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Density and Bleaching of Corals and Their Relationship to the Coral Symbiotic Community

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Abstract: Corals provide an important habitat for diverse fauna. The habitat is especially rich in branching species. Each colony harbors several species and dozens of individuals, forming an integrated symbiotic community. Factors affecting the diversity and abundance of coral symbionts are poorly understood. The present study tested experimentally the relationship between the population density of coral *Pocillopora verrucosa* and the diversity and abundance of symbionts in planted coral fragments exposed for three months. Colony size and bleaching were also considered as two additional factors. We demonstrated that, even at the early stage of colony formation, the diversity of obligate symbionts on planted corals in Nha Trang Bay was higher than the diversity of any other studied local faunas of the world's ocean. Species richness and the abundance of symbionts were positively related to colony size and density, while no impact of bleaching was found. Species richness and the abundance of obligate symbionts increased with host population density, while in facultative symbionts, these indices decreased. We hypothesized that the negative effect of host population density on species richness and the abundance of facultative symbionts is caused by the competitive pressure of obligates, which increases with their abundance. The reasons for the different responses of obligate and facultative symbionts to host density were considered.

Keywords: symbionts; *Pocillopora verrucosa*; diversity; species richness; abundance; obligate symbiont; facultative symbiont

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1. Introduction

Almost all scleractinian corals provide shelter for various invertebrate and fish species [1,2]. Some of these scleractinian corals cannot survive without the host corals (obligate symbionts), while others can be free-living (facultative symbionts) [1]. Due to their extremely high abundance and biomass, symbionts are a key component of coral-reef food webs and, by extension, entire reef ecosystems [3,4]. Another important role of symbionts in reef ecosystems is maintaining coral fitness [5–8] and protecting corals from predator attacks [9–13]. The great diversity of these organisms is partly attributed to the habitat diversity provided by scleractinian corals [14], which in turn depends on the growth form of corals and which is higher in branching coral colonies than in massive laminated or encrusting coral colonies [1]. Accordingly, the highest diversity of symbionts has been recorded in association with branching acroporid and pocilloporid corals [1,15]. In some cases, the number of species and individuals inhabiting a single coral head can reach 10–20 species and 70–80 individuals, thus forming complex symbiotic communities [16–18].

The species composition and structure of coral symbiotic communities may depend on various environmental factors, such as the morphology and the size of the host colony [19–21], host population density [20,22–24], surface chlorophyll *a* [24], wave energy [25,26], and flow regime [21,24]. The relationships between some of these factors (i.e., the size and morphology of the host colony) and the characteristics of the community are well-documented [18–22,27,28] and can be considered as a methodological basis for the analysis of coral symbiotic communities.

At the same time, the impact of other specific environmental factors on the structure of symbiotic communities has been poorly studied or remains controversial [20,22,24]. Specifically, a comparison of the diversity and the abundance of large crustaceans inhabiting coral *Madracis auretenra* (previously named *M. mirabilis*) in two sites with different colony densities showed that these two factors were higher in communities associated with individual isolated colonies than in communities with continuous aggregations. However, this effect may also be associated with the shapes of the colonies, which are different in isolated heads and continuous aggregations [20]. According to Counsell et al. [24], the density of *Pocillopora meandrina* colonies did not have a significant effect on the richness of cryptofaunal species and showed minimal variation in species-specific responses. On the contrary, a comparison of *Pocillopora damicornis* symbiont communities showed that their abundance was higher on the reef flat, where the density of corals was higher, than on the reef slope [22]. These differences were explained by the high pressure of predators on the symbionts during their host-to-host migrations on the reef slope, where the distances between coral colonies are higher, leading to a decrease in their abundance. However, the authors [22] believed that the density of the hosts was not the only factor affecting the abundance of symbionts, as the compared colonies were located in different biotopes that were subject to the influence of various environmental factors [22]. A trend toward increased diversity and abundance in coral aggregations, which was more distinct for obligate symbionts, was also shown for another coral species, *Pocillopora verrucosa* [23]. Thus, the available data on the relationship between the spatial arrangement of host corals and the structure of their symbiotic communities are contradictory and require further investigation.

