RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration

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RESEARCH ARTICLE

Effect of coral-giant clam artificial reef on coral recruitment: insights for restoration and conservation efforts

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Coral recruitment is a vital process for the maintenance and recovery of coral reefs, particularly due to their decline from global change. While it is well established that larval settlement cues significantly influence coral recruitment, the investigation of recruitment success associated with the surrounding community mainly focuses on algae. To investigate other factors controlling this process, we examined the impact of benthic invertebrate assemblages on coral recruitment using artificial reefs. Three types of artificial reefs (mono-, bi-, and tri-species) with different assemblages of three common species, *Pocillopora acuta*, *Acropora cytherea*, and *Tridacna maxima*, were studied over 8 months. This study revealed that benthic assemblages play a significant role in coral recruitment and survival. High biodiversity was found to enhance coral recruitment and inhibit potential negative cues from *A. cytherea*. Our findings underscore the importance of preserving high biodiversity using not only hard coral but a wide range of phyla, including bivalves, in coral restoration efforts. Maintaining sustainable populations is an important goal to reach in the face of the multiple threats that impact coral reefs.

Key words: assemblages, corals, giant clams, post-settlement, recruitment, restoration

Implication for Practice

- Artificial reefs with the use of adapted substrate can lead to effective coral recruitment. Environmental conditions also influence the recruitment of corals, even at a small geographical scale. Adapted artificial reefs should be designed and deployed in selected locations to enhance coral restoration efforts.
- Surrounding species highly influence coral recruitment. Transplantation of benthic assemblages should be systematically considered and studied within local ecosystems to enhance coral recruitment, post-settlement survival, and reach coral restoration objectives such as achieving population maintenance.

Introduction

Reef-building corals are habitat engineers, providing the infrastructure for one of the most productive and diverse ecosystems on the planet (Burns et al. 2019). The recruitment of coral larvae into substrate-bound juveniles is mediated by a diversity of interactions with surrounding reef organisms (Gleason & Hofmann 2011; Lei et al. 2021). This is a fundamental process that structures and sustains coral populations, making it integral to the recovery and, therefore, resilience of these communities (Pearson 1981; Kayal et al. 2018). Understanding the factors that control habitat selection, settlement, and survival of coral larvae is critical to determining how coral reefs may respond to disturbances.

Biochemical signals from crustose coralline algae (CCA) and reef biofilms are some of the most commonly identified cues known to affect coral recruitment (Webster et al. 2004; Sneed et al. 2014; Tebben et al. 2015). Numerous studies demonstrate that not only do coral larvae settle and metamorphose in response to CCA cues, but they also exhibit preferential selection of certain CCA species as a settlement substrate (Gómez-Lemos et al. 2018; Siboni et al. 2020; Lei et al. 2021). Similarly, coral larvae may respond to cues from microbial biofilms

Author contributions: IG, VB, GL designed the study; IG, CS, GL, VB conducted the study; IG, CS the field survey; IG, RH, GL did the data curation; IG, RH, GL, VB realized the analysis; VB supervised the project; IG, VB acquired the funds; all authors wrote and reviewed the manuscript.

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doi: 10.1111/rec.14145
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.14145/suppinfo

(Tebben et al. 2011; Tran & Hadfield 2011; Sneed et al. 2014). The production of a single compound, tetrabromopyrrole, by these microbes has been reported to induce settlement and metamorphosis in larvae from *Acropora*, *Porites*, *Orbicella*, and *Leptastrea* species (Sneed et al. 2014; Tebben et al. 2015). While the presence of CCA and reef biofilms is not obligatory for larval settlement (Ritson-Williams et al. 2010), they are generally credited as having a positive ecological role in steering coral recruitment.

Conversely, however, biotic interactions may also negatively impact coral recruitment processes (Edmunds et al. 2015). This applies, in particular, to other sessile reef organisms that compete with larval recruits for space and light (Chadwick & Morrow 2011). Algae, sponges, and even corals themselves employ a range of strategies to either exclude or impair swimming larvae (Chadwick & Morrow 2011; Brandt et al. 2019; Fong et al. 2019). Some coral species inhibit the recruitment of heterospecifics by releasing harmful chemicals (allelochemicals) into the surrounding water (Fearon & Cameron 1996; Koh & Sweatman 2000; Chadwick & Morrow 2011). For example, the soft coral *Sinularia flexibilis* was shown to employ allelopathy to prevent the recruitment of scleractinian coral larvae (Maida et al. 1995). Chemical extracts from the coral *Tubastraea faulkneri* increased larval mortality for 11 other species of coral yet were harmless to conspecific recruits (Koh & Sweatman 2000). Even in the case of seemingly amicable CCA, certain species have been shown to employ effective anti-settlement measures against coral recruits, including allelopathy, to modify the shape and motility of larvae (Harrington et al. 2004).

