

## Ectosymbiont community shifts driven by partial mortality in *Pocillopora* coral colonies

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**ABSTRACT:** Scleractinian corals host rich communities of specialized ectosymbiotic animals that can act as parasites or mutualists, thereby influencing coral health and survival. The structure of these communities is shaped by multiple environmental factors, many of which remain poorly understood. Here, we examine how partial mortality (PM) of live coral tissue affects the diversity and abundance of ectosymbionts in nursery-reared colonies of *Pocillopora verrucosa*. We tested the hypothesis that PM promotes a shift from obligate to facultative symbionts. We analyzed 200 one-year-old colonies, documenting colony metrics and bleaching status, and then collecting, counting, and identifying all associated symbionts. PM was observed in 36% (72) of colonies, with 62 surviving the entire experiment. Among these, only one showed PM on more than 75% of its surface, 48 on less than 25%, and 13 on 25–50%. Across all samples, we identified 79 ectosymbiotic species: 49 facultative and 17 obligate in colonies with PM, and 45 facultative and 14 obligate in healthy colonies. Generalized linear models revealed significant effects of PM and colony density on community structure, while bleaching exerted only a weak influence and colony size had no significant effect. Facultative symbionts were significantly richer and more abundant in colonies with PM, whereas obligate symbionts showed no detectable response. These contrasting patterns likely reflect differing ecological requirements and tolerance ranges of these two groups of symbionts. Our findings highlight PM as a key driver of symbiont community restructuring in *P. verrucosa*, with important implications for understanding coral-associated biodiversity and its resilience under environmental stress.

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**KEY WORDS:** *Pocillopora verrucosa*, partial mortality, obligate symbionts, facultative symbionts, diversity, abundance.

## Сдвиги в сообществах эктосимбионтов при частичной смертности колоний коралла *Pocillopora*

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**РЕЗЮМЕ:** Склерактиниевые кораллы служат хозяевами для специализированных животных-эктосимбионтов, которые могут быть паразитами или мутуалистами, тем самым влияя на здоровье и выживаемость кораллов. Структура этих сообществ определяется множеством факторов, значение многих из них остаётся недостаточно изученным. Нами изучено влияние участков отмершей поверхности (УОП) коралла на разнообразие и обилие эктосимбионтов у *Pocillopora verrucosa* в условиях культивирования. Кроме того, мы проверили гипотезу о смещении доминирования от облигатных к факультативным симбионтам по мере развития УОП. Всего было проанализировано 200 однолетних колоний кораллов. Каждую колонию измеряли, регистрировали степень обесцвечивания (бличинга), а также проводили сбор, подсчёт и таксономическую идентификацию обитающих на них эктосимбионтов. УОП наблюдались у 36% (72) колоний, из них 62 выжили к концу эксперимента. Среди этих колоний только у одной площадь УОП превышала 75% поверхности, у 48 — менее 25%, у 13 колоний — 25–50%. Во всех пробах найдено 79 видов эктосимбионтов: 49 факультативных и 17 облигатных на колониях с УОП, и 45 факультативных и 14 облигатных на здоровых колониях. Обобщённые линейные модели продемонстрировали значительное влияние УОП и плотности размещения колоний на структуру сообществ, в то время как влияние обесцвечивания было слабым, а размер колоний не оказывал статистически значимого эффекта. Факультативные симбионты были значительно разнообразнее и многочисленнее на колониях с УОП, тогда как облигатные симбионты не демонстрировали заметной реакции. Эти различия в реакции на УОП вероятно отражают разные экологические потребности и диапазоны толерантности двух групп симбионтов. Наши результаты демонстрируют, что УОП является ключевым фактором перестройки структуры симбиотического сообщества *P. verrucosa*, что важно для понимания биоразнообразия кораллов и их устойчивости к воздействию стрессовых факторов.

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**КЛЮЧЕВЫЕ СЛОВА:** *Pocillopora verrucosa*, частичная смертность, облигатные симбионты, факультативные симбионты, разнообразие, обилие.

