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Spawning, embryogenesis, settlement, and post-settlement development of the gorgonian *Plexaura homomalla*

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Abstract

Patterns of population biology and community structure can be studied by looking closely at the ontogeny and reproductive biology of reef-building organisms. This knowledge is particularly important for Caribbean octocorals, which seem to be more resilient to long-term environmental change than scleractinian corals and provide some of the same ecological services. We monitored the development of the black sea rod, *Plexaura homomalla*, a common, widely distributed octocoral on shallow Caribbean reefs, from eggs to three-polyp colonies over the course of 10 weeks. Gametes were collected *ex situ* on St. John, U.S. Virgin Islands, during spawning events that occurred 3–6 days after the July full moon. Cleavage started 3.0 hr after fertilization and was holoblastic, equal, and radial. Embryos were positively buoyant until becoming planulae at 3 days after fertilization. Planulae were competent to settle 4 days after fertilization. Symbiodiniaceae began infecting polyps ~8 days after fertilization. Overall, development was typical for Caribbean octocorals, except for an increase in the number of embryos between 3.5 and 6.0 hr after fertilization.

KEYWORDS
cleavage polyembryony, Cnidaria, *ex situ* rearing, Octocorallia, Plexauridae

1 | INTRODUCTION

Understanding the ontogeny and reproductive biology of reef-building organisms can shed light on large-scale patterns of population biology and community structure (Babcock et al., 1986; Baird et al., 2009). This information can help explain the resilience of ecosystems and populations to disturbance (Nyström & Folke, 2001; Waples et al., 2009). For example, populations can be rapidly replenished in species with reproductive capabilities that are less affected by disturbances (Lasker et al., 2020). This is particularly important for taxa like Caribbean octocorals, which have been increasing in abundance while scleractinian cover has been declining (Lenz et al., 2015; Ruzicka et al., 2013; Sánchez et al., 2019). This may be because recruitment success in Caribbean octocorals makes them more resilient to long-term disturbance than scleractinian corals (Edmunds & Lasker, 2016; Lasker et al., 2020; Tsounis & Edmunds, 2017). For example, Lasker et al. (2020) documented the return to pre-disturbance recruit densities of octocorals on St. John, US Virgin Islands, 2 years after two Category 5 hurricanes.

Successful recruitment is necessary for the maintenance of populations, and characteristics of reproduction and development in octocorals may help explain their success on Caribbean reefs. Documenting the reproductive biology and early life development of species is also important for the optimization of larval propagation methods, whether for research or restoration purposes. The general patterns of sexual reproduction in octocorals are well documented. Species are primarily gonochoric and either broadcast-spawn gametes or brood embryos (Kahng et al., 2011). Eggs are frequently yolky, cleavage is usually superficial and holoblastic, and the blastula stage is solid (Dahan & Benayahu, 1998; Lasker &

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Kim, 1996). Despite our in-depth knowledge of oogenesis, reproductive strategies, and sexual systems (see Kahng et al., 2011), the ontogenies of many conspicuous species have yet to be studied in detail.

In this study, we monitored the previously undescribed development of the black sea rod, *Plexaura homomalla* (Esper 1794), from gamete release to post-settlement development. *Plexaura homomalla* is a common member of Caribbean shallow reef communities and is typically found to a depth of 20 m (Kim & Lasker, 1997; Kinzie, 1973, 1974; Yoshioka, 1996; Figure 1). The main source of mortality is the toppling of the colony during storm events, most commonly due to the failure of the substratum (Kinzie, 1970; Yoshioka & Yoshioka, 1991). Additionally, colonies of *P. homomalla* suffer partial mortality from grazing by ovulid gastropods (Kinzie, 1974) and amphinomid annelids (Vreeland & Lasker, 1989). *Plexaura homomalla* is a relatively fast-growing octocoral (Kinzie, 1974; Yoshioka & Yoshioka, 1991) and broadcast spawns in June and July in Florida (Fitzsimmons-Sosa et al., 2004) and in August and September in Venezuela (Bastidas et al., 2005). Female colonies have a protracted period of oogenesis of 18 months (Kahng et al., 2011). In this study we detail the timeline of early development, including an observation of an increase in the number of embryos shortly after fertilization and a description of growth in the field for 8 weeks.

