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Ontogenetic shifts in Symbiodiniaceae assemblages within cultured *Acropora humilis* across hatchery rearing and post-transplantation phases

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Coral reefs have been declining worldwide due to multiple threats. Various approaches for coral restoration have been employed to increase coral populations. Sexual propagation is a crucial technique that can enhance the genetic diversity of coral offspring, thereby increasing coral reef resilience in the face of a changing environment. However, the effectiveness of using sexually reared corals for transplantation depends on many factors, including the biological traits of the coral and the physical environment. This study investigated the relationship between *Acropora humilis* and *Symbiodiniaceae* during the ontogenetic stages of the coral in *ex-situ* conditions and after transplantation to a natural reef. Coral sexual propagation techniques were conducted to produce experimental coral colonies. The fertilization rates of coral gametes averaged 98.48 ± 0.34%. However, the survival rate of juvenile corals gradually declined to 45.96 ± 1.31% at 18 months old under hatchery conditions and to 20% after transplantation to a natural reef. *Acropora humilis* associated with *Symbiodiniaceae* lineages belonging to three genera: *Symbiodinium*, *Cladocopium*, and *Durusdinium*. Reared juvenile corals developed a more specific and stable association with particular *Symbiodiniaceae* under hatchery conditions, whereas after transplantation, corals tended to contain a higher diversity of *Symbiodiniaceae* lineages. These results indicate that a shift in *Symbiodiniaceae* composition can provide long-term benefits to corals during their ontogenetic cycle and when the environment changes.

KEYWORDS

coral, endosymbiont, gamete, juveniles, coral culture, sexual propagation, ontogeny, resilience

Introduction

The establishment of a symbiotic relationship between Scleractinia corals and single-cell algae, known as zooxanthellae in the family *Symbiodiniaceae*, is essential for the development and survival of coral reefs (Decelle et al., 2018; LaJeunesse et al., 2018). Reef-building corals provide shelter and inorganic nutrients (e.g., ammonia, phosphate, CO_2) for the *Symbiodiniaceae*, which, in return, assimilate and export oxygen and photosynthetic products (such as sugars and amino acids). Within this association, a large proportion of photosynthates (64%–95%) are translocated to meet the coral's energy requirements (Muscatine, 1990; Iluz & Dubinsky, 2015; López-Londoño et al., 2022). There were 11 genera of *Symbiodiniaceae* that have been described based on morphological, physiological, ecological, and molecular evidence (Yorifuji et al., 2021; LaJeunesse et al., 2022). Four of these genera are commonly associated with Scleractinia corals, namely, *Breviolum* (clade B), *Cladocopium* (clade C), *Durusdinium* (clade D), and *Symbiodinium* (clade A) (Wham et al., 2017; LaJeunesse et al., 2018). Moreover, differences in *Symbiodiniaceae* genotypes may reflect host-specific responses to ecological or environmental gradients, as they can influence coral gene expression and present distinct ecophysiological characteristics (Berkelmans & Van Oppen, 2006; Levin et al., 2017; De Souza et al., 2022). Generally, host species in the Indo-Pacific are mostly associated with the genera *Cladocopium* and *Durusdinium*, which are found in various reef habitats (Baker, 2003; Lajeunesse, 2005). *Cladocopium* and *Durusdinium* are two well-known genera that exhibit differences in ecophysiology, which can impact their interaction with coral hosts (Hoadley et al., 2019; Abbott et al., 2021). In some reefs, for example, corals of the genus *Acropora* that host *Cladocopium* are more susceptible to bleaching, whereas those harboring *Durusdinium* can withstand higher temperatures (Sampayo et al., 2008; Thinesh et al., 2019). *Durusdinium* is considered a stress-tolerant *Symbiodiniaceae*; most corals that are frequently exposed to high temperature, irradiance, and turbidity were found to be associated with this genus (Rowan, 2004; Claar et al., 2020). However, there is evidence suggesting that reef-building host heat-evolved *Symbiodiniaceae* (e.g., *Durusdinium*) undergo poorer growth in non-stressful environments, highlighting trade-offs (Baker et al., 2013; Cunning et al., 2015). This may ultimately result in future declines in coral reefs owing to reduced calcification rates (Jones & Berkelmans, 2010).