Another factor that may have a significant impact on the symbiotic community is the bleaching phenomenon. Coral bleaching associated with anthropogenic climate change is one of the most important factors responsible for the degradation of coral reefs [29,30]. Bleaching can affect the physiological state of symbiotic fish and invertebrates, increase intra- and interspecific competition, and decrease the population density of symbionts [30–35], which, in turn, implies a change in the structure of the symbiotic community as a whole. However, the response of the entire symbiotic community to bleaching events remains unclear.

This work aimed to experimentally test the hypothesis that there is a positive relationship between the population density of hosts and the diversity and abundance of their symbionts. Taking into account that obligate and facultative symbionts can respond differently to changes in the density of the host population, we considered the effect of density on both the symbiotic community as a whole and these two components of the community separately. Since short-term bleaching happened in the area of research during the experiment, an assessment of its impact on the symbiotic community was also performed.

2. Materials and Methods

2.1. Host Coral and Sampling Location

The most diverse symbiont communities are associated with branching corals of the Acroporidae and Pocilloporidae families, which form complex three-dimensional structures with numerous well-protected microbiotopes. Of the nearly 900 species known as coral symbionts, about 250 species are associated with corals of the genus *Pocillopora* [1]. In addition, species of *Pocillopora* are fast-growing, commonly used in aquaculture [36], and widely distributed in Nha Trang Bay, Vietnam, where our study was conducted. Therefore, we chose the species *Pocillopora* cf. *verrucosa*) (hereafter *P. verrucosa*) as our object of study (Figure 1A). The symbiont fauna of *Pocillopora* ssp. has been well-documented during recent decades in several regions of the Indo–West Pacific [15,28,37–39], including Nha Trang Bay, where 16 species of obligate symbionts and 28 species of facultative symbionts were associated with *P. verrucosa* [23,40,41].

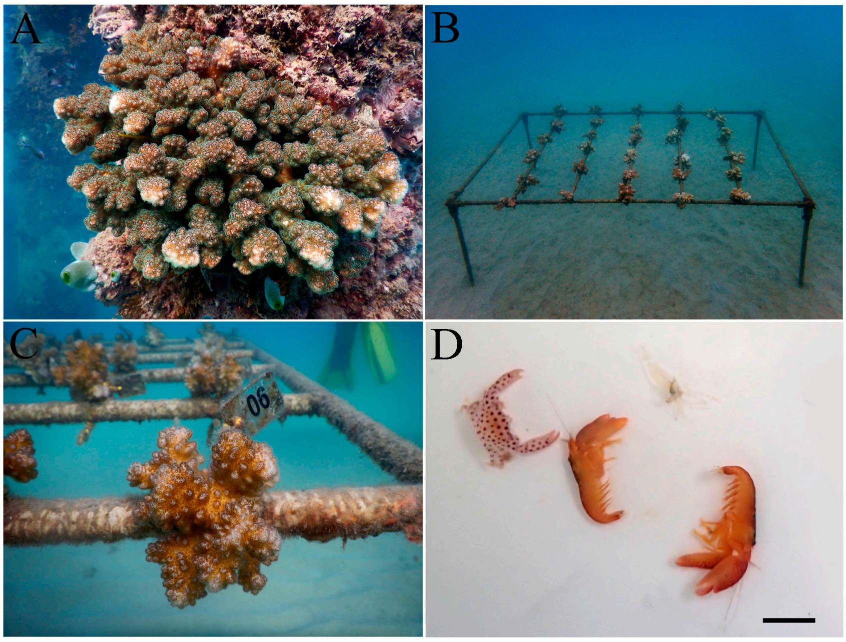

Figure 1. (**A**) *Pocillopora verrucosa* colony in its natural habitat. (**B**) Rectangular experimental frame with planted coral colonies installed on a sandy bottom. (**C**) One of the experimental colonies, close view. (**D**) Washout of one colony after three months of exposure: crab *Trapezia tigrina*, shrimps *Alpheus lottini* and *Palaemonella rotumana* are recognizable, scale bar 5 mm.

Experimental studies were carried out from 26 April 2020 to 23 July 2020 in the Dam Bay Research Station coastal area located in the Nha Trang Bay of the South China Sea, Vietnam (Figure 2). Fixed rectangular nurseries for coral planting were installed on the sandy bottom among bioherms at a depth of 3 m (Figures 1B and 2C). Planted colonies were raised above the ground to a height of 40 cm.

