 2013)
		Skeleton growth	**4 traits:** Tissue thickness (m > f) Extension rate (m > f) Calcification rate (m > f) Skeletal density (m > f)	Central Mexican Pacific (ETP)	(Tortolero-Langarica et al., 2017)
		Skeletal isotopic signals	**2 traits:** $\delta^{18}O$ (f > m) $\delta^{13}C$ (m > f)	South Gulf of California (ETP)	(Cabral-Tena et al., 2013)
		Morphological traits	**3 traits:** Corallite diameter (f > m) Corallite density (m > f) Number of adjacent corallites (m > f)	South Gulf of California (ETP)	(González-Espinosa et al., 2018)
		Phenotypic integration	**1 trait:** Trait integration (m > f)	Central Mexican Pacific (ETP)	This study
Porites lobata	Gonochoric spawner	Skeleton growth	**3 traits:** Tissue thickness (m > f) Extension rate (m > f) Calcification rate (m > f)	Central Mexican Pacific (ETP)	(Tortolero-Langarica et al., 2016)
	Gonochoric spawner	Morphological traits and phenotypic integration	**3 traits:** Corallite area (m > f) Corallite diameter (m > f) Trait integration (f > m)	Central Mexican Pacific (ETP)	This study
Pavona gigantea	Hermaphrodite spawner	Skeleton growth	**3 traits:** Tissue thickness (h > m > f) Skeletal density (m > h > f) Calcification rate (h > m > f)	Central Mexican Pacific (ETP)	(Tortolero-Langarica et al., 2017)
Montastraea cavernosa	Gonochoric spawner	Skeleton growth	**3 traits:** Tissue thickness (m > f) Skeletal density (m > f) Calcification rate (m > f)	Southern Mexican Caribbean (Caribbean)	(Mozqueda-Torres et al., 2018)
Dichocoenia stokesi	Gonochoric spawner	Skeleton growth	**2 traits:** Extension rate (m > f) Calcification rate (m > f)	Southern Mexican Caribbean (Caribbean)	(Cruz-Ortega et al., 2020)
Dendrogyra cylindrus	Gonochoric spawner	Skeleton growth	**2 traits:** Skeletal density (m > f) Calcification rate (m > f)	Southern Mexican Caribbean (Caribbean)	(Cruz-Ortega et al., 2020)

* protandrous bidirectional sex change.

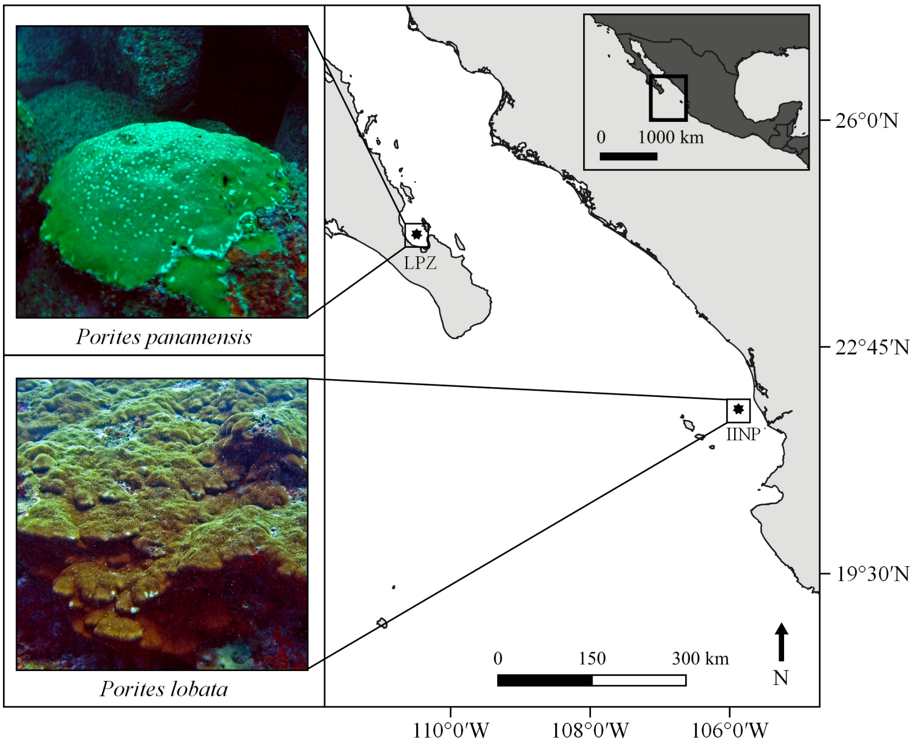

FIGURE 1
Study sites in the central Mexican Pacific. Black star denotes collection sites. Collection sites were Bahía de La Paz (LPZ) for *P. panamensis* and Isla Isabel National Park (IINP) for *P. lobata*. Colonies from *P. panamensis* were collected and described in previous study done by González-Espinosa et al (2018).