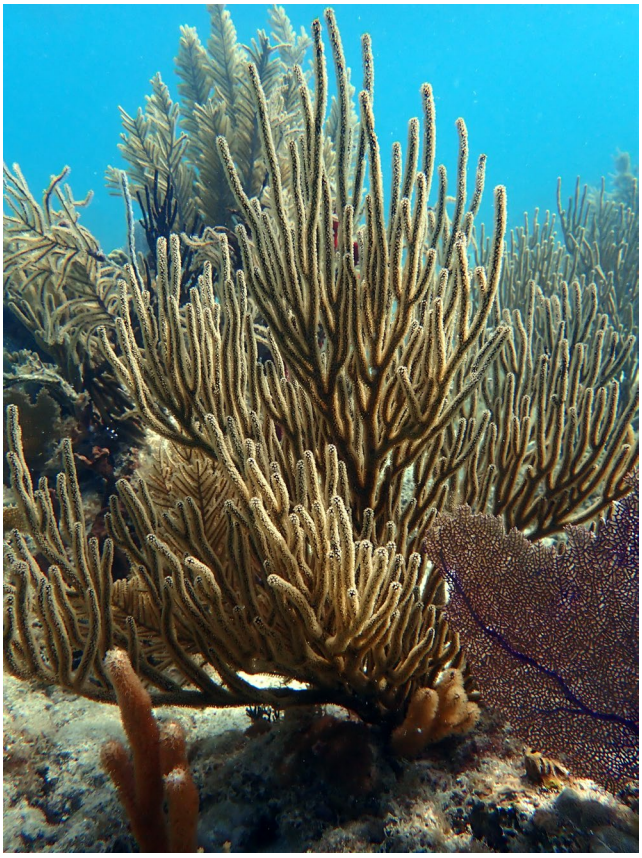

FIGURE 1 Photograph of the black sea rod, *Plexaura homomalla*. The colony is ~65 cm tall

2 | METHODS

Eleven female and four male branches of *Plexaura homomalla* were collected from adult colonies on an octocoral-dominated reef in Round Bay, St. John, USVI (18.345°N, 64.681°W), on July 14–15, 2019, between 3.0 and 6.0 m depth. All branches collected were about 15 cm long. We determined whether colonies were gravid in the field by cutting a 5-cm piece diagonally and looking for spermaries or eggs. Colonies were transported to the Virgin Islands Environmental Research Station and maintained in a sea table (i.e., flow-through, open-topped aquarium) with unfiltered running seawater pumped from Great Lameshur Bay (18.318°N, 64.724°W) from a depth of 1.5 m. Exchange rate in the sea table was ~200 L/hr (60% of the volume hourly). Two EcoPlus 1/10 HP water chillers (Hawthorne Gardening Company, Vancouver, WA) were run in series, and set to a temperature of 27°C to reduce temperature variability. This reduced water temperature 0.5°C during the day (daily temperature range 27.0–29.4°C) and maintained temperature at 27°C at night. Two submersible circulation pumps (Maxi-Jet 900 and Mini-Jet 404 [Marineland Spectrum Brands Pet LLC, Blacksburg, VA]) were placed within the tank to create a circular flow within the sea table that caused branch tips to occasionally sway.

We began monitoring for signs of spawning (e.g., eggs being released, present in the water column, or at the water surface) for 5 hr starting at sunset on each of seven nights starting one night after the full moon (July 17–23, 2019). Bastidas et al. (2005) found that colonies of *P. homomalla* spawned six and seven nights after the full moon in Venezuela, and we began monitoring one night after the full moon in order to capture the entire spawning period. As soon as eggs were observed, pumps and water input were shut off. Eggs and sperm were collected together with 60-mL syringes as they were released from the colonies and were stored in water from the tank for 30 min to ensure fertilization. We were unable to determine the exact moment of fertilization for any given egg, so we refer to the time at which gametes were collected as $t = 0$.

Embryonic development was documented on two consecutive spawning nights (four and five nights after the full moon). On the second night of spawning (four nights after the full moon), 100 eggs were placed in an isolated container (i.e., no external water sources), and the number of cells was counted in triplicate by two different observers (KJT and CDW). Counts were taken every 0.5 hr from 2.5 to 7 hr after fertilization, and then hourly until 10 h after fertilization. Cell divisions were tracked until embryos had 64 cells. Observations of gross morphology were made at 15, 18, 21, and 24 hr after fertilization, and then daily for 3 days. Once planulae became competent to settle, they were provided with 14 × 14 × 1 cm stoneware clay tiles onto which they settled and metamorphosed into primary polyps. Nine days later, the tiles were deployed onto an octocoral-dominated reef (18.309°N, 64.719°W) and monitored 2, 4, and 10 weeks after fertilization. Settlement and survival rates on these tiles in the presence of varying levels of algal turf cover are reported in Wells et al. (2020).