Evidently, both positive and negative interactions with surrounding sessile organisms can greatly determine the success of coral recruitment. However, while it is beneficial to address the impact of a single organism or species on a critical ecological process, there is also a necessity to consider wider community composition. There remains a limited understanding of the synergistic impacts of two or more sessile organisms (assemblages) on these processes. For example, Tebben et al. (2015) showed that the supposed beneficial interaction between coral larvae and reef biofilms may be altered without the presence of CCA cues. This suggests a complementary interaction between microbial and CCA cues, wherein microbial cues by themselves cannot or do not elicit an ecologically realistic response in coral larvae. Whether coral recruitment may be altered depending on the composition of local macro species assemblages, especially those that also recruit larvae, is still unclear. Recruitment studies often focus on the same key players (e.g. CCA, biofilms), leaving aside other benthic engineers such as mollusks and sponges. Understanding how local assemblages may influence coral recruitment not only reveals valuable insights for natural reefs, but is also critical to consider for in situ restoration and conservation practices, especially coral transplants, artificial reefs, and coral nurseries.

Active coral transplantation efforts are growing in response to global coral decline (Lirman & Schopmeyer 2016) but are often done at small spatial scales (<1 ha) mostly because they remain expensive (Bayraktarov et al. 2015). While these restoration projects often focus their efforts on minimizing competition between coral transplants, they generally fall short when factoring in wider ecological processes, such as larval recruitment (Silliman et al. 2015). Ladd et al. (2018) showed that while the majority of studies investigated transplanted coral growth and survivorship, only 19% incorporated ecological processes. The repercussions of restoration design on coral recruitment are often neglected, with only 5% of this subset reviewing impacts on fish and coral recruitment.

Despite our effort to understand the ecology of surface colonization in marine ecosystems, our knowledge of the impact of benthic sessile species on coral recruitment has scarcely advanced. Here, we hypothesize that coral reef diversity contributes to coral recruitment and that heterogeneous benthic assemblages are the key to coral restoration. To our knowledge, coral reef restoration programs do not typically include non-coral invertebrates despite their importance. Invertebrates, including mollusks, are reef engineers who represent a large part of coral reef biodiversity and contribute to ecosystem structuring and maintenance processes (Reid 2017). Artificial reefs constructed for this study were composed of three common engineer species: one giant clam species, *Tridacna maxima*, and two coral species, *Pocillopora acuta* and *Acropora cytherea*. These three species were previously found to cooperatively impair the growth of biofouling algae, indicating their influence on the colonization of surrounding benthic surfaces (Guibert et al. 2019). Aiming to overcome the gaps in coral recruitment studies, we tested the settlement specificity of coral recruits by measuring the larval metamorphosis preferences and post-settlement survival in response to variations of these benthic assemblages.

Methods

Coral and Giant Clam Collection

Coral and giant clam collection was described previously (Guibert et al. 2020). Briefly, five colonies of two coral species, *Acropora cytherea* and *Pocillopora acuta*, were collected in the Moorea lagoon, French Polynesia (17°30′S, 149°50′W fringing reef Linareva; Rouzé et al. 2015). Each colony was cut into nubbins, producing a minimum of 45 small fragments. Fifty giant clams, *Tridacna maxima*, were purchased at a French Polynesian distributor on Reao Island (18°28′S, 136°25′W; Company identification number—N°Tahiti: 139519). The coral nubbins and giant clams were farmed separately on underwater racks in a garden in the Moorea lagoon near the InterContinental Resort and Spa Moorea (17°29′S, 149°53′W) for 6 months before the experiment. Routine maintenance was carried out every 2 weeks to avoid any excessive proliferation of algae on coral nubbins and racks.

Experimental Design

Small artificial reefs of benthic assemblages were constructed using coral nubbins and giant clams (Fig. 1). Artificial reefs were installed and monitored in 3 nearby sites at Manava Beach Resort and Spa Hotel, formerly named the Pearl Resort Hotel, during the main period of Pocilloporidae and Acroporidae