2.2 Morphological traits and analysis of modularity

2.2.1 Morphological traits and comparison between sexes

Five morphological traits were selected for analysis (Table 2) based on their potential to delimit between *Porites* species (Brakel, 1977; Weil, 1992; Budd et al., 1994) and reveal sexual dimorphism in *P. panamensis* (González-Espinosa et al., 2018). A Nikon D5300 digital camera was used to capture images for corallite density (Figure 2A). Due to the small size of corallites of *P. lobata* (Figure 3C), high-resolution images were also obtained using a Hitachi S-3000N Scanning Electron Microscope (SEM). Those SEM images were used to measure morphological traits in 10 random corallites per colony (Figure 2B; Table 2). Previous studies done on extinct and extant *Porites* species have found an average from 5-10 corallites best represent the colony by tempering the variability among single corallites (Foster 1986; Weil, 1992; López-Pérez 2013; González-Espinosa et al., 2018; Tisthammer and Richmond, 2018). We selected only mature corallites and avoided the smallest corallites as they could be new corallites recently formed by extratentacular budding (Pichon, 2011) or broken corallites that would give imprecise measurements. Morphological traits were analyzed using ImageJ ver. 1.60 software (https://imagej.nih.gov/ij/) (Schindelin et al., 2015). Images were calibrated with a grid with standard dimensions. Statistical analyses were performed using colony means. After testing the data for normality (Kolmogorov–Smirnov test) and homogeneity of variances (Levene test), the Student's t-test was used to determine trait differences between sexes in *P. lobata*.

We performed a canonical discriminant analysis (CDA) comparing sexual dimorphism observed in *P. lobata* (this study) with data for *P. panamensis* (https://doi.org/10.5061/dryad.5d6sp) from González-Espinosa et al (2018). We performed a random partition of 50% of the total colonies of *P. panamensis* from the dataset to perform analysis with a similar sample size in both *Porites* species. We used four out of five morphological traits (corallite density, corallite diameter, distance of adjacent corallites, and number of adjacent corallites; Table 2) to perform the CDA. Corallite area was not used because it was not measured by González-Espinosa et al. (2018) All statistical analyses were conducted with STATISTICA 7 software (www.statsoft.com).

2.2.2 Analysis of modularity

The four morphological traits used in the CDA (Table 2: traits 1-4) were also used for the modularity analysis. Integration

TABLE 2 Morphological traits descriptions used in this study.

Morphological trait	Abb.	Description	Sampling per colony	Unit	Measurement method
1. Corallite density	CDe	Total number of corallites per cm^2.	3-6 squares of 1 cm^2	Count	Fragment image
2. Corallite diameter	CDi	Mean value between the linear distance from the initial-point of the dorsal septum to the initial-point of the ventral septum, and from the initial-point of the lateral septum to the end of the other lateral septum.	10 corallites (20 measurements)	mm	SEM image
3. Adjacent corallites	AC	Count of the total number of adjacent corallites.	10 central corallites	Count	SEM image
4. Distance of adjacent corallites	DaC	Average of the lineal distance from the centre of the corallite to the centre of the closest and farthest adjacent corallite.	10 corallites (20 measurements)	mm	SEM image
5. Corallite Area	CAr	Area of the whole corallite.	10 corallites	mm^2	SEM image

References: Multiple studies used previously for *Porites* delimitations along geographical locations: Brakel (1977); Weil, 1992; Budd et al. (1994); González-Espinosa et al. (2018). Abb., Abbreviation.
All morphological traits were averaged to colony means (one measurement per trait per colony) to avoid corallite variability (more details in Materials and Methods).