## Introduction

Symbiosis, first formally defined by de Bary (1879), describes close, long-term interactions among organisms of different species. Such interactions range from mutualism, where both partners benefit, to parasitism, in which one partner harms the other while obtaining food or shelter. Boundaries between these categories are often blurred: species once considered commensals — benefiting without affecting the host — or even parasites may in fact provide mutualistic benefits (Zapalski, 2011; Martin, Britayev, 2018). A system composed of two or more symbionts is termed a “symbiome”. By this definition, virtually all plants and animals

are symbiomes, hosting a variety of micro- and macro-organisms (Sapp, 2003). Scleractinian coral colonies represent a particular example of a symbiome.

Coral colonies function as discrete ecosystems, physically bounded by the colony’s structure and maintained by their interactions with associated symbionts (Gates, Ainsworth, 2011). Coral hosts provide shelter, reproductive habitat, and nutritional resources to a range of associated organisms (Glynn, Enochs, 2011; Stella *et al.*, 2011). In return, symbionts supply nutrients and energy (Knowlton, Rohwer, 2003; Gates, Ainsworth, 2011), protect against disease (Pollock *et al.*, 2013) and predators (Glynn, 1980; DeVantier *et al.*, 1986; DeVantier, Endean, 1988;

Pratchett, 2001; Rouzé *et al.*, 2014), remove fouling organisms (Coen, 1988; Stachowicz, Hay, 1999), and clear sediments or detritus from coral surfaces (Stewart *et al.*, 2006).

Coral symbionts can be classified by interaction type (mutualist, commensal, parasite), size (micro- vs. macro-symbionts), degree of host dependence (obligate vs. facultative symbionts), and location (endosymbionts vs. ectosymbionts). Obligate symbionts depend entirely on their coral host to survive and often show morphological or behavioral adaptations for life with specific hosts (Munday, 2004; Stella *et al.*, 2010; Limviriyakul *et al.*, 2016). Facultative symbionts usually lack such adaptations and use coral as a habitat or substrate (Black, Prince, 1983; Enochs, Manzello, 2012). Research on coral symbioses has largely focused on obligate endosymbionts, especially dinoflagellate algae (*Symbiodinium* LaJeunesse, 2017) (e.g., Baker, 2003; Stat *et al.*, 2006; Andradi-Brown *et al.*, 2019; Bonacolta *et al.*, 2023), whereas ectosymbionts remain comparatively understudied (Patton, 1966; Patton, 1994; Stella *et al.*, 2011; Pisapia *et al.*, 2020; Britayev *et al.*, 2023a; Lishchenko *et al.*, 2024).

Ectosymbionts include both conspicuous epibenthic animals (e.g., fishes, mollusks) and cryptobionts—mobile or sessile animals inhabiting spaces between branches, cavities, or dead skeletons of reef builders (Reaka-Kudla, 1997; Enochs, 2012; Enochs, Manzello, 2012). They represent the majority of known coral-associated invertebrates (Stella *et al.*, 2011), with branching scleractinian corals serving as their primary habitat (Stella *et al.*, 2010). The composition and relative abundance of ectosymbiont groups are shaped by multiple factors, including environmental conditions (temperature, salinity, wave action) and host colony traits (morphology, size, condition, relative density). Documented drivers include temperature (Tkachenko *et al.*, 2022), depth, hydrodynamics, location on the reef, and chlorophyll *a* (Franklin *et al.*, 2013; Gove *et al.*, 2015; Counsell *et al.*, 2018; Pisapia *et al.*, 2020), as well as colony morphology (Patton, 1966, 1994; Stella *et al.*, 2011; Britayev, Mikheev, 2013; Graham, Nash, 2013), size (Abele, Patton, 1976; Caley *et al.*, 2001; Counsell *et al.*, 2018), relative density (Gotelli, Abele, 1983; Lewis, Snelgrove, 1990; Britayev, Mikheev, 2013; Britayev *et al.*, 2023a), and bleaching

(Munday, 2004; Stella *et al.*, 2014; Froehlich *et al.*, 2021; Britayev *et al.*, 2023a), as well as partial mortality (PM) of coral polyps (Stella *et al.*, 2010; Enochs, 2012; Leray *et al.*, 2012; Head *et al.*, 2015; Counsell *et al.*, 2018; Pisapia *et al.*, 2020).