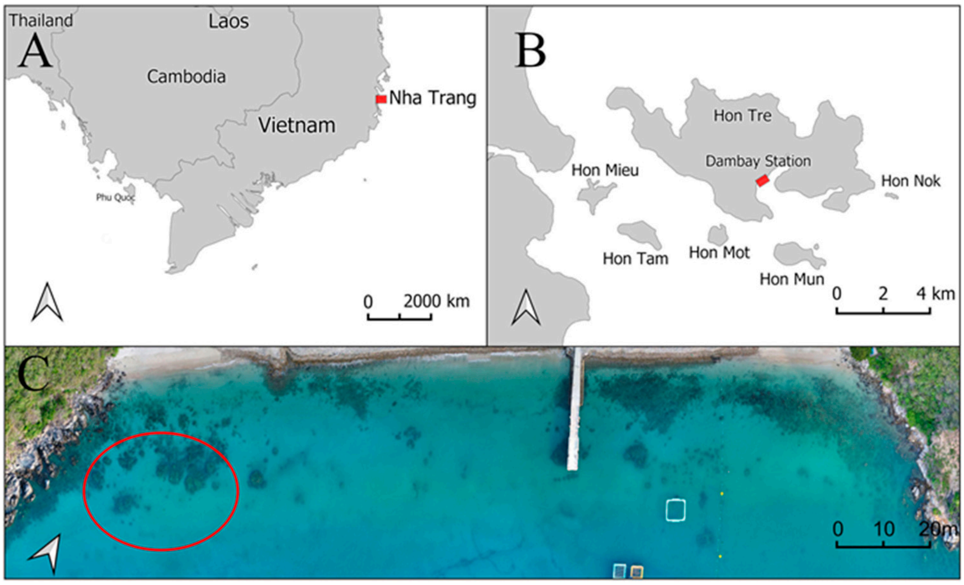

Figure 2. Location of the study area on the coast of Vietnam (**A**,**B**) and sampling site in Dam Bay ((**C**), orthophotoplan taken from a height of 20 m). The area where experimental constructions with planted colonies of *Pocillopora verrucosa* are located is circled in red.

A temperature logger (HOBO U22-001) was deployed at a depth of 3 m to monitor the temperature regime in the area of the experiment. It recorded the temperature twice per day. During the observation period, the daily temperatures varied from 25.3 to 31.2 °C. Seasonal upwelling mitigates thermal anomalies [42], thus the average daily temperatures exceeded 30 °C for only six days in June 2020 and for three days during the first ten days of July 2020 (Figure S1).

2.2. Experimental Design

For the experiment, fragments of coral branches 4–6 cm high were collected from the large colonies grown in the same area at the coral nursery. Fragments were measured before planting. The volume between coral branches is the major factor influencing the number of animals inhabiting a coral, as this is the space where the animals live. As demonstrated earlier, this volume is highly correlated with the total coral colony volume, calculated by multiplying the height and the large and small diameters [43]. Therefore, in this study, we used these three parameters to determine the volume of colonies, as this process speeds up measurements when processing a large number of colonies. The fragments were then washed in an emulsion of clove oil (15 drops per liter) to anesthetize and remove symbionts. Then, fragments were examined with the naked eye and all found symbionts were removed. After processing, the fragments were planted on five rectangular frames 1.5 × 1.0 m in size to form settlements of different densities (20, 30, 40, 50, and 60 fragments per frame; 200 fragments in total). The distance between individual fragments was 20, 13.3, 10, 8, and 6.7 cm, respectively.

During the experiment, individual photo registration of the coral colonies and their cleaning from fouling and debris were carried out twice a month. Bleaching was assessed, based on the images of colonies according to the 6-point Siebeck's color reference card [44]. Often the bleaching of *Pocillopora verrucosa* is characterized by spotting: colonies are darkest in the central part and lightest at the ends of the branches. Therefore, the arithmetic mean of the scores of the lightest and darkest colony parts was used to estimate the level of bleaching of each individual colony. Since the impact of bleaching on symbionts develops gradually [31], the accumulated bleaching score for the last 2 censuses of colonies before sampling (3 July 2020 and 21 July 2020) was used for statistical analysis. After exposure for three months in the sea (Figure 1C), the colonies were removed from the frames, measured, photographed, and washed in clove oil emulsion (Figure 1D). Then, they were carefully examined and the remaining symbionts were collected with tweezers. Washouts from the colonies were sieved through a 1 mm diameter mesh. All symbionts found in the washouts and on the colony were fixed in 70% ethanol.