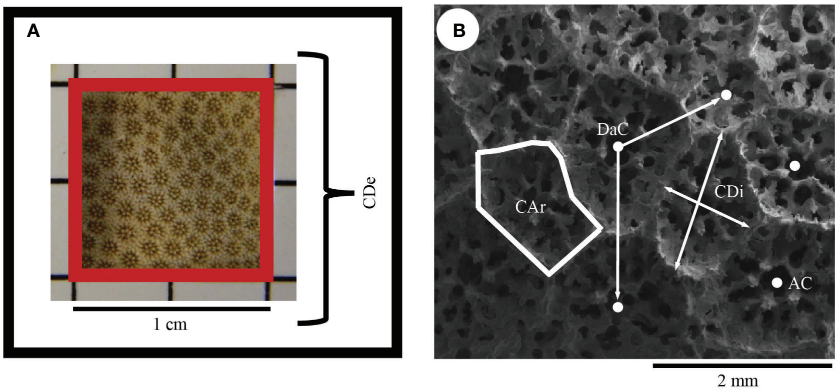

FIGURE 2
Morphological traits used to detect sexual dimorphism. **(A)** corallite density (CDe) **(B)** corallite diameter (CDi), number of adjacent corallites (AC), distance of adjacent corallites (DaC), and corallite area (CAr). Descriptions of each morphological trait are summarized in Table 2.

between morphological traits was analyzed using conditional independence tests and independence graphs (Magwene, 2001). This method reveals the interaction between two traits after removing the effect of other traits and provides insight into whether traits are evolving in a coordinated manner or independently. Due to the number of traits measured in each species, second-order partial correlation coefficients (PCC) for both *Porites* species were computed from log-transformed data. The PCC was estimated for each set of two variables, controlling for the remaining variables (two). The PCC analyses were performed using STATISTICA 7.

Weak trait interactions were removed from the model by statistically comparing the PCCs for edge exclusion deviance (Magwene, 2001). The strength of the interactions was calculated by the edge strength (Magwene, 2001; Paz-García et al., 2015). For this model, we used four categories to classify the strength of the interactions based on the edge strengths results: weak integration (0-0.2), regular integration (0.21-0.4), strong integration (0.41-0.6), and very strong (>0.6) integration between traits. A graphic model was constructed for each species and sex (2 species × 2 sex), resulting in 4 different models in total. The resulting graphical model represents morphological traits in nodes and integration among traits by lines. The edge strength was represented in the graphical model as followed: weak integration (thin dotted line), regular integration (thick dotted line), strong integration (thin continuous line), and very strong integration (thick continuous line). The modularity level in each graphical model will depend on the strength (line thickness) and the number of trait connections (lines) for each model.