The influence of PM on the structure of ectosymbiont communities remains poorly understood. While some studies report higher symbiont diversity in PM-affected colonies compared to healthy ones (Stella *et al.*, 2010; Enochs, 2012; Leray *et al.*, 2012; Head *et al.*, 2015), others document a negative impact on associated fauna (Munday, 2004; Stella *et al.*, 2014; Froehlich *et al.*, 2021). One hypothesis is that PM drives community restructuring, with obligate symbionts declining and facultative symbionts increasing in richness and abundance (Coles, 1980; Enochs, Manzello, 2012; Leray *et al.*, 2012).

Here, we test this hypothesis in *Pocillopora verrucosa* (Ellis et Solander, 1786) by: (1) characterizing the composition and structure of the ectosymbiont fauna of colonies with and without PM, (2) assessing significance of the differences between the two colony groups, and (3) identifying the species and functional groups responsible for the observed patterns.

## Material and methods

Branching colonies of *P. verrucosa* were selected as the study model system because approximately one-third of known coral symbionts are associated with this genus (Stella *et al.*, 2011; Britayev *et al.*, 2023a). These corals exhibit rapid growth, are suitable for aquaculture (Highsmith, 1982; Combillet *et al.*, 2022), and are abundant in Nha Trang Bay, where they are used in long-term experiments.

Our experiment was conducted from 23 July 2020 to 2 April 2021 at the Marine Research Station of the Coastal Branch of the Vietnam–Russia Tropical Research and Technology Center in Dam Bay, Nha Trang Bay, Vietnam (12°11'40" N, 109°17'25" E) (Fig. 1). Colony fragments measuring 5–7 cm in length were attached to metal frames at 3 m depth after selection to minimize variation in morphology, thereby reducing potential bias in associated communities. Details of the experimental setup are provided in Britayev *et al.* (2023a).

In total, 200 colonies were outplanted on 28 April 2020 for acclimatization. After three months, colonies were cleaned of all ectosymbionts and returned to the frames for a nine-month exposure period. At the end

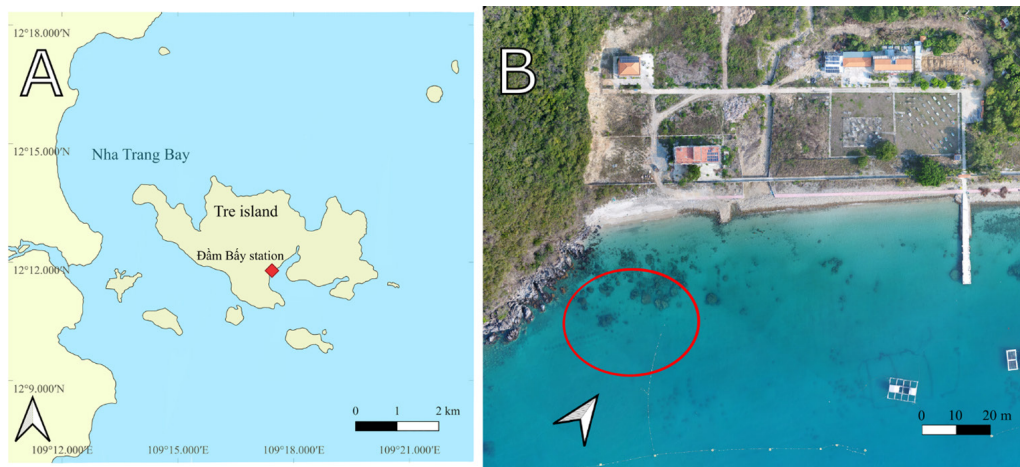


Fig. 1. Localities of material collection. A — Nha Trang Bay, with the location of the Dam Bay research station marked. B — aerial photograph of the research area, the location of the coral frames is marked by a red ellipse.

of this period, colonies were retrieved, placed in individual plastic bags, and transported to the laboratory.

In the laboratory, colonies were measured (two perpendicular diameters  $\times$  height) to estimate colony volume, photographed, and visually examined for PM and bleaching. PM extent was initially scored as <25%, 25–50%, and >50% tissue loss, but was ultimately treated as a binary variable (presence/absence) for statistical analysis. Bleaching was assessed using the six-point coral health scale of Siebeck *et al.* (2006), evaluating the darkest and lightest areas of the colony (excluding young branch tips, which had not yet accumulated symbiotic algae). The overall bleaching score was calculated as the arithmetic mean of the values for these two zones. Dead colonies were excluded from analyses.