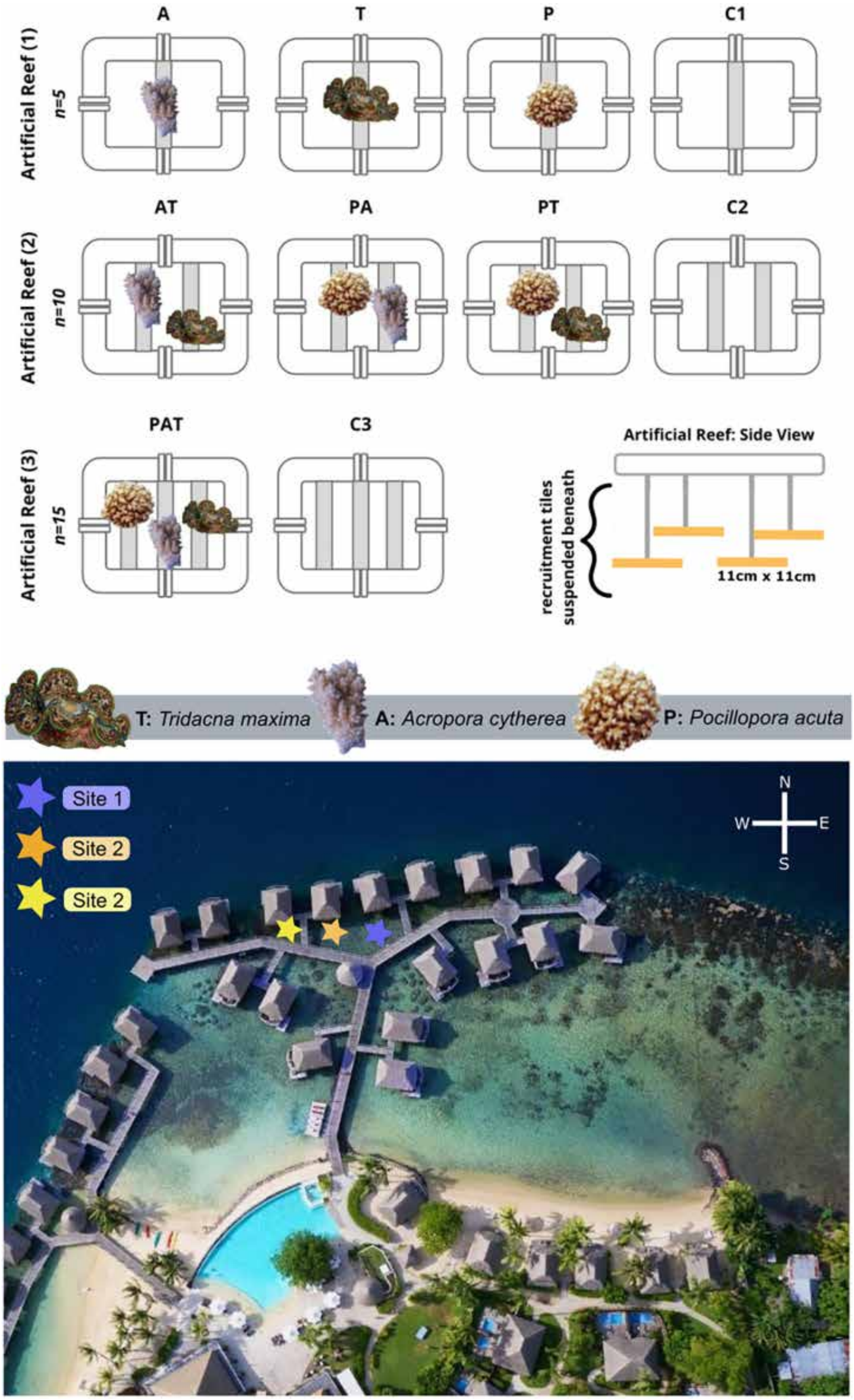

Figure 1. Design of the experiment and map of the study sites. Four types of artificial reefs were deployed at each site to accommodate one, two, three species, or none (control). A total of four recruitment tiles were placed beneath each artificial reef. Two species of corals and one species of giant clams were used: *Pocillopora acuta*, *Acropora cytherea*, and *Tridacna maxima*. The artificial reefs were installed in replicate in three close sites with site 1 in the middle of the Manava Beach Resort lagoon and sites 2 and 3 closer to one of the bridges. The Pearl River (Papeahi) flows in the lagoon greater than 200 m away from site 1. The Manava Beach Resort and Spa Hotel, formerly named the Pearl Resort Hotel, is located at the northeast coast of Moorea (French Polynesia). Map Image: www.tahiti.com.

recruitment from November (3/11/2015) to May (5/2/2016) (Gleason 1996; Adjeroud et al. 2007*a*). Located on the northeast coast of Moorea, the Manava Beach Resort Hotel is positioned within the lagoon adjacent to a reef spanning approximately 200 m near the Irihoriu pass. The three sites were spaced 5–10 m apart within a 20 m^2 area, intentionally situated away from the beach to prevent tourists from swimming by. Only a few alive coral colonies were found near the sites, and the species of interest for this study were not observed around the Manava Beach Resort and Spa Hotel.

Benthic assemblages were composed of either one, two, or three species: *P. acuta* (P); *A. cytherea* (A) and *T. maxima* alone (T); *P. acuta* + *A. cytherea* (PA); *A. cytherea* + *T. maxima* (AT); and *P. acuta* + *A. cytherea* + *T. maxima* (PAT) (Fig. 1). For each assemblage, five specimens of each species were used for one artificial reef: $n = 5$ per site for each mono-specific reef (resulting in a total of $n = 15$ for the three sites), $n = 10$ for each bi-species reef (total $n = 30$ for the three sites), and $n = 15$ for tri-species assemblages (total $n = 45$ for the three sites). Each organism was spaced 12 cm apart. The artificial reefs varied in size and shape according to the assemblages and, therefore, the number of species. To account for this diversity, three artificial reefs of each type and control reefs without organisms (C3, C2, and C1) were deployed at the three sites. Artificial reefs were spaced 1 m apart. Recruits were sampled using four clean, unglazed terracotta tiles (11 × 11 cm) placed 15 cm below the artificial reef using a stainless steel threaded adjusting stem secured to the center of the tiles and artificial reef with a stainless wing nut. Regular observations were carried out to monitor the health of the nubbins and giant clams. Given the lack of observed algae growth, the artificial reef and specimens did not require maintenance. Light and temperature were recorded every 15 minutes at each site using a Hobo data logger (P/NU22-001, Onset, Bourne, Massachusetts).