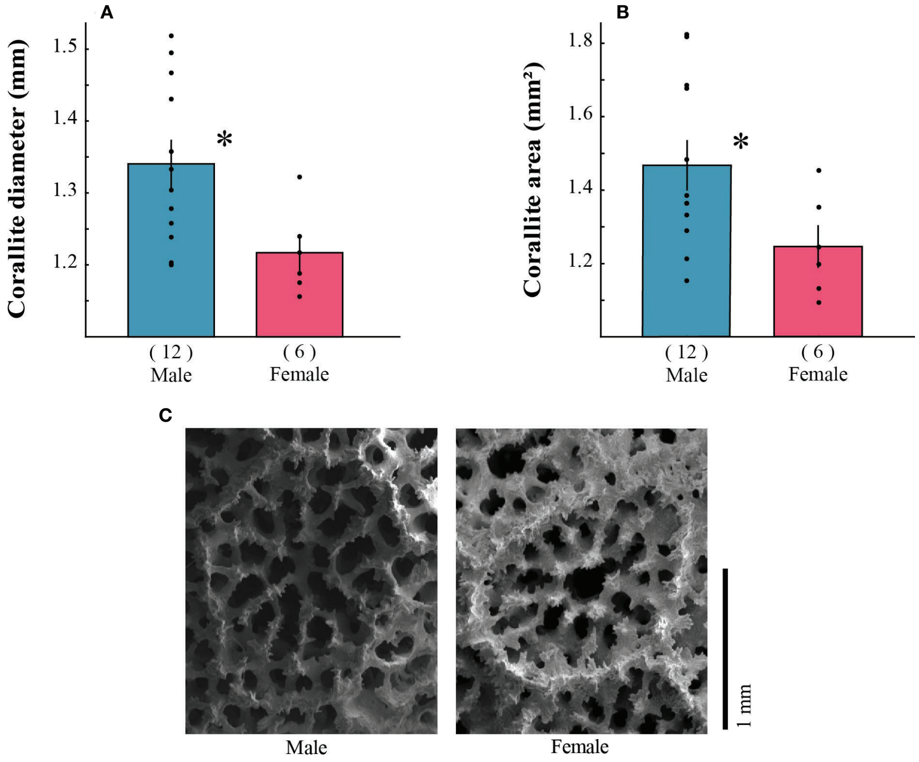

FIGURE 3
Sexual dimorphism in morphological and corallite traits of *Porites lobata* corals **(A, B)**. Mean values (± standard error) of male (blue) and female (red). Black dots represent the data points per colony. Numbers in parenthesis indicate the number of colonies. Significance level: t-test, * $p < 0.05$. Visual representation of corallites of *P. lobata* **(C)**.

3 Results

3.1 Corallite traits

We analyzed 49 colonies for the CDA and modularity analysis: 18 from *Porites lobata* (12 males, 6 females) and 31 from *Porites panamensis* (12 males, 19 females). In *P. lobata*, two morphological traits were significantly larger in male colonies than female colonies (Figure 3; Supplementary Table S1). Male colonies had larger corallite areas (by 17%; p = 0.047) and diameters (by 10%; p = 0.024) than females (Figure 3; Supplementary Table S1). For *P. panamensis*, González-Espinosa et al. (2018) found the opposite: females had wider corallite diameters than males (p = 0.020), while males had higher corallite density (p = 0.016) and number of adjacent corallites (p = 0.005).

Sexual dimorphism in corallite size was statistically supported for both species in the CDA (Wilk's λ= 0.11596, $F_{(12,111)} = 11.676$, p 0.0001, Figure 4, Supplementary Table S2). For the CDA, the first axis explained 86.1% of the variance and the second axis explained an additional 10.4% between the species and sexes (Figure 4). The CDA resulted in a correct classification rate above 66%, with an average of 77% for males and females from both species (Supplementary Table S3).

3.2 Modularity

Patterns of modularity differed between sexes for both species (Figure 5; Supplementary Tables S4, S5). The distance between adjacent corallites (DaC) showed the highest level of integration between traits in all four models (Figure 5), while corallite density (CDe) also showed higher coordination between traits in both species (Figure 5). Female colonies showed higher trait integration (i.e., higher strength and number of trait connections) than male colonies in *P. lobata*, while *P. panamensis* showed the opposite pattern.

For *P. lobata*, while the number of integrated traits was similar between sexes (two integrated traits for males, three for females), the connections between traits were different (Figures 5A, B; Supplementary Table S4). Corallite density was integrated with adjacent corallites (AC) in both sexes, but the other associations varied between the sexes. Corallite density, the distance of adjacent corallites, and the number of adjacent

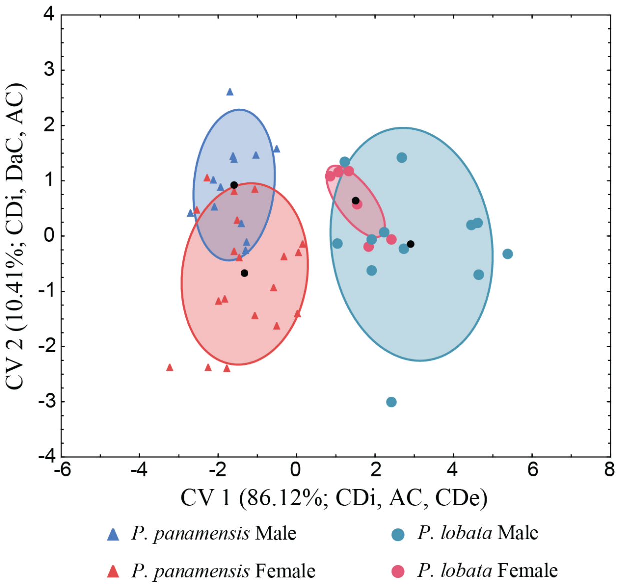

FIGURE 4
Canonical discriminant analysis between *Porites lobata* and *Porites panamensis* morphological traits. Each symbol represents one colony. *P. panamensis*: Male (N= 12), Female (N= 19), *P. lobata*: Male (N= 12), Female (N= 6). CDe, corallite density; CDi, corallite diameter; AC, adjacent corallites; and DaC, distance of adjacent corallites.

corallites were the most integrated traits in female colonies, showing two connections (Figure 5B). In contrast, male colonies showed a unique connection between corallite diameter (CDi) and the distance of adjacent corallites (Figure 5A).