Colonies were rinsed with clove-oil emulsion (15 drops  $L^{-1}$  seawater, 3 min exposure) to anesthetize symbionts and then inspected for larger, non-anesthetized symbionts. The rinsed solution was then filtered through a 1 mm mesh to retain anesthetized symbionts. Microscopic or internally hidden fauna that could not be collected without destroying the coral were not counted. All collected organisms were photographed and fixed in 70% ethanol.

Identifications were based on morphological characters to the lowest possible taxonomic level, using standard identification keys and original descriptions (Banner, Banner, 1975; Banner, Banner, 1982; Bruce, 1998; Castro *et al.*, 2004; Ho, Ng, 2005; Naderloo, 2017), with nomenclature verified in the World Register of Marine Species (WoRMS Editorial Board, 2025). Symbionts were then classified as obligate or facultative based on published accounts of host dependence and adaptation (Coles, 1980; Black, Prince, 1983; Stella *et al.*, 2011; Britayev, Mikheev, 2013).

In this study, “facultative symbionts” also include species with uncertain adaptation status.

Symbiotic community metrics included: species richness — number of species per infracommunity (per colony) and component community (pooled colonies); mean species richness — average number of species per colony hosting symbionts; and mean abundance — average number of individuals per colony hosting symbionts. These parameters were calculated for the entire symbiotic community, and separately for obligate and facultative symbionts. Rare species (found in only one colony or with prevalence <1%; Table S1) were excluded to reduce the influence of accidental occurrences (Tate, Heiny, 1995).

Effects of host colony size and PM on community metrics were tested using generalized linear models (GLZs). The Poisson distribution provided the best fit to the dependent variables, as indicated by Pearson’s goodness-of-fit statistics (lowest  $\chi^2$ ,  $p > 0.05$ ). The logarithmic link function was selected based on the lowest Akaike information criterion (AIC) value. Factor significance was evaluated using the Wald test (W), with  $p < 0.05$  considered statistically significant. Analyses were conducted in Statistica 13.5.0.17.

## Results

### Colony characteristics

The volume of 9-month-old colonies ranged from 30 to 2640  $cm^3$  (mean  $\pm$  standard error,  $598.8 \pm 333.5 cm^3$ ). Colonies with PM (Fig. 2C) ranged from 30 to 1170  $cm^3$  ( $443.1 \pm 245.8 cm^3$ ), whereas healthy colonies (Fig. 2A) ranged from 49 to 2640  $cm^3$  ( $674.2 \pm 344.9 cm^3$ ), a significantly higher value ( $p \leq 0.05$ ).



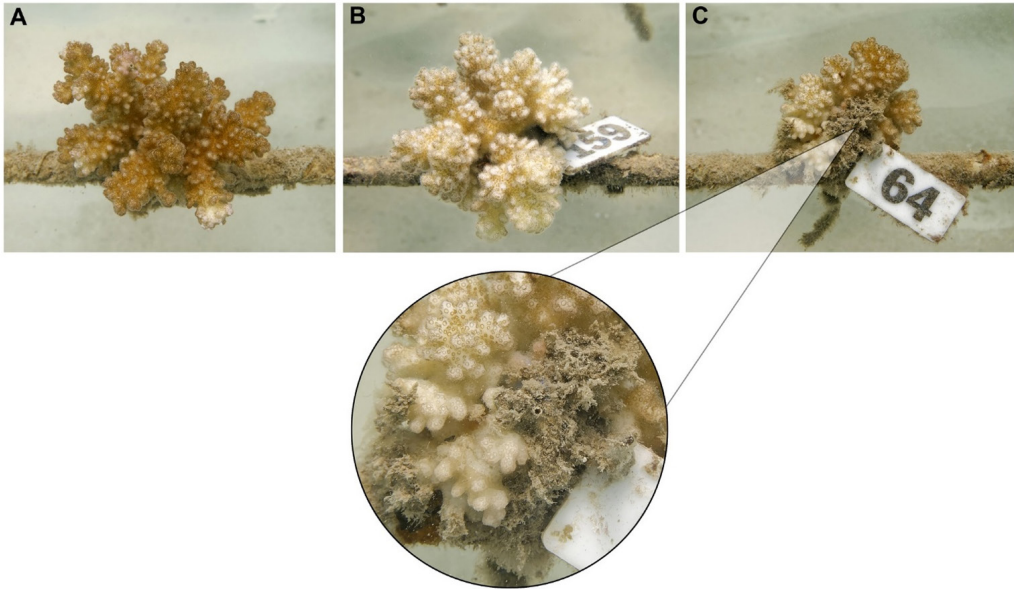


Fig. 2. Physiological states of colonies of *Pocillopora verrucosa*. A — healthy; B — bleached; C — bleached with partial mortality.