On the third night of spawning (five nights after the full moon), more detailed observations of embryo development were conducted by counting the number of cells in 11 embryos in triplicate every 10 min for the first 2 hr after fertilization and then every 5 min for the next 4 hr. Individual embryos were kept in separate containers. We stopped counting the number of cells after embryos reached 128 cells because further divisions became difficult to detect.

3 | RESULTS

Ex situ spawning in *Plexaura homomalla* occurred ~2 hr after sunset on four consecutive nights, three to six nights after the full moon in July 2019. Spawning was synchronous. Branches released either eggs or an indistinct cloud of sperm. While spawning was observed for up to 4 hr on four consecutive nights in our aquarium system, individual colonies spawned for up to 2 hr on a maximum of three consecutive nights. Colonies displayed extended polyps during spawning. We collected all eggs released on the third and sixth nights after the full moon. Nearly all the eggs were collected on the fourth and fifth nights and no eggs were released on the seventh night. The total number of eggs collected from the nine female branches were 35, 7381, 6002, and 123 on the third, fourth, fifth, and sixth nights after the full moon, respectively. Eggs and early-stage embryos were positively buoyant, spherical, and 600–800 μm in diameter (Figure 2A), with high yolk content. Three days after the last night of spawning (9 days after the full moon), colonies were checked for gametes to determine whether they would spawn the following month. No eggs or developed spermaries were observed.

Cleavage began 3 h after fertilization and was holoblastic, equal, and radial (Figure 2B,C; Table 1). Cleavage started at one pole of the fertilized egg and traveled across its circumference, with increased furrow formation after each division. Cleavages to 8-, 16-, 32-, and 64-celled embryos led to blastulae with distinct blastomeres (Figure 2B,C). Development from 8 cells to 64 cells took about 45 min (Figure 3; Table 1). Of the 100 eggs or embryos monitored on the second night of spawning (four nights after the full moon), 13

TABLE 1 Median and range of time to reach stages of development in the gorgonian *Plexaura homomalla*

Development stage	Median time	Range
Oocyte	0 hr	0–3.7 hr
2-cell	3.0 hr	2.8–3.7 hr
4-cell	3.3 hr	2.8–3.8 hr
8-cell	3.4 hr	2.8–3.8 hr
16-cell	3.7 hr	3.0–3.9 hr
32-cell	3.8 hr	3.4–4.2 hr
64-cell	4.3 hr	4.1–4.6 hr
Stereoblastula	4.9 hr	4.8–6 hr
Gastrula	15 hr	5–36 hr
Planula	3 days	2.5–4 days
Settlement (polyp)	5 days	5–8 days
3-polyp colony	71 days	

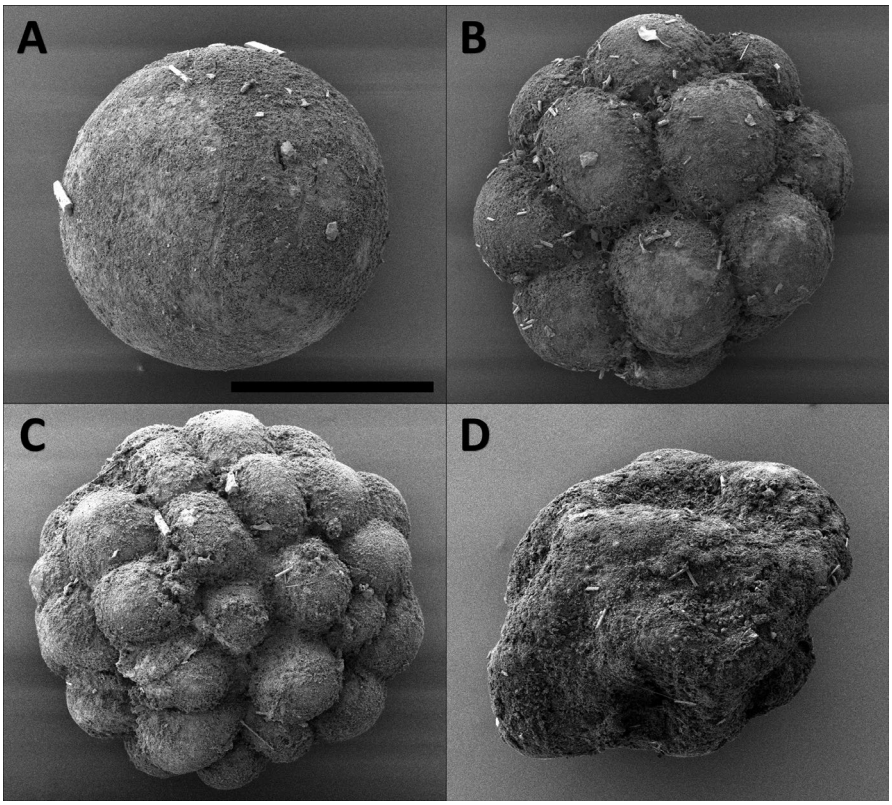

FIGURE 2 Scanning electron microscope images of early development events of the gorgonian *Plexaura homomalla*. **A** Egg or embryo. **B** 16-cell embryo. **C** 32-cell embryo. **D** Early-stage gastrula. Scale bar =300 μm