While females of *P. lobata* showed slightly higher integration than males, the pattern was reversed in *P. panamensis*, where males showed a higher integration of traits (4 connections between traits; Figure 5C, Supplementary Table S5) than females (1 connection between traits; Figure 5D, Supplementary Table S5). Corallite density and distance between adjacent corallites were the most integrated traits in both sexes (Figures 5C, D).

4 Discussion

4.1 Sexual dimorphism in corals

The broadcast spawning coral *Porites lobata* is sexually dimorphic both in corallite morphology and at the level of correlated change among corallite traits (Figures 3–4B, Supplementary Tables S1, S4, S6). Sexual dimorphism in scleractinians has been reported for corallite size in solitary corals (Kramarsky-Winter and Loya, 1998; Loya and Sakai, 2008; see Table 1), for skeletal growth, and for calcification rates (see Table 1), as well as for corallite morphology (González-Espinosa et al., 2018). In two gonochoric broadcast spawners from the family Fungiidae (Kramarsky-Winter and Loya, 1998; Loya and Sakai, 2008), small individuals are males whereas large individuals were females. In three massive Caribbean species (Mozqueda-Torres et al., 2018; Cruz-Ortega et al., 2020), skeletal growth rates are higher for male colonies than female colonies. Likewise, in the eastern Pacific, *P. lobata* (Tortolero-Langarica et al., 2016), *P. panamensis* (Cabral-Tena et al., 2013; Tortolero-Langarica et al., 2017), and the hermaphrodite broadcast spawner *Pavona gigantea* (Tortolero-Langarica et al., 2017) show sexual dimorphism in annual skeletal growth, all with faster growth in male colonies. Carricart-Ganivet et al. (2013) found differences between sexes in skeletal growth and density banding in *Siderastrea siderea*, although a more recent study on this same species employing smaller sample sizes (and at a different location) failed to reveal any differences (Benson et al., 2019).

Previous studies have suggested that female colonies may have less energy to invest in growth due to the high energetic cost of producing eggs (Hall and Hughes, 1996; Cabral-Tena et al., 2013. Males, in contrast, may be able to invest more energy in growth due to the lower energetic cost of sperm production. These previous studies (Table 1), along with our new results for corallite morphology, suggest that sexual dimorphism in corals may be common, regardless of phylogenetic lineage (seven genera), geographical location (Red Sea, East China Sea, Caribbean, and eastern Pacific) or spawning mode (broadcast spawner and brooder, this study), and that intersexual differences in corallite integration may facilitate plasticity that allows species to acclimate to different environmental conditions.