Over the 12-month experiment, 10 out of 200 colonies died (5% background mortality), all of which had shown PM prior to death. PM occurred in 36% of colonies (72/200), typically at low severity: of the 62 PM-affected colonies that survived to the end, 48 had <25% affected surface, 13 had 25–50%, and only one exceeded 75%.

**Taxonomic composition of the ectosymbiont community**

A total of 79 ectosymbiont species were identified, including 31 at species level, 8 at genus level, and 40 at higher taxonomic levels (Table 1), with crustaceans being the most diverse (37 species). Of all symbionts, 17 were obligate (predominantly crustaceans: twelve crab species belonging to *Trapezia* and *Cymo*, and four shrimp species), but there was also one fish, *Paragobiodon modestus* (Regan, 1908); 62 were facultative (Table S1).

Among obligate symbionts, the most frequent were the crabs *Trapezia septata* Dana, 1852 (92.6%), *T. serenei* Odinetz, 1983 (83.7%), and the shrimp *Alpheus lottini* Guérin, 1829 (77.4%) (Table S1). However, facultative symbionts were more taxonomically diverse, including 21 crustaceans, 18 annelids, 15 mollusks, and smaller numbers (1–5 each) of turbellarians,

Table 1. Taxonomic composition and number of species of the ectosymbiont community associated with colonies of *Pocillopora verrucosa*.

Taxa	O	F
<b>Crustacea</b>	16	21
Decapoda	16	15
Amphipoda	0	5
Tanaidacea	0	1
<b>Annelida</b>	0	18
Polychaeta	0	17
Sipuncula	0	1
<b>Turbellaria</b>	0	1
<b>Mollusca</b>	0	15
Gastropoda	0	13
Bivalvia	0	2
<b>Osteichthyes</b>	1	1
<b>Ophiuroidea</b>	0	5
<b>Tunicata</b>	0	1

Higher taxa marked in bold, O — obligate; F — facultative species.