2.3. Identification and Categorization of the Species

Each animal was identified to the lowest possible taxonomic level in the laboratory, based on specialized literature [40,41,45–47]. All specimens associated with the colonies of *P. verrucosa* were assigned to one of two main groups—"obligatory symbionts" and "facultative symbionts"—according to the existing literature [1,23,27,37]. The latter group includes both species known as facultative symbionts and poorly studied species with an uncertain status. Juveniles of *Trapezia* spp. crabs, which cannot be identified to the species level, were used only for comparison of the abundance of main groups of symbionts. The identified material is deposited in the A.N. Severtsov Institute of Ecology and Evolution Russian Academy of Sciences (IPEE RAS), Moscow, Russia.

The biodiversity (i.e., the total number of symbionts and the number obligate symbionts and facultative symbionts separately), species richness (i.e., the median number of species per one colony of infested hosts), and abundance (i.e., the median number of individuals per one colony of infested hosts) were used in the analysis of the environmental impacts on the structure of the symbiotic community. The terms were used following Bush et al. [48], with minor changes.

2.4. Statistical Analysis

Generalized linear models (GLZ) were used to assess the impacts of host colony volume, colony density, and bleaching on species richness and the abundance of symbionts [49]. The value of the fit criterion χ^2 was used to test the distributions of dependent variables and the results of the Kolmogorov–Smirnov test were applied to supplement the estimation. The test showed that the values of all dependent variables were distributed following the Poisson distribution pattern. The Akaike information criterion (AIC) was applied to determine the best link function for the model. The models based on the identity-link function were characterized by the lowest values of AIC. Therefore, they were selected to test the impacts of given factors on the symbiotic community.

The impact of each factor was assessed using the Wald test (W). The factor's influence was considered significant if the test results were statistically significant ($p < 0.05$). To describe the effect of host colony density on community characteristics, linear trends were plotted, based on average values for each density. All tests were performed in Statistica v. 12.0.

3. Results

3.1. Taxonomic Composition

A total of 69 animal species was found on 200 coral colonies, 26 of which were identified at the species level, 10 at the genus level, and 33 at the family or higher taxonomic level. The richest taxonomic group was crustaceans (subphylum Crustacea), which included 41 species, of which the majority, 33 species, belong to the order Decapoda. They were followed in descending order by polychaetes (13 species), mollusks (9 species), and brittle stars (2 species). Fish, sipunculans, nemerteans, and turbellarians were represented by one species each (Table S1).

Of the species found, 21 were obligate symbionts and 48 were facultative symbionts. Among obligates, the most diverse taxa were crabs of the genera *Trapezia* (9 species) and *Cymo* (6 species). In addition, three species of shrimp and one species each of molluscs and fish were recorded (Table S1). The total number of symbiont species and the number of facultative symbionts increased with the sample size and approached the asymptote when the sample size was about 160 colonies. For obligate symbionts, saturation occurred much earlier, with a sample size of about 40 colonies (Figure 3).