The diversity of *Symbiodiniaceae* assemblages, when flexible in coral hosts, might provide them with the ability to rapidly cope with environmental conditions (Cunning et al., 2015; Goulet et al., 2017). Rapid acclimatization and/or adaptive bleaching of corals under a changing climate can occur through "switching" (uptake of exogenous *Symbiodiniaceae* from the environment) and "shuffling" (changes in the endogenous *Symbiodiniaceae* community composition) (Buddemeier and Fautin, 1993). These mechanisms represent an opportunity for corals to turn over their community of *Symbiodiniaceae* from currently susceptible to more stress-resistant genera/strains (Baker et al., 2013; Boulotte et al., 2016; Quigley et al., 2016). Coral–*Symbiodiniaceae* shuffling is a phenomenon more common than complete switching mechanisms.

Additionally, switching requires sensitive techniques and temporal monitoring on the same coral (Goulet, 2006; Rouzé et al., 2019). Most corals can optimize their photosynthetic and metabolic performance in response to prevailing environmental conditions by changes in their *Symbiodiniaceae* community compositions (Cunning et al., 2018; Wang et al., 2022). For instance, the proportion of *Durusdinium* in *Orbicella faveolata* increased differently in response to short- and long-term heat stress exposure, depending on the severity of the disturbance (Cunning et al., 2015). Similarly, several studies have revealed that a large-scale spread of heat-stress tolerant symbionts is correlated with corals living in warmer oceans (Pettaya et al., 2015; Jain et al., 2021); this rapid shift in *Symbiodiniaceae* can potentially enhance the corals' survival in the face of unstable environmental conditions. Nevertheless, this mechanism may not be sufficient to ensure the survival of all corals under the predicted conditions of future climate change, which can vary depending on the severity of stress, geographic locations, coral taxa, etc. (Berkelmans & Van Oppen, 2006; Cunning et al., 2018).

Several variables influence the structure of the *Symbiodiniaceae* assemblage in coral, including biological traits (e.g., age, life-history strategies) and environmental factors (e.g., temperature, light) (LaJeunesse et al., 2010; Stat et al., 2013). The distinct modes of *Symbiodiniaceae* cell acquisition (vertical and horizontal) can significantly impact the *Symbiodiniaceae* community in coral offspring (Ali et al., 2019; Swain et al., 2021). For example, the early developmental stages of horizontal symbiont transmission is often correlated with increased diversity of the *Symbiodiniaceae* communities within corals (Yuyama et al., 2012b; Yamashita et al., 2014). Conversely, vertical symbiont transmission is associated with lower *Symbiodiniaceae* diversity, but greater stability and co-evolution of *Symbiodiniaceae* with their parental colony (Chamberland et al., 2017; Quigley et al., 2017b). Offspring of broadcast spawner corals (aposymbiotic larvae and/or primary polyps) acquire symbiont cells from the surrounding environment, leading to the establishment of distinct *Symbiodiniaceae* community assemblages (Yamashita et al., 2014; Nitschke et al., 2016). Most newly recruited *Acropora* corals are associated predominantly with *Durusdinium* and *Symbiodinium* in both *ex-situ* and *in-situ* environments, whereas the parent colony is significantly associated with *Cladocopium* and/or *Symbiodinium* (Gómez-Cabrera et al., 2008; Yamashita et al., 2013). Consequently, the *Symbiodiniaceae* community can shift during the ontogeny in *Acropora* spp., potentially allowing them to acquire suitable *Symbiodiniaceae* to cope with environmental stress (Abrego et al., 2012; Rouzé et al., 2016; Yuyama et al., 2016).

Ongoing climate change significantly impacts coral reefs around the world (Hoegh-Guldberg et al., 2017; Thirukanthan et al., 2023). Mass bleaching events in Thai waters have become frequent, primarily due to elevated seawater temperatures and river flooding, which results in hyposalinity (Chavanich et al., 2009; True, 2012). *Acropora* corals are known to be a predominant species around Sattahip Bay in the upper Gulf of Thailand (Viyakarn et al., 2009; Chankong & Manthachitra, 2013). However, nearly all *Acropora* spp. perished after a mass bleaching event in 2010, especially at Samae San Island. *Acropora humilis* is particularly