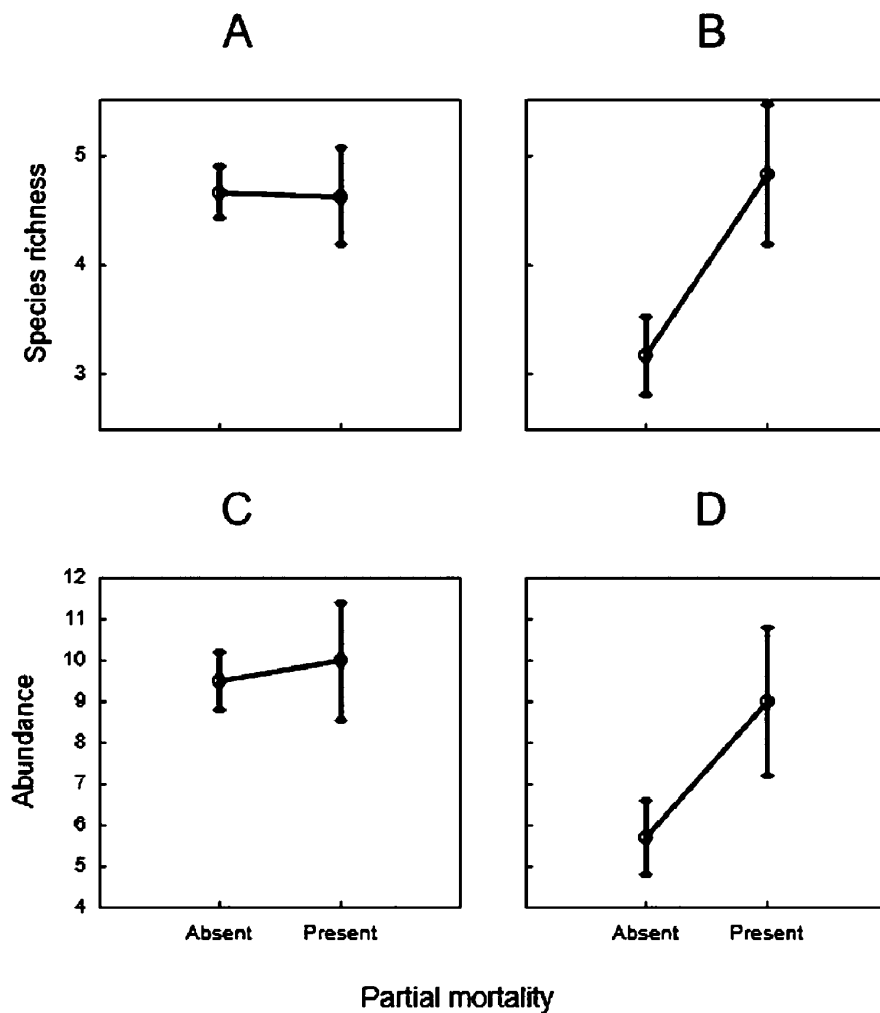


Fig. 3. Effect of partial mortality on the average species richness and abundance of symbionts. Vertical bars represent  $\pm$  standard errors. A, C — obligate; B, D — facultative.

echinoderms, tunicates, and bony fishes (Table S1), with the *Amphipoda* gen. sp. 1 (64.7%), the crab *Domecia hispida* Eydoux & Souleyet, 1842 (43.2%), and the shrimp *Cuapetes* sp. (27.4%) being the most common.

Rare species accounted for 12% of obligate species but 35% of facultative species (Table S1).

Sixty-six symbiont species were recorded on PM-affected colonies (49 facultative, 17 obligate), with three obligates—the crabs *Trapezia guttata* Rüppell, 1830 and *Cymo barunae* Ho and Ng, 2005, and the fish *P. modestus*—being only found on PM-affected colonies. Healthy colonies hosted 59 species (14 obligate, 45 facultative),

including 13 facultative species absent from PM-affected colonies.

#### Effects of PM and environmental parameters

Across all colonies PM was associated with significantly smaller volumes ( $Z = 4.96$ ;  $p < 0.00001$ ), an effect significant only at higher planting densities (40 and 60 colonies per frame:  $Z = 3.87$ ,  $p = 0.00011$  and  $Z = 2.64$ ,  $p = 0.0084$ ). The variance in colony volume explained by the models (22.7%) was partitioned between PM presence (10.2%) and colony density (12.4%). Bleaching did not show a significant effect, and

Table 2. Symbiotic communities in *Pocillopora* spp. from different tropical Indo–West Pacific regions.

Research location	CS	NC	NS	O/F	Source
Nha Trang Bay, Vietnam (9-month)		190	79	17/62	Current study
Nha Trang Bay, Vietnam (3-month)	<i>P. verrucosa</i> (Ellis et Solander, 1786)	200	69	21/48	Britayev <i>et al.</i> , 2023
Red Sea, Saudi Arabia		40	36	12/23	Britayev <i>et al.</i> , 2017
Pacific coast of Panama		35	61	7/54	Abele, Patton, 1976
Lizard Island, the Great Barrier Reef		50	102	15/87	Stella <i>et al.</i> , 2010
Heron Island, the Great Barrier Reef	<i>P. damicornis</i> (Linnaeus, 1758)	70+	107	15/84	Patton, 1966, 1974; Austin <i>et al.</i> , 1980 (summarized)
Rottneest Island, Australia		54	67	8/59	Black, Prince, 1983
Point Quobba, Australia		12	45	10/35	Black, Prince, 1983
Oahu, Hawaii	<i>P. meandrina</i> Dana, 1846	18	127	11/116	Coles, 1980
Oahu, Hawaii		751	91	9/82	Counsell <i>et al.</i> , 2018
Oahu, Hawaii	<i>P. grandis</i> Dana, 1846	210	48	9/39	Brush, 2024
Moorea, French Polynesia	<i>Pocillopora</i> spp.	36	52	12/40	Pisapia <i>et al.</i> , 2020
Culebra Bay, Costa Rica		40	132	5/127	Salas-Moya <i>et al.</i> , 2021

CS — coral species; NC — number of colonies; NS — total number of species; O — obligate; F — facultative; O/F — ratio of obligate to facultative species.

most volume variance was attributable to factors not taken into account in the model.