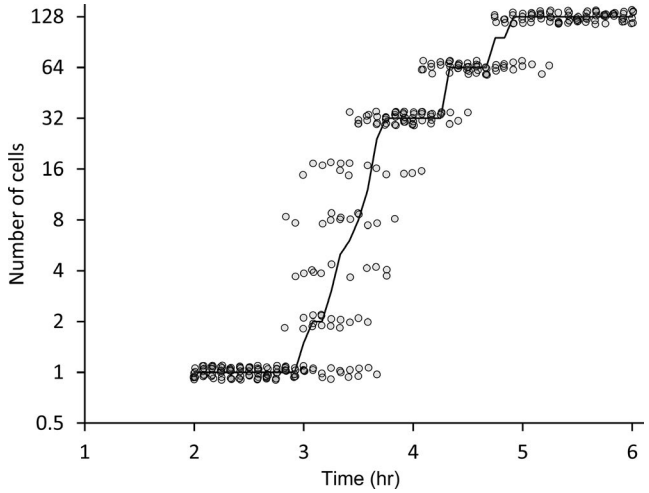

FIGURE 3 Development of 11 eggs or embryos of the gorgonian *Plexaura homomalla*, 2–6 hr after fertilization, monitored at 5-min intervals. Each point represents one observation. Cells started dividing ~3 hr after fertilization and had all reached 128+ cells by 5.5 hr after fertilization. The solid black line is the median number of cells. Values have been spread on the *x*- and *y*-axes to reduce overlap

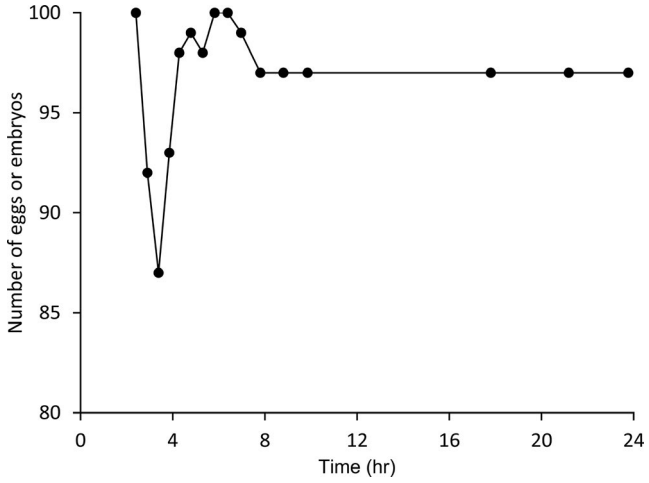

FIGURE 4 Number of eggs or embryos of the gorgonian *Plexaura homomalla* alive in the first 24 hr of development, starting with 100 eggs on the second night of spawning (four nights after full moon). Mortality was high between 2.5 and 3.5 hr. At 3.5 hr, some 64+ cell embryos broke into fragments. The number of embryos stabilized after 8 h during the blastula stage

died (i.e., lysed) between 2.5 and 3.5 hr after fertilization (Figure 4). A spherical stereoblastula was formed 4.9 h after fertilization, and by 15 hr after fertilization all embryos were irregularly shaped gastrulae, appearing like a raisin (Figure 2D; Table 1). Embryos that did not progress through stages at a steady rate (i.e., too fast or slow) frequently died. Particularly noteworthy, at 3.5 hr after fertilization, the number of embryos increased from 87 to 100 (Figure 4). This increase in number, counted in triplicate, was not observed among the 11 individuals monitored on the third night of spawning (five nights after the full moon).

Two days after fertilization, the embryos were ovoid and less buoyant than the preceding day. By 3 days after fertilization, embryogenesis was complete, and planulae had formed (Figure 5A, Table 1). Planulae were slightly negatively buoyant, pear shaped to ovoid, and were capable of swimming at a speed of ~0.5 cm/s. They had the ability to become elongated but could quickly return to a pear shape. Planulae could be found crawling on the surfaces of the culture container but did not stick inside the glass pipettes during water changes. By Day 4, planulae were clearly competent to settle. They readily attached to surfaces at that time, and it was difficult to transfer planulae without forceful flushing of the water to remove them from the sides of the pipette. This behavior has been observed in *Antillogorgia elisabethae*, *Plexaura kuna*, and *Pseudoplexaura porosa* as an indicator of competence (H. Lasker, unpubl. data).