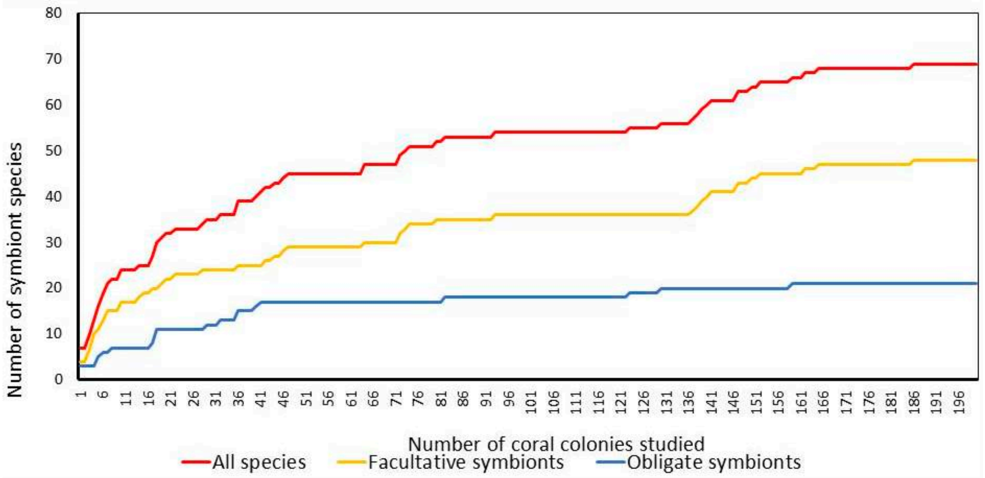

Figure 3. Accumulation of symbiont species as a function of sample size, both for the total species pool and for obligatory and facultative species associated with *Pocillopora verrucosa* (n = 200 colonies).

3.2. The Impact of Colony Size, Bleaching and Host Density on Symbiotic Assemblages

The generalized linear models used to assess the influence of environmental factors on the composition and structure of the symbiotic assemblage demonstrated that the volume of the host colony significantly affected both the species richness of all symbionts

(W (1) = 9.64, $p < 0.002$) and the species richness of obligate symbionts (W (1) = 7.88, $p < 0.005$) and facultative symbionts (W (1) = 3.89, $p < 0.05$) separately. The volume of the host colony also had a significant effect on the abundance of all symbionts (W (1) = 30.77 and $p < 0.0001$), on the abundance of obligate symbionts alone (W (1) = 21.02, $p < 0.0001$), and on the abundance of facultative symbionts alone (W (1) = 13.34, $p < 0.0001$). In general, an increase in the volume of the host colony led to an increase in both the number of symbiont species and the number of individuals.

During the observation period, we recorded partial bleaching, in which the state of the colonies varied from 2 to 4 points on Siebeck's scale from colony to colony during the period of observation. According to the test results, bleaching did not significantly affect either the richness (W (2) = 0.17, $p = 0.920$) or the abundance of the symbiotic community as a whole (W (2) = 0.37, $p = 0.830$). Similar results were obtained in the analysis of the effect of bleaching on species richness and the abundance of obligate symbionts alone (W (2) = 0.91, $p = 0.635$ and W (2) = 0.69, $p = 0.710$, respectively) and facultative symbionts alone (W (2) = 0.04, $p = 0.982$ and (W (2) = 1.62, $p = 0.444$, respectively).

Significant differences in the species richness of all symbionts (W (4) = 11.65, $p < 0.020$), obligate symbionts (W (4) = 11.52, $p < 0.021$), and facultative symbionts (W (4) = 19.20, $p < 0.0001$) were observed between the frames with different population densities of host coral (Figure 4). Similar differences were found in the abundance of all symbionts (W (4) = 18.40, $p < 0.001$), obligate symbionts (W (4) = 22.23, $p < 0.0001$), and facultative symbionts (W (4) = 45.35, $p < 0.0001$) (Figure 5).