Recruitment Analysis

Following Penin and Adjeroud (2013), the recruitment tiles of each artificial reef ($n = 90$) were simultaneously collected, three were bleached and sun-dried and one was stored at −20°C for further analyses. Coral recruits on all the surfaces (upper, sides, lower) of the three tiles were photographed and identified using a dissecting microscope. Due to their stage of development, recruits were identified according to family, classified as either Pocilliporidae or other (Babcock et al. 2003; Penin et al. 2010). For each recruit, the number of corallites was counted to assess their size.

Statistical Analysis

All statistical analyses were performed using the R v4.2.3 (R Core Team, 2014). To test the difference between the proportion of recruits according to categorical variables (sites, assemblages, structures), a chi-square test of independence (independence test) or a goodness of fit was performed. When required (values <5), the p value was computed for a Monte Carlo test (Hope 1968) with 1,000 replicates. To test the difference in the number of recruits (a) between assemblages and (b) between groups of assemblages (containing *P. acuta*, or not), a multivariate generalized linear mixed model using a Markov chain Monte Carlo approach (package: MCMCglmm v2.35) was used, with site included as a random effect. A permanova (package vegan) was performed for the analysis of the size of recruits. All data and scripts used in this work are available at https://github.com/iguibert/Recruits.

Results

In total, 207 recruits were identified as Pocilloporidae and 26 as other (Table S1). Site 1 showed the highest number of recruits overall ($n = 130$), followed by site 2 ($n = 60$) and site 3 ($n = 43$; Supplement S1; Table S1). The total number of all recruits was significantly different between sites (chi-square test, $p < 0.001$; Supplement S1). Statistical analysis based on the recruit family demonstrated that the site had an effect on the number of Pocilloporidae recruits (chi-square test, $p < 0.001$) but not for the other recruits. Indeed, the number of recruits for others was low, with no significant difference between sites ($n = 11$, 6, and 9), while the number of Pocilloporidea significantly decreased ($n = 119$, 54, and 34) from site 1 to site 3, respectively. The shape of each artificial reef had no significant effect on the total number of recruits between sites (chi-square test, $p = 0.51$). Inter-assemblage comparisons within each site were then performed, showing that the proportion of total recruits per assemblage was similar per site regardless of the number of recruits (chi-square test, $p = 0.53$; Table S1). Therefore, the observed differences between sites are solely attributed to variations in Pocilloporidae recruitment. Light intensity and temperature exhibited notable variations across sites. However, while there were significant disparities in environmental parameters among sites, these differences do not correlate consistently with variations in the number of recruits. Thus, a direct link between observed recruitment fluctuations at each site and the variations in environmental parameters cannot be established. (Supplement S1; Table S2).

Overall, the site effect on recruitment was due to a quantitative effect without disproportionate recruitment based on structures or assemblages according to a specific site, which allowed pooling of the data by assemblages from all sites (Fig. 2). Across all sites, the type of assemblage had a significant effect on the total number of recruits. The tri-species assemblage (PAT) recruited the most, followed by assemblages PT, P, and PA, respectively (GLMM, $p < 0.05$). Assemblages containing *Acropora cytherea* (A, AT) recruited the least out of all the assemblages, with even fewer recruits on average than the *Tridacna maxima*-only (T) or control (C) assemblages (Fig. 3A). Based on the presence or absence of *Pocillopora acuta*, assemblages that did contain *P. acuta* had significantly more recruits than those without (GLMM, $p < 0.05$; Fig. 3B).

At the family level, even if other recruits showed a significant preference for the PA assemblage ($n = 11/26$—chi-square test, $p < 0.001$), this had no impact on the overall result, indicating that in this study, the assemblage effect mainly concerns