Planulae began settling 5 days after fertilization. Settlement was asynchronous; some planulae settled as late as 8 days after fertilization. Typically, planulae landed on a surface, crawled around, and either attached to the substratum or swam back into the water column. Endosymbiotic dinoflagellates (Symbiodiniaceae) were not apparent at settlement (Figure 5B). Tentacles on some polyps started to turn brown by 8 days after fertilization, indicating the establishment of the Symbiodiniaceae endosymbionts. Primary polyps started producing purple sclerites 12–18 days after fertilization (Figure 5C). Two to four polyp colonies formed between 4 and 10 weeks after fertilization (Figure 5D, Table 1).

4 | DISCUSSION

This study provides the first detailed description of the spawning, embryogenesis, larval behavior, settlement, and post-settlement development in *Plexaura homomalla* (Figures 2–5, Table 1). We observed spawning in July. In Florida, colonies of *P. homomalla* spawned after the full moon in both June and July (Fitzsimmons-Sosa et al., 2004). We cannot rule out the possibility of spawning in June, but we are confident that spawning did not occur in August. After spawning in July, colonies lacked detectable eggs, which take 18 months to develop (Kahng et al., 2011). Compared to field observations from Venezuela (Bastidas et al., 2005), we observed spawning 1–2 lunar cycles earlier, spawning lasted for twice the duration on each night, and took place over twice as many nights. Colonies released few gametes on the first and last days of spawning (three and six nights after the full moon) in comparison to peak spawning nights (four and five nights after the full moon). During such small spawning events, observations in a laboratory setting may be advantageous for detecting early-spawning colonies that release just a few gametes. The temporal difference between spawning times at different locations has been observed with other octocoral species and has been related to differences in local temperature (De Putron & Ryland, 2009; Pakes & Woollacott, 2008). Differences in the hour at which spawning began and the duration of spawning between our observations and those of Bastidas et al. (2005) could be an artifact of collecting and conditions in the laboratory (e.g., light pollution or stress).

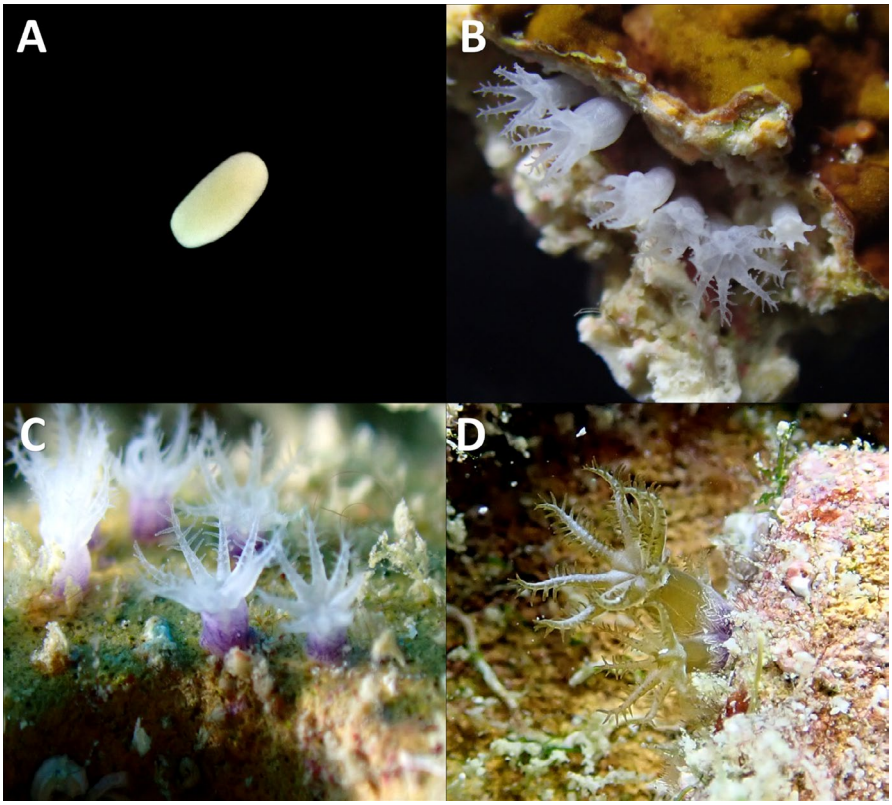

FIGURE 5 Photographs of the early development of the gorgonian *Plexaura homomalla*. **A** Planula larva (~1 mm long). **B** Twelve-day-old polyps (polyp columns are ~0.1 cm tall in panels B,C. **C** Eighteen-day-old polyps with developed purple sclerites. **D** Seventy-one-day-old colonies (column of the main polyp of the colony is ~0.4 cm tall)