susceptible to environmental stressors. All populations of *A. humilis* have failed to recover after bleaching events, even when temperatures have returned to normal (unpublished data). As such, stock enhancement may serve as a means to mitigate coral reef degradation and foster recovery (Omori, 2019; Koch et al., 2022). Both asexual reproduction (coral fragmentation) and sexual reproduction (sexually propagated corals) are recognized as sources for coral transplantation (Omori et al., 2016; Randall et al., 2020). Our research group is focused on preserving the remaining populations of *A. humilis* using sexual propagation techniques, as they generate genetically diverse offspring that could enhance coral reef resilience (Randall et al., 2020; Shaver et al., 2022). To evaluate the resilience potential of corals, it is essential to investigate the relationship between the coral and their symbionts, especially at a young stage when they are more susceptible to shifts in their *Symbiodiniaceae* in response to environmental changes.

In this context, we aimed to examine the *Symbiodiniaceae* community within *A. humilis* from the early developmental to juvenile stages under hatchery conditions and after transplantation to the reef site. An experimental coral was prepared using a sexual propagation technique, employing a method initiated by the Reef Biology Research Group in collaboration with the Akajima Marine Science Laboratory, Japan. Investigating the composition and variability of *Symbiodiniaceae* communities provides insight into how coral symbioses interact throughout the ontogenetic cycle and post-transplantation. This knowledge can aid in developing restoration strategies tailored to specific reef ecosystems and environmental conditions, thereby increasing the likelihood of successful coral reef restoration and conservation.

Materials and methods

Coral species and study sites

Acropora humilis is an important reef-building coral, noted for its rapid growth and high calcification rates, which are approximately 5 mm/year–15 mm/year (Shaaban et al., 2015; Mohammed & Dar, 2017) (Figure 1). This species is prevalent in shallow reefs and reef slope habitats in Thai waters, encompassing both the Gulf of Thailand and the Andaman Sea. However, *A. humilis* is highly sensitive to environmental changes. Most colonies around Samae San reefs have been unable to recover following mass bleaching events. This study was conducted at three different sites: Sattahip, Chon Buri in the upper Gulf of Thailand; the Tao Mo Island (TMI: 12° 38′ 33.78″ N 100° 51′ 40.13″ E); Samae San Island, which functions as a coral hatchery (SSI: 12° 35′ 05.51″ N 100° 57′ 14.50″ E); and Had Na Baan (HNB: 12° 35′ 12″ N 100° 57′ 12″ E) (Figure 2A). Each site was selected for its accessibility and the specific type of experiment conducted.

The Tao Mo Island is situated within the military harbor of the Royal Thai Navy. A burgeoning reef community has established itself on the hard substrate with depths of approximately 5 m–10 m along an 800-m stretch of artificial breakwater adjacent to the island. A high density of mature *A. humilis* colonies, ranging from 10 cm to 120 cm in diameter, was observed at depths of 5 m–7 m.