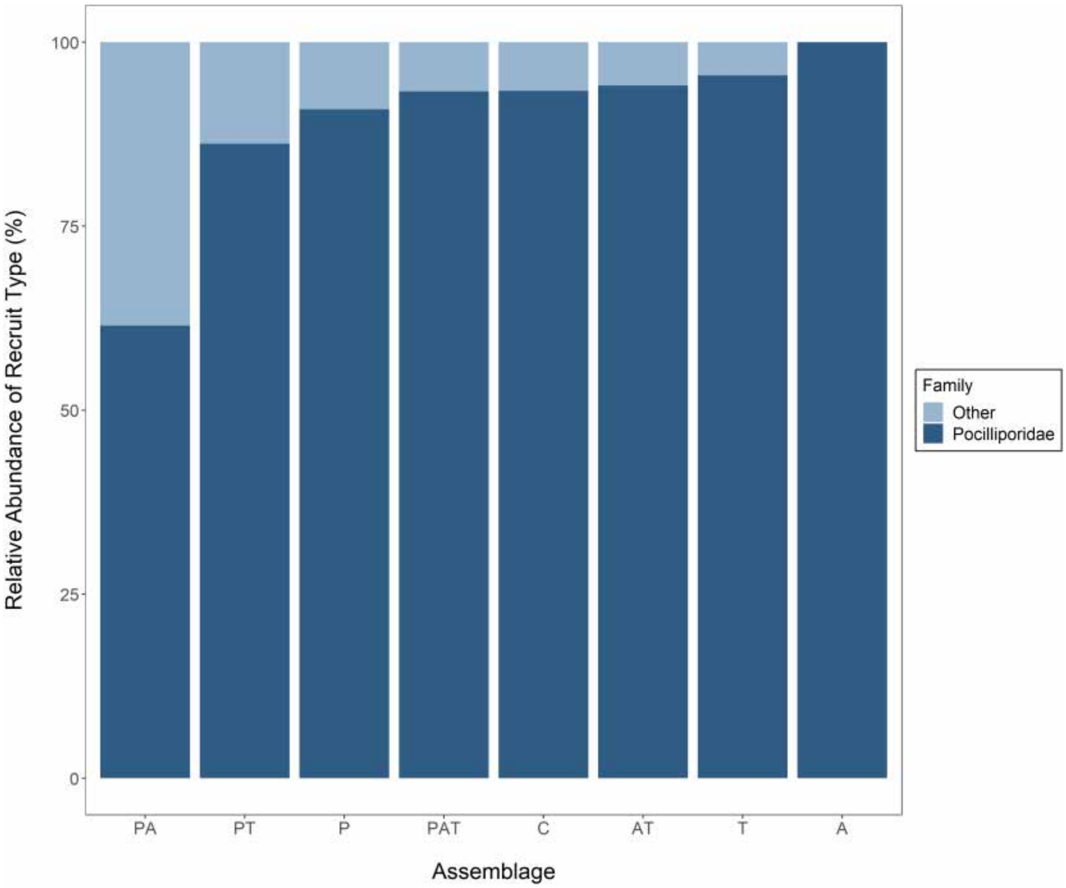

Figure 2. Relative abundance of Pocilloporidae (dark blue) and other (light blue) recruits per assemblages. PAT—*Pocillopora acuta*, *Acropora cytherea*, and *Tridacna maxima*; AT—*A. cytherea* and *T. maxima*; PT—*P. acuta* and *T. maxima*; PA—*P. acuta* and *A. cytherea*; A—*A. cytherea*; P—*P. acuta*; T—*T. maxima*; and C—control.

Pocilloporidae recruits. Assemblages PAT (mean = 3.5 ± 2.13), PT (mean = 3.13 ± 1.89), and P (mean = 3 ± 2.21) recruited the most Pocilloporidae (Table S1).

The size of each recruit was quantified by the number of corallites (Table S1). All recruits, regardless of the family, were found to be larger in size at site 1 compared to both of the other sites (permanova factor Site, $p < 0.001$), with Pocilloporidae recruits being consistently larger (i.e. had more corallites) than other recruits (permanova factor Family, $p < 0.001$). The size of Pocilloporidae recruits ranged from 1 to 74 corallites, with a mean of 14.31 (±13.37). The size of other recruits only ranged from 1 to 6 corallites, with a mean of 1.76 (±1.39). However, there was a higher abundance of small (<20 corallites) and mid-size Pocilliporidae recruits (20–40 corallites), with the majority of recruits (82%) having less than 20 corallites (Fig. 4). The number of recruits showed an exponential decline as the size of the recruits increased (Fig. 4).

Discussion

Understanding the process of coral recruitment is a vital objective for coral reef ecosystems, particularly considering their decline because of global change (Hughes et al. 2017; Edmunds 2022). Alongside stressors, it is well established that larval settlement cues from biofilms influence coral recruitment (Tebben et al. 2015; Da-Anoy et al. 2017). Despite the characteristic diversity of coral reefs, artificial reef experiments using species other than scleractinian corals are lacking (Clements & Hay 2019). The investigation of recruitment success associated with the surrounding community mainly focuses on algae, leading to incomplete knowledge of other factors controlling this process (Chan et al. 2018). The current study addresses these gaps by examining the impact of benthic invertebrate assemblages on coral recruitment. By employing artificial reefs, we demonstrated that these assemblages play a role in coral recruitment and survival, a finding that is of utmost importance for restoration and conservation concerns.

The benthic assemblages used in this study had a significant impact on both the total number of recruits and the family recruited, highlighting the importance of biodiversity in coral recruitment dynamics. The maturity of coral nubbins is achieved after 22 months or more (Zakai et al. 2000; Shafir & Rinkevich 2010), whereas the nubbins we used in this study were less than 12 months. However, a recent study conducted by Rapuano et al. (2023) demonstrated that fragments (approximately 1 cm) from six sexually mature coral