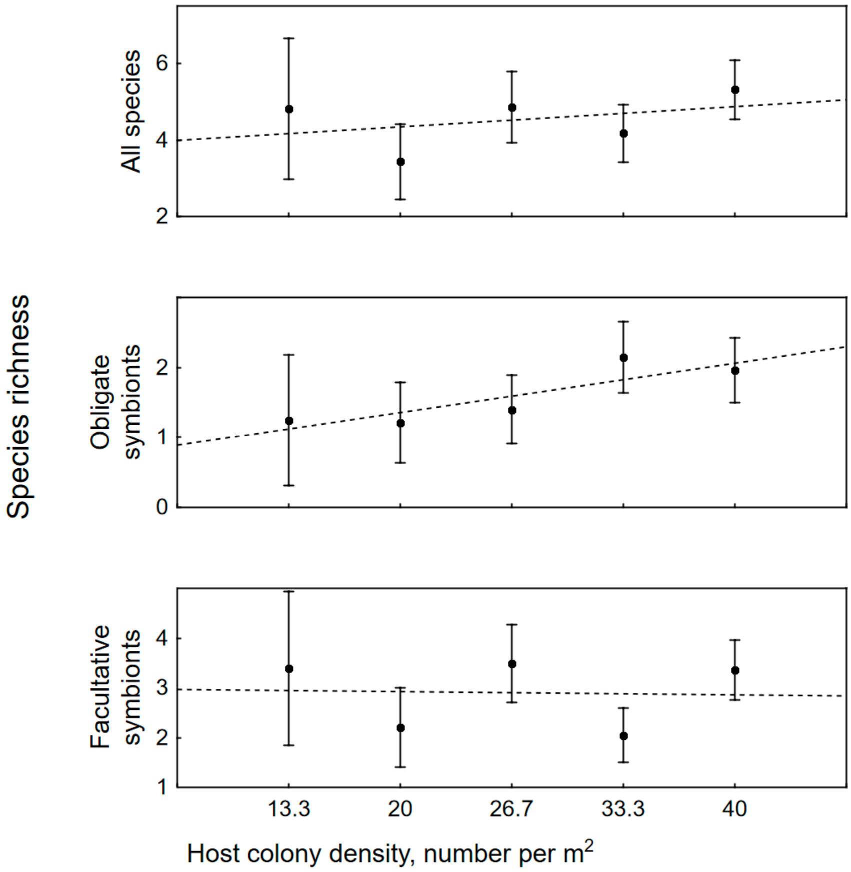

Figure 4. Effect of colony density on species richness of symbionts (mean number of species per colony ± SE).

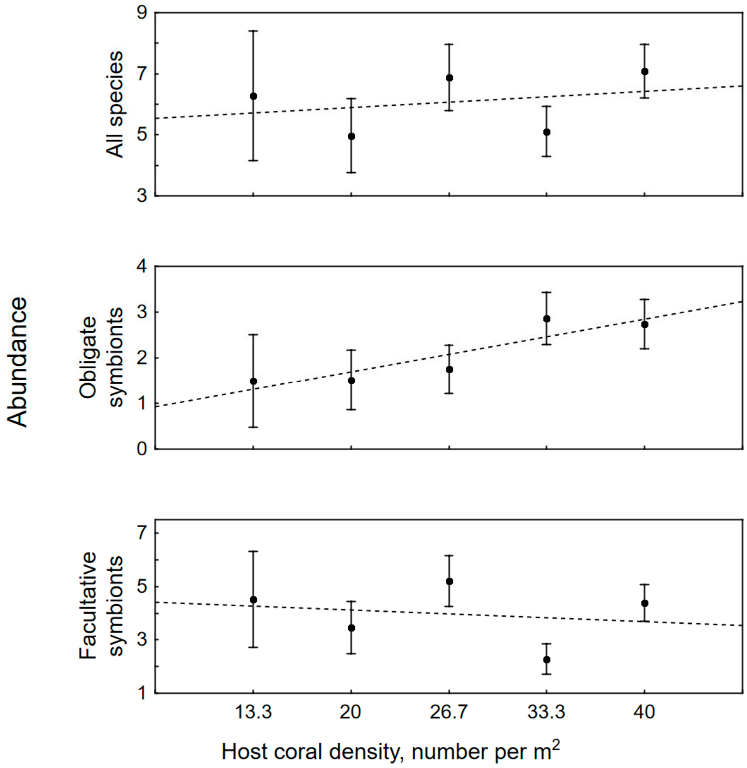

Figure 5. Effect of colony density on abundance of symbionts (mean number of individuals per colony ± SE).

However, host density had different impacts on obligate symbionts and facultative symbionts (Figures 4 and 5). The impact was positive and pronounced on species richness and the abundance of obligate symbionts ($SR = 0.89 + 0.24D$ and $A = 0.92 + 0.38D$, respectively, where SR is species richness, A is the abundance of symbionts, and CD is the density of colonies), whereas the impact on these indices of facultative symbionts was slightly negative ($SR = 2.97 - 0.02CD$ and $A = 4.40 - 0.15CD$). Due to the opposite effects of colony density on these two ecological groups, the impact of this factor on the community as a whole was weakened ($SR = 3.99 + 0.18CD$ and $A = 5.54 + 0.18CD$).