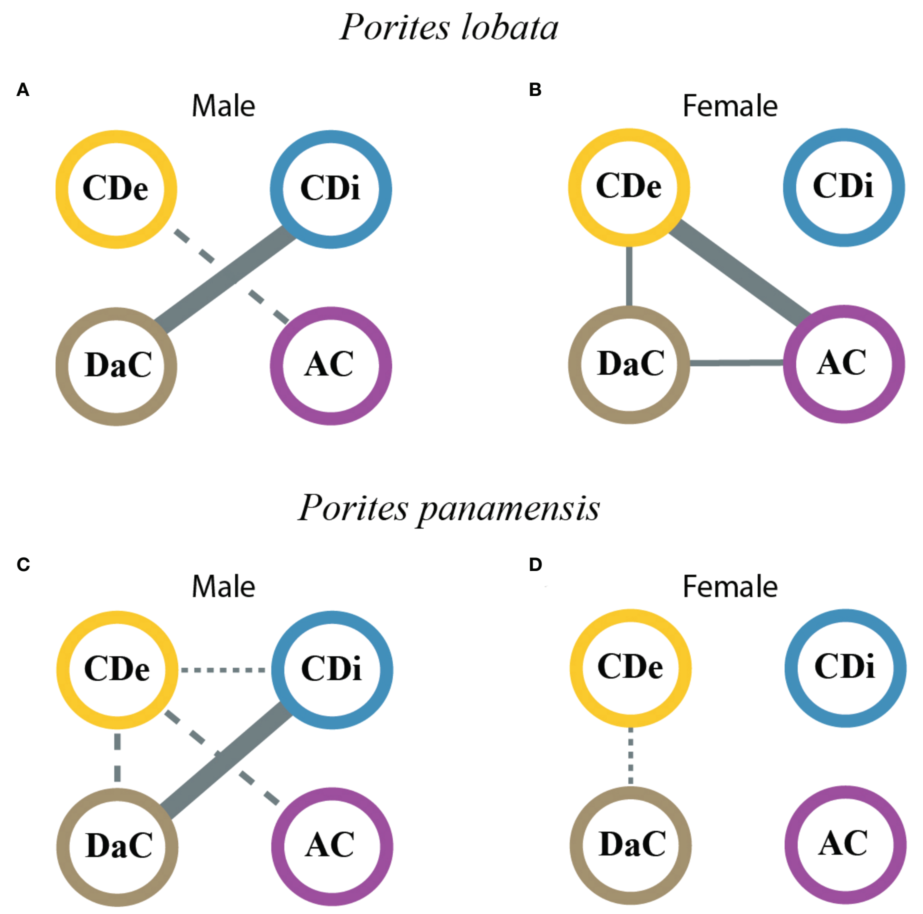

FIGURE 5
Modularity differences between sexes of *Porites lobata* **(A, B)** and of *Porites panamensis* **(C, D)** Graphical models of the level of modularity of male **(A, C)** and female **(B, D)** colonies, where modularity is indicated by the number of trait connections (lines) and their strength (thicker= stronger coordination).

4.2 Sexual dimorphism in corallite size

Sexual dimorphism tied to corallite size operates differently in the broadcast spawner *P. lobata* (this study) than in its brooding congener *P. panamensis* (González-Espinosa et al., 2018). In *P. lobata*, corallite area was larger in male colonies than in female colonies (Figure 3; Supplementary Table S1). In contrast, *P. panamensis* showed larger corallites in female colonies compared to male colonies (González-Espinosa et al., 2018). Gamete production in different coral species is influenced by the number and size of gamete-producing mesenteries in each polyp, which in turn are limited by the space available inside a polyp (Hall and Hughes, 1996). As a result, a larger polyp in male or female (correlated with a larger corallite area) could increase fecundity (Hall and Hughes, 1996; Shlesinger et al., 1998; Leuzinger et al., 2003), as in other broadcast spawning invertebrates (Evans and Sherman, 2013). The patterns observed between species may be due to different constraints imposed on females in the two spawning modes. Broadcast spawning females produce far smaller eggs and there is no higher energy investment in larvae development within their polyps as brooders (Shlesinger et al., 1998; Glynn et al., 2017). If broadcast spawning females are already near their energetic limits of gamete production, there may be little selective pressure for larger female corallites, while larger male colonies may still be favored to increase sperm production to avoid low fertilization success due to sperm dilution (Oliver and Babcock, 1992). These could explain the differences between sexes in corallite size of *P. lobata* (Figure 3).

Corallite area has also been linked to trophic strategy, with variation in polyp size resulting from a trade-off between optimizing for autotrophy (small size) or heterotrophy (large size) (Conti-Jerpe et al., 2020). *Porites* species employ both autotrophic and heterotrophic nutritional sources (Palardy et al., 2005; Grottoli et al., 2006). A larger corallite area in males could enhance the capture of particulate organic matter and planktonic prey. Such heterotrophic nutrition sources, and the greater energy reserves they confer, may lead to a higher tolerance to bleaching when the autotrophic benefits of symbiosis are disrupted (Conti-Jerpe et al., 2020; Liu et al., 2022). As stressful warming events occur more frequently (Sully et al., 2019), future studies should test whether corallite size dimorphism results in physiological responses such as calcification rates and bleaching threshold between sexes.

The production of gametes is the most energetically costly physiological activity for corals, especially for female colonies (Hall and Hughes, 1996), sometimes limiting other processes such as skeletal extension and calcification (Cabral-Tena et al., 2013; Tortolero-Langarica et al, 2016; Tortolero-Langarica et al, 2017). While reproductive output increases with polyp size, the ratio of reproductive output to somatic tissue decreases with a higher polyp diameter (Leuzinger et al., 2003). Larger polyps require thicker skeletal elements for support, thereby reducing the space available for reproductive tissue (Leuzinger et al., 2003). Based on this inverse relationship and the high energetic cost of gamete production, if there is no selective pressure for female corals to increase their corallite size (as the pressure of larger sizes in female brooders), a reduced size in corallite size should be favored. Interestingly, the opposite trend has been observed in two solitary broadcast spawning fungiids, where females have larger polyps than males (Kramarsky-Winter and Loya, 1998; Loya and Sakai, 2008). Sexual size dimorphism can vary depending on different selective pressures as seen in *P. panamensis* (González-Espinosa et al., 2018). Further studies should bring more insight into sexual dimorphism in scleractinian corals.