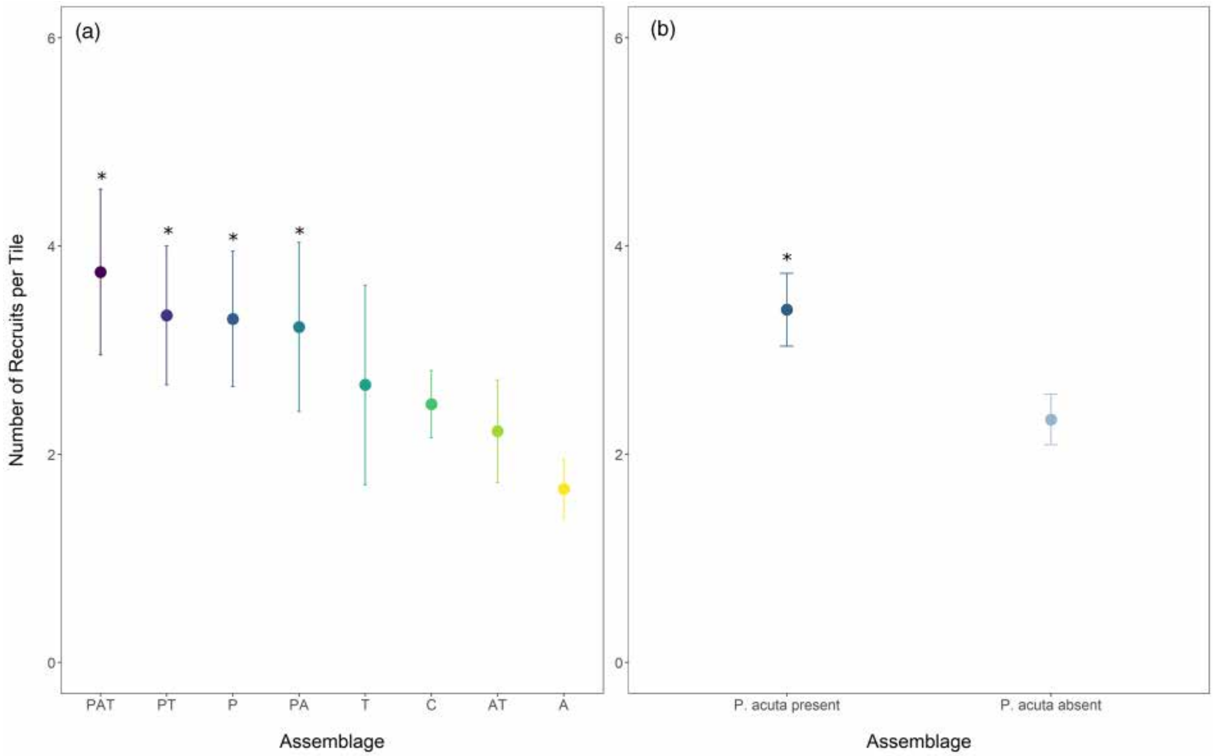

Figure 3. Average number of coral recruits per assemblages (A) and per group with or without *Pocillopora acuta* nubbins (B). Lines represent ±SE and stars represent significant differences. PAT—*P. acuta*, *Acropora cytherea*, and *Tridacna maxima*; AT—*A. cytherea* and *T. maxima*; PT—*P. acuta* and *T. maxima*; PA—*P. acuta* and *A. cytherea*; A—*A. cytherea*; P—*P. acuta*; T—*T. maxima*; and C—control.

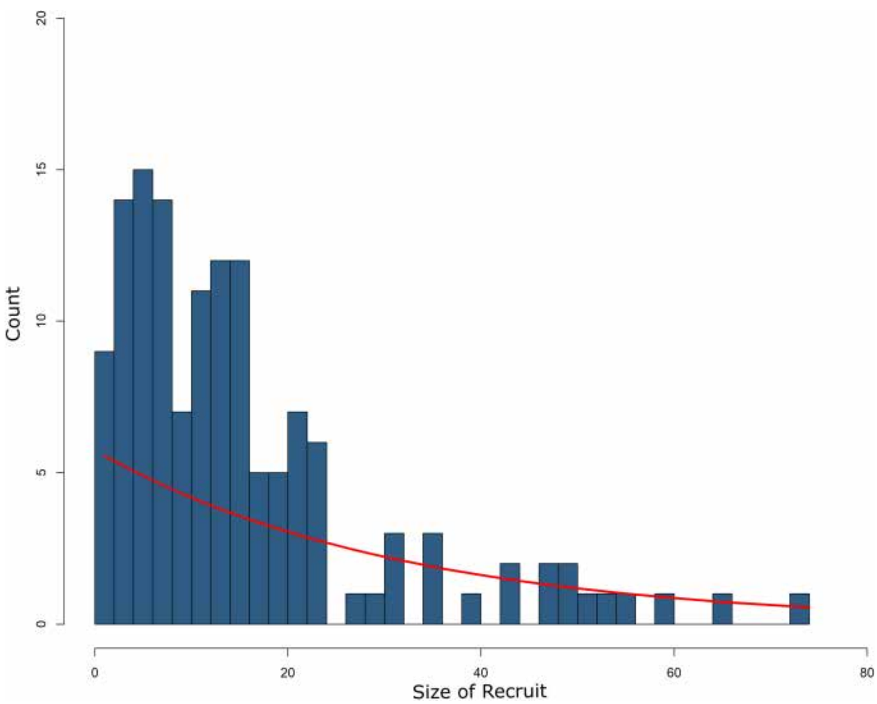

Figure 4. Size distribution of live Pocilloporidae recruits across all sites. Dark blue line represents the number of recruits as a function of size (number of coralites).