Compared to the closely related *Plexaura kuna* LASKER, KIM, & COFFROTH 1996, spawning times were similar relative to the full moon (i.e., several days after full moon), spawning took place over approximately the same number of days, and colonies spawned for similar amounts of time (Brazeau & Lasker, 1989; Lasker et al., 1996). Additionally, embryogenesis was nearly identical (Lasker et al., 1996). As in *P. homomalla* (Table 1), embryos of *P. kuna* were 64 cells by 4 hr after fertilization, gastrulae by 12 hr after fertilization, and planulae by 36 hr after fertilization (Lasker et al., 1996). These similarities indicate that octocorals share many ontogenetic features and that these components have a broad phylogenetic basis.

One unexpected observation was the increase in the number of embryos on the second night of spawning (four nights after full moon; Figure 4). The observation is consistent with polyembryony (i.e., splitting of embryos), although polyembryony was never directly observed. This phenomenon has not yet been described in octocorals but has been reported in reef-building scleractinian corals (Chamberland et al., 2017; Heyward & Negri, 2012). In both scleractinian studies, embryos generated from polyembryony developed into competent, albeit smaller, planulae that successfully settled. Further observations are necessary to fully document the phenomena and understand the possible mechanisms behind this increase in number of embryos. Heyward and Negri (2012) found that, during turbulent conditions, small breaking waves could induce fragmentation in scleractinians during the 2- to 16-cell stages. Embryos of *P. homomalla* were left in still water during this study. A comprehensive survey for polyembryony in octocorals is needed to determine whether this is a potential phenomenon in octocorals or whether this behavior is limited to a smaller number of taxa and circumstances in anthozoans.

If *P. homomalla* has the capability of splitting embryos, then inducing polyembryony may help in experiments where the number of embryos is limited or in coral restoration efforts (Randall et al., 2020). Restoration efforts for octocorals have most focused on propagating colony fragments (cf. Espitia, 2013; Linares et al., 2008; Montseny et al., 2019; Oren & Benayahu, 1997). However, propagation based on settling larvae will be necessary for species such as alcyonaceans, which lack axes and cannot be propagated using colony fragments (Steinberg et al., 2020). Bramanti et al. (2007) examined field settlement to tiles, which could be transported to new areas, but *ex situ* development of larvae may be important in repopulating areas where natural settlement is too low to reestablish populations (Vanderklift et al., 2020). Inducing polyembryony, if the larvae are equally likely to survive, could be an effective technique to increase the numbers of larvae available to remediation projects.

In this study, we found that development in *P. homomalla* is consistent with patterns described in other species except for the increase in number of embryos; although polyembryony remains undescribed in octocorals, it is known to occur within the scleractinians and should be explored further in octocorals. A widespread effort to document early life history, reproductive biology, and the ecological processes that influence recruitment in the octocorals could be key to understanding their success on Caribbean reefs.

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REFERENCES

Babcock, R. C., Bull, G. D., Harrison, P. L., Heyward, A. J., Oliver, J. K., Wallace, C. C., & Willis, B. L. (1986). Synchronous spawnings of 105 scleractinian coral species on the Great Barrier Reef. *Marine Biology*, *90*(3), 379–394. https://doi.org/10.1007/BF00428562

Baird, A. H., Guest, J. R., & Willis, B. L. (2009). Systematic and biogeographical patterns in the reproductive biology of scleractinian corals. *Annual Review of Ecology, Evolution, and Systematics*, *40*(1), 551–571. https://doi.org/10.1146/annurev.ecolsys.110308.120220

Bastidas, C., Cróquer, A., Zubillaga, A. L., Ramos, R., Kortnik, V., Weinberger, C., & Márquez, L. M. (2005). Coral mass- and split-spawning at a coastal and an offshore Venezuelan reefs, southern Caribbean. *Hydrobiologia*, *541*(1), 101–106. https://doi.org/10.1007/s10750-004-4672-y

Bramanti, L., Rossi, S., Tsounis, G., Gili, J. M., & Santangelo, G. (2007). Settlement and early survival of red coral on artificial substrates in different geographic areas: Some clues for demography and restoration. *Hydrobiologia*, *580*, 219–224

Brazeau, D. A., & Lasker, H. R. (1989). The reproductive cycle and spawning in a Caribbean gorgonian. *Biological Bulletin*, *176*(1), 1–7. https://doi.org/10.2307/1541882