4. Discussion

For the first time, we obtained representative data on the composition of symbiotic assemblages of the coral *Pocillopora verrucosa* at the early stage of colony formation. Due to the large samples, we can conclude that the fauna of symbionts are well-represented in our samples. Facultative symbionts are often opportunistic species that do not have close relationships with their host coral, and their diversity is driven mainly by external environmental factors (e.g., the diversity of surrounding habitats) [18]. The faunae of these facultative symbionts continue to increase slowly with an increase in the number of samples. This applies, to a lesser extent, to obligate symbionts and a given coral size group. According to our results, a sample of 40 colonies can be considered sufficient for assessing their species diversity. However, the larger size of the sample we used in the present research allowed a more accurate assessment of the local diversity of obligate species. As a result, the local species diversity of obligate symbionts recorded in the framework of the present study (21 species) was noticeably higher than it was for larger colonies in other regions of the Indo–Pacific [18], including the richest local symbiotic communities of the Great Barrier Reef (15 species) [16,37,38,43], even though the present study was performed on small colonies inhabited by communities at an early stage of formation. These data are consistent with the exceptionally high diversity of crinoid symbionts reported earlier in Nha Trang Bay [50], which was probably related to the proximity of this region to the center of marine biodiversity, the Coral Triangle [51]. The present result on coral symbiont biodiversity is, in fact, one of the first reports on symbiont biodiversity in coral farms. Therefore, we can assume that another important function of coral farms (in addition to coral propagation) is the maintaining and conservation of coral-reliant invertebrates.

Our study revealed that the structure of symbiotic communities of the coral *P. verrucosa* is significantly affected by two of the three studied parameters: the size of colonies and their density. At the same time, no significant effect of bleaching on species richness and the abundance of communities was found.

Previously, it was shown that the deterioration of colonies' fitness during bleaching leads to a change in intra- and interspecies relationships in the community of obligate symbionts [34]. The most pronounced consequences of bleaching are the displacement of female *Trapezia cymodoce* crabs and shrimp *Alpheus lottini* from corals by male crabs and a sharp decrease in the clutch size in the remaining female crabs [31,32,34]. Obligate symbionts were absent from completely bleached colonies [52]. These data imply that bleaching should lead to a decrease in species richness and the abundance of obligate symbionts. However, our findings do not support this hypothesis.

The observed discrepancy in the assessment of bleaching consequences for symbiotic communities is probably related to the different levels of bleaching recorded in our work and in the studies of other authors. Specifically, several authors [31,32,52] considered colonies as being in the "bleaching" state when they were completely bleached (white). This state probably corresponds to 1 point of Siebeck's color reference card [44] or to "complete bleaching" in the work of Stella et al. [34]. At the same time, we did not observe colonies with a bleaching level below 2 points, which was in good agreement with the temperature regime in the area during the experiment (Figure S1). In contrast to 2019, when the temperature anomaly reached Bleaching Alert Level 2 in Nha Trang Bay [42], the temperature in the hottest months (May–July) of 2020 did not exceed the coral bleaching threshold. The partial bleaching observed by us (2–2.5 points) was probably caused by a slight excess above the threshold of 30 °C in June and the beginning of July. Therefore, we concluded that the level and duration of bleaching observed in the framework of this study were insufficient to induce changes in the structure of symbiotic communities.

Generally, coral-colony size is positively associated with symbiont abundance and diversity [18,19,37,43]. However, this parameter is not always a good predictor of symbiont abundance. Other factors, such as exposure at low tides, differences in host-colony structure, intraspecific interactions, and spatial distribution, can also affect the symbiotic community [18,21,23,24,28,53]. In particular, our study revealed the significant effect of the population density of *P. verrucosa* colonies on symbionts. This result is consistent with the often-observed positive correlation between host population density and the abundance in communities of parasites [54]. It may be partly explained by the general epidemiological density-dependence theory of infection transmission [55].