4.3 Sexual dimorphism in corallite modularity

The integration of corallite traits in *P. lobata* was slightly higher for females than for males (Figures 4A, B; Supplementary Table S4). Integration may constrain the elements of a module (the corallite here) to evolve in concert due to directional selection on just one or a few traits in the module (Magwene, 2006; Villmoare, 2013; Klingenberg, 2014). Integration between corallite traits in *P. lobata* was much lower overall than in *P. panamensis* (Figure 5, Supplementary Tables S4, S5). Less integration, and thus weaker constraints, could allow for greater morphological plasticity in this broadcasting species (Klingenberg, 2014). Indeed, high morphological plasticity is characteristic of the corallites and whole colonies of *P. lobata* (Forsman et al., 2009). Intraspecific corallite variation is also high, showing differences between inshore and offshore colonies (Tisthammer and Richmond, 2018).

In contrast, in the brooding *P. panamensis*, corallite trait integration was lower in females than in males (Figure 4, Table S4). Each polyp in a female colony of *P. panamensis* can brood a single larva that can reach a diameter of 800 µm (Carpizo-Ituarte et al., 2011), potentially placing selective pressure on females to increase the internal space within each corallite to harbor larger larvae (González-Espinosa et al., 2018). Strong selection for larger corallites in females could alter the degree of integration of traits between colonies of different sexes and allow female colonies independence of trait change and greater morphological plasticity. Such plasticity could free them to vary their corallite structure depending on the environment (Todd, 2008) to cope with energetic constraints. This potential plasticity could include (1) increase in the size to accommodate larger larvae, (2) increase their energy supply by having a higher density of dinoflagellate algal symbionts, and (3) enable the polyps to feed on bigger particles. These hypotheses could be tested by measuring larvae size, Symbiodiniaceae density, and total lipid content and fatty acid composition as proxies for food uptake. Liu et al. (2022) tested two factors of the three proposed and found that corallite area increases the food uptake (i.e., higher levels of total lipid content and unsaturated fatty acids) but is not correlated with Symbiodiniaceae density in massive corals.

Sexual dimorphism in *P. lobata* and *P. panamensis* was supported by morphological and modularity analyses. Our findings also indicate that corallite diameter and area may be used to identify the sex of *P. lobata* colonies with modest accuracy. Due to this, these traits can potentially serve as target characteristics in other corals to better understand their reproductive biology. The distinct patterns of sexual dimorphism observed between reproductive modes (larger females in a brooder vs. larger males in a spawner) may be related to the different selective pressures that each sex faces.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Ethics statement

Permission to collect samples of *P. lobata* was granted by The Secretariat of Agriculture, Livestock, Rural Development, Fisheries and Food of Mexico (SAGARPA) (permit No. DGOPA.04552.040711.1798). The permitted collections were made in October 2013 at Isla Isabel National Park. Field collections were made by JJAT-L, APR-T, ALC-M, and with the support of the authorities on both National Parks.

Author contributions

DAP-G, EFB and RMP-P conceived and designed this study. JJAT-L, APR-T, ON-L, RAC-T and ALC-M conducted field work and processing of samples. RMP-P conducted imaging capture and measurements. RMP-P, DAP-G, EFB and MEH conducted data analysis. RMP-P and DAP-G wrote the manuscript. MEH contributed to improvements in the text. All authors contributed to the article and approved the submitted version.

Funding

This work was funded by the project 10023 of PEP Program of CIBNOR to EFB, grant PROMEP-220265 to APR-T, P/PIFI-2010-14MSU0010Z-10 to ALC-M, NGS-55349R-19 to APR-T, PROCER/CCER/DROPC/09/2016 to ALC-M, Marine BioGenomics funding and National Geographic Society.

Acknowledgments

We acknowledge Ariel Cruz Villacorta, Noemí Bocanegra Castillo, Arminda Mejía Rebollo, Claudia Pérez Estrada, and Enrique Morales Bojórquez of CIBNOR for assistance in laboratory work. We thank Erick Treviño Balandra for his assistance in the statistical analyses and the Marine BioGenomics group for support and suggestions in the early stages of preparing the manuscript.

Conflict of interest

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.1068391/full#supplementary-material

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