The Samae San Island (SSI) holds particular significance as the largest (4 km²) of nine islands under the protection of the Royal Thai Navy, contributing to the Plant Genetic Conservation Project initiated by Her Royal Highness Princess Maha Chakri Sirindhorn.
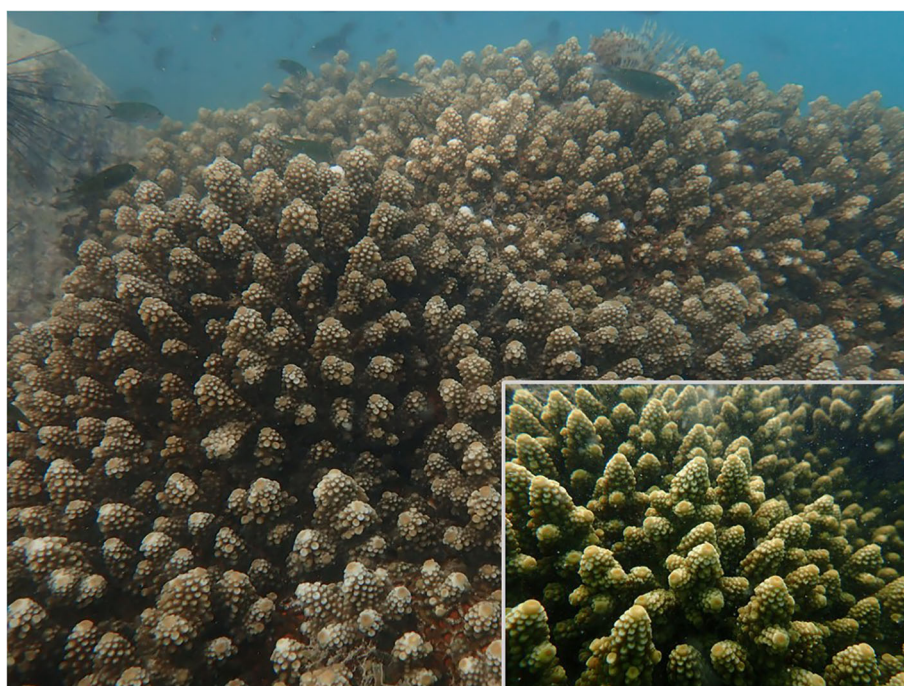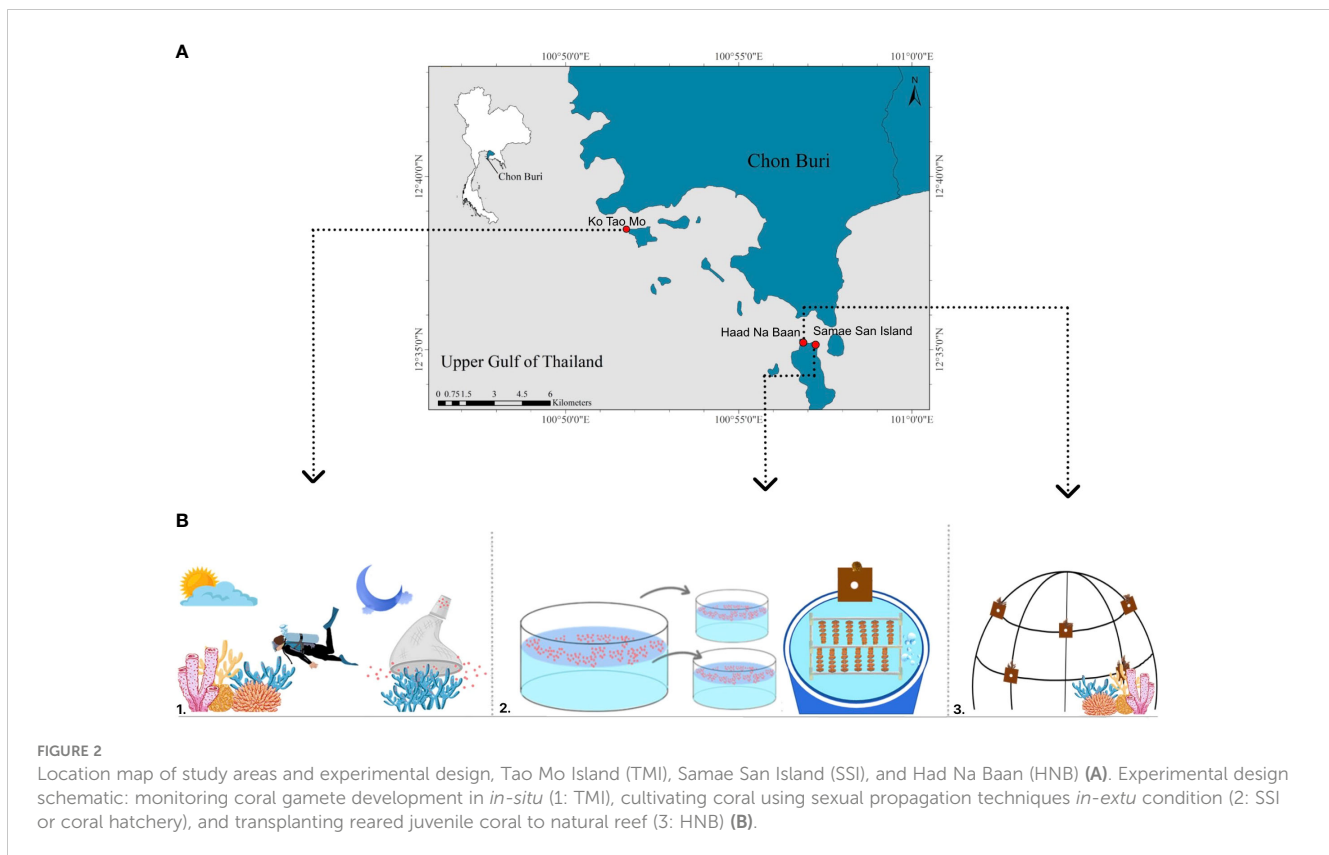

FIGURE 1
Parent colony of *Acropora humilis*.