species were capable of reproduction after 0.5–1 year, thereby suggesting that nubbins can retain their reproductive capacity as long as the initial colony has reached puberty. Nevertheless, the authors acknowledge that this capacity may be species-specific and that natural disturbances from natural reefs can impede the reproduction of coral nubbins. In addition, while self-recruitment on artificial reefs containing *Pocillopora acuta* is possible, Pocilloporidae recruits were the most abundant type of recruits across all assemblages, including those that did not contain any *P. acuta* (Fig. 2). It is challenging to state if the nubbins used in this study produced larvae. In the event of local recruitment, and given the close proximity of the artificial reefs, the role of biodiversity remains an important player. Furthermore, the average number of recruits was significantly higher in the most diverse assemblage, PAT, highlighting the critical role of biodiversity in coral recruitment. The number of recruits was higher in the artificial reef composed of live organisms compared to the control reef without live organisms, demonstrating the importance of a healthy reef for coral recruitment (Mallela & Crabbe 2009).

For a variety of taxa, there is evidence that the presence of conspecifics has a positive influence on recruitment (Vermeij & Sandin 2008; Da-Anoy et al. 2017). Despite Pocilloporidae being generally regarded as an opportunistic family (Adjeroud et al. 2007*b*; Penin et al. 2010), the presence of *P. acuta* positively impacted their recruitment. Indeed, artificial reefs hosting only *P. acuta* assemblages (P) showed a greater total number of recruits, with a majority of recruits belonging to the Pocilloporidae family. Recruitment in French Polynesia occurs throughout the year, peaking at its maximum between September and March (Gleason 1996; Adjeroud et al. 2007*a*), which coincides with the deployment phase of our study (December–May). Previous studies conducted in Moorea, using recruitment tiles, have similarly reported higher recruitment for Pocilloporidae (Adjeroud et al. 2007*a*; Penin & Adjeroud 2013). The high abundance of these recruits in Moorea is attributed to the substantial density of *Poccillopora* on the outer reef slope (Adjeroud 1997), in addition to their biological characteristics, such as an important production of larvae and high potential of colonization (Magalon et al. 2005; Adjeroud et al. 2007*a*). It is worth noting that *P. acuta* releases monthly larvae all year round while other Pocilloporidae species have a yearly production of larvae (Puisay et al. 2021; Harnay & Putnam 2023) which could potentially explain the high abundance of Pocilloridae recruits through local recruitment.

In contrast, certain taxa have been observed to exert a negative influence on coral recruitment. For example, *Acropora hyacinthus* has been found to significantly inhibit coral recruitment, resulting in no recruitment at all of Acroporid or Poccilloporid in some regions (Wallace 1985; Baird & Hughes 1999). *Acropora* is often recognized as an aggressive genus (Sheppard 1979; Riegl & Purkis 2009). In this study, *Acropora cytherea* leads to no recruitment of non-Pocilloporidae recruits. This phenomenon may be attributed to the relatively small number of recruits from other species in general, or it could suggest that *A. cytherea* inhibits the recruitment of species that produce settlement cues for larvae (e.g. CCA; Baird & Hughes 1999) and/or releases potentially harmful chemicals on its own (Fearon & Cameron 1997) targeting non-Pocilloporidae recruits. Nevertheless, the relationship between *A. cytherea* and the health of the recruits was unclear, as the highest number of dead recruits was observed in the assemblage of *A. cytherea* with *P. acuta* (PA) but not *A. cytherea* alone (A).

Interestingly, our study found that the combination of three species in an assemblage enhanced coral recruitment and may inhibit potential negative cues from *A. cytherea*. The three species together (PAT) lead to a higher number of recruits compared to the association of *A. cytherea* with either *P. acuta* (PA) or *Tridacna maxima* (AT). This finding again highlights the importance of biodiversity in supporting coral recruitment. Moreover, our study provides novel evidence that giant clams can increase coral recruitment of Pocilloporidae. This finding is not surprising, as coral is often found growing on clam shells as a hard substrate (Neo et al. 2015; Mehrotra et al. 2022). Indeed, the intimate relationship between coral and giant clams has been described as specialized mutualism for the *T. maxima* species (Morton 1990). Moreover, PAT assemblage has been shown to inhibit biofouling (Guibert et al. 2019), potentially reducing spatial competition with algae for coral larvae (Birkeland et al. 1981) and creating favorable conditions for coral recruitment.

Despite the considerable attention given to tropical coral reefs, the processes controlling coral recruitment are still not fully understood. The temporal variation in recruitment remains an important process to understand. Although biodiversity plays a vital role in controlling coral recruitment, our results also indicate that environmental variation had an impact on recruitment. The three sites studied were located in close proximity to each other, yet site 1 had the highest recruitment, followed by site 2 and then site 3. The difference in light exposure and temperature, with site 1 receiving light all day, while site 2 was shaded for part of the day and received the least light of the three sites, could explain why site 1 had the highest recruitment. However, these factors fail to explain why site 2 had a higher recruitment than site 3. It is highly possible that multiple factors were at play here. Site 1, being the closest site to the Pearl River, could have benefitted from a high nutrient flow, which, combined with high light intensity and temperature, may have enhanced coral recruitment.