Chamberland, V. F., Snowden, S., Marhaver, K. L., Petersen, D., & Vermeij, M. J. A. (2017). The reproductive biology and early life ecology of a common Caribbean brain coral, *Diploria labyrinthiformis* (Scleractinia: Faviinae). *Coral Reefs*, *36*(1), 83–94. https://doi.org/10.1007/s00338-016-1504-2

Dahan, M., & Benayahu, Y. (1998). Embryogenesis, planulae longevity, and competence in the octocoral *Dendronephthya hemprichi*. *Invertebrate Biology*, *117*(4), 271–280. https://doi.org/10.2307/3227029

De Putron, S. J., & Ryland, J. S. (2009). Effect of seawater temperature on reproductive seasonality and fecundity of *Pseudoplexaura porosa* (Cnidaria: Octocorallia): Latitudinal variation in Caribbean gorgonian reproduction. *Invertebrate Biology*, *128*(3), 213–222. https://doi.org/10.1111/j.1744-7410.2009.00170.x

Edmunds, P. J., & Lasker, H. R. (2016). Cryptic regime shift in benthic community structure on shallow reefs in St. John, US Virgin Islands. *Marine Ecology Progress Series*, *559*, 1–12. https://doi.org/10.3354/meps11900

Espitia, P. G. (2013). Attachment, survivorship, and fecundity of *Eunicea flexuosa* (Cnidaria: Octocorallia) transplants. (Master of Science Thesis). Nova Southeastern University, Fort Lauderdale, FL, USA.

Fitzsimmons-Sosa, K., Hallock, P., Wheaton, J., Hackett, K. E., & Callahan, M. K. (2004). Annual cycles of gonadal development of six common gorgonians from Biscayne National Park, Florida, USA. *Caribbean Journal of Science*, *40*(1), 144–150.

Heyward, A. J., & Negri, A. P. (2012). Turbulence, cleavage, and the naked embryo: A case for coral clones. *Science*, *335*(6072), 1064. https://doi.org/10.1126/science.1216055

Kahng, S. E., Benayahu, Y., & Lasker, H. R. (2011). Sexual reproduction in octocorals. *Marine Ecology Progress Series*, *443*, 265–283. https://doi.org/10.3354/meps09414

Kim, K., & Lasker, H. R. (1997). Flow-mediated resource competition in the suspension feeding gorgonian *Plexaura homomalla* (Esper). *Journal of Experimental Marine Biology and Ecology*, *215*(1), 49–64. https://doi.org/10.1016/S0022-0981(97)00015-4

Kinzie, R. A., III (1970). The ecology of the *Gorgonians* (Cnidaria, Octocorallia) of Discovery Bay, Jamaica. (Ph.D.). Yale University, New Haven, CT, USA.

Kinzie, R. A., III (1973). The zonation of West Indian gorgonians. *Bulletin of Marine Science*, *23*(1), 93–155.

Kinzie, R. A., III (1974). *Plexaura homomalla*: The biology and ecology of a harvestable marine resource. In F. M. Bayer & A. J. Weinheimer (Eds.), *Prostaglandins from* Plexaura homomalla*: Ecology, utilization and conservation of a major medical marine resource* (pp. 22–38). University of Miami Press.

Lasker, H. R., Brazeau, D. A., Calderon, J., Coffroth, M. A., Coma, R., & Kim, K. (1996). *In situ* rates of fertilization among broadcast spawning gorgonian corals. *The Biological Bulletin*, *190*(1), 45–55. https://doi.org/10.2307/1542674

Lasker, H. R., & Kim, K. (1996). Larval development and settlement behavior of the gorgonian coral *Plexaura kuna* (Lasker, Kim and Coffroth). *Journal of Experimental Marine Biology and Ecology*, *207*(1), 161–175. https://doi.org/10.1016/S0022-0981(96)02625-1

Lasker, H. R., Martínez-Quintana, Á., Bramanti, L., & Edmunds, P. J. (2020). Resilience of octocoral forests to catastrophic storms. *Scientific Reports*, *10*(1), 4286. https://doi.org/10.1038/s41598-020-61238-1

Lenz, E. A., Bramanti, L., Lasker, H. R., & Edmunds, P. J. (2015). Long-term variation of octocoral populations in St. John, US Virgin Islands. *Coral Reefs*, *34*(4), 1099–1109. https://doi.org/10.1007/s00338-015-1315-x

Linares, C., Coma, R., & Zabala, M. (2008). Restoration of threatened red gorgonian populations: An experimental and modelling approach. *Biological Conservation*, *141*(2), 427–437. https://doi.org/10.1016/j.biocon.2007.10.012