PM had no significant effect on mean species richness ( $W = 0.04$ ,  $p = 0.84$ ) or abundance ( $W = 1.7$ ,  $p = 0.19$ ) of obligate symbionts, with  $<0.5\%$  variance explained (Fig. 3A, C). Colony density explained 29.9% of variance in obligate symbiont species richness, while colony density and volume explained 38.5 and 3.6% of variance, respectively.

By contrast, PM significantly increased both mean species richness ( $W = 16.87$ ,  $p < 0.05$ ) and abundance ( $W = 40.98$ ,  $p < 0.05$ ) of facultative symbionts (Fig. 3B, D). However, PM accounted for only  $\approx 5\%$  of richness variance and 3.2% of abundance variance. Colony density instead explained 17.3% and 15.0% of variance in richness and abundance, respectively, whereas bleaching affected only mean abundance, with a minor effect (0.52%).

Due to the strong PM effect on facultative symbionts, total mean species richness ( $W = 6.94$ ,  $p = 0.01$ ) and abundance ( $W = 26.70$ ,  $p < 0.05$ ) were higher on PM-affected colonies.

Nevertheless, PM explained only 2.3 and 1.7% of variance in these metrics, while colony density remained the dominant variance predictor (30.0% for richness, 31.9% for abundance), and colony volume explained only a small proportion (1.6%).

## Discussion

### Variability of ectosymbiont richness in *Pocillopora* spp.

The symbiont diversity observed in this study was comparable with that reported from other Indo-Pacific regions, with the number of obligate species (17) exceeding most previous records (Table 2), likely reflecting the larger sample size (190 colonies) and the proximity of the study site to the Coral Triangle – recognized as a global hotspot of marine biodiversity (Hoeksema, 2007). Facultative species richness was also high and within the range observed for other tropical Pacific areas (Table 2). However, this metric is less informative for assessing host-specific effects, as it primarily reflects habitat heterogeneity and local invertebrate diversity.

### Prevalence of PM, colony size, and symbiont richness

PM prevalence in *Pocillopora* spp. varies widely, typically ranging from 44 to 69% (Pisapia, Pratchett, 2014, 2016; Pisapia *et al.*, 2015, 2020). Our observed prevalence (36%) was slightly lower and consistent with background PM levels — i.e., those occurring in the absence of major disturbances such as mass bleaching or salinity shocks (Jokiel *et al.*, 1993; Glynn, 2000). PM is a key indicator of colony health and a potential predictor of mortality, with >5% colony cover persisting for weeks indicating a 50% mortality risk within 3–5 months for branching corals (Cumming, 2002). Yet only 14% of PM-affected colonies in our study died, likely because severity was low — 77% of affected colonies had <25% surface loss.

As PM causes polyp death and consequently reduces colony growth rates (Meesters *et al.*, 1994), smaller colony sizes in affected colonies were expected. Since colony size can positively influence symbiont richness (Abele, Patton, 1976; Gotelli, Abele, 1983; Britayev *et al.*, 2017), reduced richness in affected colonies was also predicted. Surprisingly, PM-affected colonies hosted more species overall than healthy ones (66 vs. 59), and this trend was also observed for both facultative and obligate symbionts (Table S1). Given that our healthy-colony sample size was nearly twice as large, these results are unlikely due to chance.

PM-affected colonies must divert energy from growth and other metabolic functions to tissue repair (Meesters *et al.*, 1994), likely becoming less attractive to obligate symbionts that rely closely on the host's metabolic activity. Interestingly, the three obligate symbionts found exclusively on PM-affected colonies — *T. guttata*, *C. barunae*, *P. modestus* — are rarely found on healthy *Pocillopora* spp. in this region (Britayev, Mikheev, 2013; Britayev *et al.*, 2023b). This suggests that they may be competitively excluded from healthy colonies by other obligate symbionts, forcing them to occupy less favourable, “peripheral” habitats created by PM. In this way, PM-driven microhabitat heterogeneity may enhance richness in both facultative and, unexpectedly, obligate symbiont species.