We suggest that the positive effect of host density on symbiotic communities is related to the recruitment patterns of symbiont populations. The recruitment of obligate symbionts occurs in two ways: by the settlement of larvae from plankton and by the immigration of symbionts from other colonies. Coral-colony aggregations may be more attractive for settling larvae than single colonies, due to the effect of high concentrations of metabolites [56]. Migrations of juvenile and adult invertebrate symbionts from host to host are a common phenomenon in marine communities, which has been experimentally confirmed [57–59], including for coral symbionts [53,60]. The reasons for migration may be the search for a partner, a lack of space and food in the colony, and aggressive intra- and interspecies interactions [53]. However, obligate symbionts associated with the host throughout their life cycle are poorly adapted to the environment and are vulnerable to predators during migration. Therefore, the mortality of symbionts migrating from host to host in dense aggregations of hosts should be lower [53], which may lead to increased diversity and an abundance of symbionts in host aggregations.

Previously, we suggested that the effect of host density would be more pronounced on obligate symbionts than on facultative symbionts [23]. The data obtained confirm this suggestion (Figures 4 and 5). This difference between the two ecological groups of symbionts is probably the result of a lack of functional relationships between opportunistic facultative symbionts and their hosts. Therefore, the attraction of settling larvae by host metabolites and host-to-host migrations is unlikely or impossible for them. Moreover, although the differences were not statistically significant, we found a negative relationship between the density of the host population and species richness and the abundance of facultative symbionts (Figures 4 and 5). We believe that this could be the result of the competitive pressure of obligate symbionts on facultative symbionts, which increased with an increase in species richness and the abundance of obligates. Earlier, a similar conclusion was drawn by Patton [16], who observed an increase in the abundance of facultative symbionts on *Acropora* colonies from which the obligate symbionts were removed. However, this hypothesis requires further experimental verification.

5. Conclusions

Our studies showed that even at the early stage of the formation of *Pocillopora verrucosa* colonies, they are already inhabited by obligate and facultative symbionts. The diversity of obligate symbionts appeared to be the highest for all the studied local symbiont faunas of the world's ocean. We demonstrated that, contrary to expectations, the effect of bleaching on symbiotic communities was not recognizable. This is probably due to the absence of colonies in the state of “complete bleaching” (1 point) in our samples, as the observed bleaching did not exceed 2–2.5 points on the bleaching color scale [44]. However, it is possible that the observed partial bleaching may affect symbionts at the population level.

It was shown that, in general, coral population density positively affects species richness and the abundance of symbiotic communities. However, coral population density had the opposite effect on obligate and facultative symbionts. With an increase in density, these indices increased in obligate symbionts, while they slightly decreased in facultative symbionts. We believe that the positive effect of the host density on symbiotic communities is related to the peculiar properties of recruitment of obligate symbiont: (1) attracting settling larvae, due to the effect of high concentration of metabolites in dense host aggregations, and (2) reducing mortality of migrating symbionts in host aggregations. We hypothesize that a slight negative effect of the host density on species richness and the abundance of facultative symbionts is caused by the increase in the competitive pressure of obligates when there is an increase in their abundance. However, further experimental studies are necessary to verify this hypothesis.

Due to the vital role of symbionts in functioning coral colonies [4,6,7], young colonies transplanted from coral nurseries to the natural environment should contain a set of symbionts to maintain their fitness and to protect them from predators. Therefore, our data on the effect of density on the symbiotic community should be considered when planning the optimal fragment density in coral farms and when planting seedlings in coral reef restoration.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/d15030456/s1: Table S1: title; List of symbiont taxa found on experimental colonies in association with the coral *Pocillopora verrucosa*; Figure S1: title; Temperature dynamics for 3 months from April to July 2020 at a depth of 3 m, obtained using HOBO® u22-001 thermologgers at the experimental site in Dam Bay.

Author Contributions: Conceptualization, T.A.B. and F.V.L.; methodology, T.A.B., F.V.L. and Y.A.B.; software, F.V.L.; formal analysis, T.A.B., F.V.L. and Y.A.B.; investigation, T.A.B., F.V.L., Y.A.B., T.H.N. and R.A.P.; resources, F.V.L., T.A.B. and T.H.N.; data curation, T.A.B.; writing—original draft, T.A.B.; writing—review and editing, T.A.B., F.V.L., Y.A.B., T.H.N. and R.A.P.; visualization, T.A.B., F.V.L., Y.A.B. and R.A.P.; supervision, T.A.B.; funding acquisition, T.A.B. and T.H.N. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: All data used in this study have been made available online; the corresponding links are indicated in the text.

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Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

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