Montseny, M., Linares, C., Viladrich, N., Olariaga, A., Carreras, M., Palomeras, N., Gracias, N., Istenič, K., Garcia, R., Ambroso, S., Santín, A., Grinyó, J., Gili, J.-M., & Gori, A. (2019). First attempts towards the restoration of gorgonian populations on the Mediterranean continental shelf. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *29*(8), 1278–1284. https://doi.org/10.1002/aqc.3118

Nyström, M., & Folke, C. (2001). Spatial resilience of coral reefs. *Ecosystems*, *4*(5), 406–417. https://doi.org/10.1007/s10021-001-0019-y

Oren, U., & Benayahu, Y. (1997). Transplantation of juvenile corals: A new approach for enhancing colonization of artificial reefs. *Marine Biology*, *127*(3), 499–505. https://doi.org/10.1007/s002270050038

Pakes, M. J., & Woollacott, R. M. (2008). Reproduction of the gorgonian *Plexaura flexuosa* in Bermuda. *Journal of Experimental Marine Biology and Ecology*, *357*(2), 121–127. https://doi.org/10.1016/j.jembe.2008.01.003

Randall, C. J., Negri, A. P., Quigley, K. M., Foster, T., Ricardo, G. F., Webster, N. S., Bay, L. K., Harrison, P. L., Babcock, R. C., & Heyward, A. J. (2020). Sexual production of corals for reef restoration in the Anthropocene. *Marine Ecology Progress Series*, *635*, 203–232. https://doi.org/10.3354/meps13206

Ruzicka, R. R., Colella, M. A., Porter, J. W., Morrison, J. M., Kidney, J. A., Brinkhuis, V., Lunz, K. S., Macaulay, K. A., Bartlett, L. A., Meyers, M. K., & Colee, J. (2013). Temporal changes in benthic assemblages on Florida Keys reefs 11 years after the 1997/1998 El Niño. *Marine Ecology Progress Series*, *489*, 125–141. https://doi.org/10.3354/meps10427

Sánchez, J. A., Gómez-Corrales, M., Gutierrez-Cala, L., Vergara, D. C., Roa, P., González-Zapata, F. L., Gnecco, M., Puerto, N., Neira, L.,

& Sarmiento, A. (2019). Steady decline of corals and other benthic organisms in the SeaFlower Biosphere Reserve (Southwestern Caribbean). *Frontiers in Marine Science*, *6*, 1–13. https://doi.org/10.3389/fmars.2019.00073

Steinberg, R. K., Dafforn, K. A., Ainsworth, T., & Johnston, E. L. (2020). Know thy anemone: A review of threats to octocorals and anemones and opportunities for their restoration. *Frontiers in Marine Science*, *7*(590), 1–18. https://doi.org/10.3389/fmars.2020.00590

Tsounis, G., & Edmunds, P. J. (2017). Three decades of coral reef community dynamics in St. John, USVI: A contrast of scleractinians and octocorals. *Ecosphere*, *8*(1), e01646. https://doi.org/10.1002/ecs2.1646

Vanderklift, M. A., Doropoulos, C., Gorman, D., Leal, I., Minne, A. J. P., Statton, J., Steven, A. D. L., & Wernberg, T. (2020). Using propagules to restore coastal marine ecosystems. *Frontiers in Marine Science*, *7*, 724. https://doi.org/10.3389/fmars.2020.00724

Vreeland, H. V., & Lasker, H. R. (1989). Selective feeding of the polychaete *Hermodice carunculata* Pallas on Caribbean gorgonians. *Journal of Experimental Marine Biology and Ecology*, *129*(3), 265–277. https://doi.org/10.1016/0022-0981(89)90108-1

Waples, R. S., Beechie, T., & Pess, G. R. (2009). Evolutionary history, habitat disturbance regimes, and anthropogenic changes: What do these mean for resilience of Pacific salmon populations? *Ecology and Society*, *14*(1), 3.

Wells, C. D., Martínez-Quintana, Á., Tonra, K. J., & Lasker, H. R. (2020). Welcome to the jungle: Algal turf negatively affects recruitment of a Caribbean octocoral. bioRxiv, 2020.2005.2027.119404. 10.1101/2020.05.27.119404

Yoshioka, P. M. (1996). Variable recruitment and its effects on the population and community structure of shallow-water gorgonians. *Bulletin of Marine Science*, *59*(2), 433–443.

Yoshioka, P. M., & Yoshioka, B. B. (1991). A comparison of the survivorship and growth of shallow-water gorgonian species of Puerto Rico. *Marine Ecology Progress Series*, *69*(3), 253–260. https://doi.org/10.3354/meps069253

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