### Environmental drivers of symbiotic community structure

We examined four potential drivers — bleaching, colony volume, planting density, and PM. Model performance was moderate, explaining 19.1–42.4% of variance, suggesting additional unmeasured factors may be important. However, our experimental design minimized environmental variability by placing all colonies at the same site — in close proximity — and depth.

The strongest predictors of symbiont richness were host density (12.4% of variance explained), as previously reported (Britayev *et al.*, 2023a), and PM (10.2%). Bleaching had negligible effect on symbiont communities (<0.5% of variance explained), likely due to mild temperature conditions and the absence of severe bleaching during the study period (Britayev *et al.*, 2023a).

Host density emerged as the most important factor for both obligate and facultative symbiont richness and abundance, consistent with previous findings for coral-associated symbiont communities (Gotelli, Abele, 1983; Arneberg *et al.*, 1998; Britayev, Mikheev, 2013; Britayev *et al.*, 2023a). Nevertheless, contrary to expectations and previous reports (Abele, Patton, 1976; Britayev *et al.*, 2017, 2023a; Counsell *et al.*, 2018), colony volume had minimal impact on symbiont communities (<0.5% of variance in most metrics; 3.6% for abundance of obligate symbionts). This pattern, also reported by Pisapia *et al.* (2020), may result from strong territorial interactions among dominant symbionts, such as species of *Trapezia* or *A. lottini* (Castro, 1978; Vannini, 1985; Huber, 1987), with limited recruitment of new individuals regardless of available space.

### Differential responses of facultative and obligate symbionts to PM

Our results align with Stella *et al.* (2010) in showing an overall positive effect of PM on community richness and abundance, but responses differed by guild. Facultative species' abundance and richness increased significantly with PM, while obligate species were almost unaffected. However, positive effects on diversity and abundance of facultative symbionts have also been reported alongside negative effects on obligate symbionts (Coles, 1980; Enochs, Manzello, 2012; Leray *et al.*, 2012).

These patterns reflect fundamental ecological differences. Obligate symbionts are tightly



linked to live coral tissue (Munday, 2004; Stella *et al.*, 2010, 2011a; Limviriyakul *et al.*, 2016), establishing deep trophic relationships (Coles, 1980) and generally avoiding algal- or sessile-fouled PM areas (Castro, 1976). Their diversity and abundance often decline as live coral cover is reduced (Leray *et al.*, 2012). In contrast, facultative symbionts primarily use coral as structural habitat and can persist without live tissue (Coles, 1980; Black, Prince, 1983; Enochs, 2012), being able to colonize both living and dead colonies (Coles, 1980). PM areas covered with mixed fouling provide novel shelter opportunities, often supporting higher facultative richness than healthier colonies (Coles, 1980; Enochs, Manzello, 2012; Leray *et al.*, 2012).

In our case, PM prevalence was high but severity low, creating sufficient heterogeneity to benefit facultative species without substantially reducing habitat quality for obligate symbionts. This may also explain the net-positive effect of PM on total symbiont richness observed here.

## Conclusions

Our study provides a comprehensive assessment of the ectosymbiotic fauna associated with *P. verrucosa* in Nha Trang Bay (Vietnam), and examines the influence of bleaching, colony size, planting density, and PM on symbiotic community composition and structure. We recorded remarkably high diversity — 17 obligate and 62 facultative species — likely reflecting both the large sample size and the proximity to the Coral Triangle, a global hotspot of marine biodiversity.

Seasonal bleaching and colony size had no significant effect on symbiont community structure, whereas colony density and, to a lesser extent, PM explained a substantial proportion of the observed variation. PM was associated with a shift in community composition, with facultative symbionts showing higher richness and abundance, while obligate symbionts tended to decline. However, this response depended on PM severity: high prevalence combined with low severity could enhance facultative diversity without significantly reducing the obligate component.

These findings highlight the complex, context-dependent effects of host health and habitat structure on coral-associated communities and underscore the potential role of PM in shaping biodiversity at fine ecological scales.

## Supplementary data

The following supplementary data are available online:

Suppl. Table 1. Taxonomic composition of the symbiotic fauna associated with colonies of *Pocillopora verrucosa*.

## Conflict of interest

The authors declare no conflicts of interest.

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