Coral recruitment and post-settlement survival are critical for the maintenance and recovery of coral reefs facing disturbance (Randall et al. 2020), as they play a critical role in shaping the structure of tropical reefs and ensuring the growth and survival of early life stages of stony corals. Despite the importance of post-settlement processes, there is a lack of information on recruitment size distribution. In our study, the frequency of Pocilloporidae recruits followed an exponential decrease according to their size, suggesting that small recruits (<30 corallites) are highly vulnerable. Indeed, a survivorship size threshold has been identified for most corals with decreasing mortality once they exceed 50 mm in size (Doropoulos et al. 2015). This finding is important for enhancing our understanding of the population dynamics of Pocilloporidae corals in French Polynesia and emphasizing the significance of identifying factors that influence coral recruitment and post-settlement survival, as it was observed in the absence of environmental stress.

Previous studies have demonstrated the effect of environmental stressors on coral recruits. For instance, temperature alone can decrease the survival of *Porites astreoides* recruits by more than 20% (Fourney & Figueiredo 2017), and when combined with acidification, can lead to a 32% decrease in the survival of *Acropora millepora* recruits (Brunner et al. 2021). To face these challenges and mitigate the unprecedented loss of hard corals, reef restoration provides a potential solution to positively impact all coral life stages by maximizing post-settlement survival while growing adult corals. Our research has demonstrated that artificial reefs seeded with coral nubbins and mollusks can enhance coral recruitment depending on the assemblage used. However, many coral restoration projects are poorly designed and fail to reach their objectives (Bostrom-Einarsson et al. 2020). For example, 28% of the restoration projects studied by Bostrom-Einarsson et al. (2020) used only one species, most of which were fast-growing hard corals. While co-culturing techniques have been used, they involved the culture of coral recruits alongside grazers only. The use of echinoderms (Toh et al. 2013; Craggs et al. 2019) and herbivorous gastropods (Villanueva et al. 2013) has also been shown to increase coral recruit survival. To our knowledge, only one study has examined the effect of coral transplantation combined with giant clam restoration with a focus on the fish community, highlighting the importance of coral and clams to reef fishes (Cabaitan et al. 2008). Our findings suggest that restoration efforts could focus on preserving high biodiversity using not only hard coral but also a wide range of phyla, including bivalves. This could particularly be the case in French Polynesia, where *T. maxima* are an integral component of the coral reef. Coral restoration research would benefit from integrating multispecies and ecological processes into coral restoration to enhance restoration design and success. Providing efficient material (Leonard et al. 2022) and stable substrate (Ferse et al. 2013) could be coupled to transplantation for better success. We demonstrated that environmental parameters, such as light and assemblages, have an important impact on coral recruitment, even at a small geographic scale. Achieving population maintenance is an important goal to reach in the face of the multiple threat that impacts coral reefs and local effort should be made to determine the best assemblages and locations to use in order to fine-tune coral recruitment and post-settlement survival.

In light of the significant threats facing coral reefs, it remains urgent to gain a better understanding of the spatiotemporal dynamics of coral recruitment (Edmunds 2022). Despite the gain in knowledge in this area over the past few decades, the processes controlling coral recruitment remain poorly understood, representing a true "black box" (Edmunds 2022).

This study began to shed light on this black box, providing novel insights into the temporal variability of coral recruitment in relation to surrounding biotic factors. For the first time, we demonstrated that the surrounding biodiversity, including the presence of both coral and bivalves, plays a crucial role in determining the number, taxonomic composition, and health of coral recruits. Given the pivotal role of environmental conditions in shaping coral recruitment, future coral reef restoration projects should prioritize the examination of local biotic interaction to maximize recruitment success and post-settlement survival. In this context, a permaculture-based approach, utilizing local biodiversity to enhance coral recruitment and survival, may prove particularly effective for reef restoration initiatives. In conclusion, this study underscores the importance of considering the complex ecological processes underlying coral recruitment and highlights the need for continued research efforts to promote the sustainability and resilience of coral reef ecosystems.

Acknowledgments

This work was supported by LabEx Corail, CNRS Funding, and the Walter Zellidja Grant from the Academie Française. I.G., PhD, was supported by Sorbonne University—Doctoral School 129. We acknowledge the InterContinental Resort and Spa Moorea and the Moorea Dolphin Center for providing a coral garden-protected area. We are grateful to the Manava Beach Resort and Spa Hotel for allowing us to work in their Hotel. We also thank F. Lerouvreur, P. Ung, E. Morin, and all the students from CRIOBE who helped us on the field.

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Supporting Information

The following information may be found in the online version of this article:

Supplement S1. Supplementary figures of environmental data and recruits per site.
Table S1. Recruits' data.
Table S2. Environmental data.

Coordinating Editor: Phanor Montoya-Maya

Received: 6 December, 2023; First decision: 11 February, 2024; Revised: 1 March, 2024; Accepted: 9 March, 2024