FIGURE 2
Location map of study areas and experimental design, Tao Mo Island (TMI), Samae San Island (SSI), and Had Na Baan (HNB) **(A)**. Experimental design schematic: monitoring coral gamete development in *in-situ* (1: TMI), cultivating coral using sexual propagation techniques *in-extu* condition (2: SSI or coral hatchery), and transplanting reared juvenile coral to natural reef (3: HNB) **(B)**.

The coral hatcheries on SSI have been developed for cultivating and conducting experiments on corals.

Had Na Baan (HNB) features a shallow reef community, extending from approximately 3 m–7 m in depth on SSI. In this area, artificial dome-shaped structures constructed from stainless steel have been installed for the purpose of an out-planting experiment (Figure 2B).

Coral cultivation and sample collection

We sampled 10 coral fragments and gametes from 10 parent colonies at TMI during the spawning event in February from 20:00 to 20:30 h, in 2016. A gamete collector—a net with a plastic cup receptor at the end tip—was placed over the coral colony at the initial sign of spawning. Coral gametes, being positively buoyant, floated toward the surface, allowing collection into the plastic cup. Once spawning concluded, a lid sealed each cup before it was moved to the surface. All cups containing coral gametes were then stored in containers filled with seawater and transported directly to the coral hatchery on SSI for *ex-situ* fertilization. The gametes from each cup were gently poured into a container with 40 L of filtered seawater to facilitate fertilization. Fertilized oocytes underwent three washes with filtered seawater to remove excess sperm cells. The embryos were then distributed into five culture tanks, each containing 400 L of filtered seawater. To assess fertilization success, we counted the number of fertilized (embryos exhibiting cell division) and unfertilized (no cell division or abnormal cell development) embryos in each culture tank after 8 h, using a microscope, in five replicates (Suzuki et al., 2013; Omori, 2019). Seawater was replaced daily by 50% for 3 days to

diminish impurities in the culture tanks. Terracotta tiles (5 × 5 × 1 cm), preconditioned for 2 months on the reef to promote crustose coralline algae (CCA) growth and subsequently cleaned of biofouling, were introduced to the tanks to encourage coral larva attachment. During the initial 24 h of settlement, we avoided aeration and water flow in the tanks to minimize disturbance. Continuous aeration and seawater flow were resumed after coral larvae settlement until the experiment concluded. We did not control water temperature and light intensity in the culture tanks. The settled coral was grown in flow-through systems, with each tank receiving a continuous filtered water flow at an average rate of 0.38 L/min. Sand filtration was employed to enhance water quality before entering the culture tanks. There were 10 individual colonies of settled corals randomly sampled from each tank at ages of 3, 6, 12, and 18 months. For 1-month-old corals, 15 coral spats were sampled in 10 replicates. All samples were preserved in 95% absolute ethanol for *Symbiodiniaceae* community analysis. The survival of post-settlement coral was recorded every 3 months up to 18 months, with survival rates based on the initial number of settled spats from the five culture tanks. Algae and other biofouling on the coral colonies were regularly removed.

Coral cultivation and maintenance protocols were adapted from Omori (2005) and Omori and Iwao (2014). At 18 months, 10 plates with reared coral colonies were transferred to HNB and affixed to artificial dome-shaped structures. We monitored the transplanted coral health bimonthly and cleared biofouling as necessary. Additionally, 10 replicates of 9-month-old (from the same batch as this experiment) and five replicates of 2-, 3-, 4-, and 5-year-old post-transplantation corals (from different hatchery batches) were collected for *Symbiodiniaceae* community analysis. Physical factors,

such as light intensity and temperature, were recorded at SSI (2016-2017), TMI (2016), and HNB (2018) using HOBO data loggers.

DNA extraction and next-generation sequencing

Coral samples, including parent colonies and reared corals at 1, 3, 6, 12, and 18 months of age, as well as post-transplant colonies (after 9 months and 2, 3, 4, and 5 years of transplantation), were utilized for DNA extraction, respectively. A small coral fragment was air-dried to remove any excess ethanol and then pulverized using a mortar and pestle prior to proceeding with further analysis. Total genomic DNA from each sample was extracted utilizing the DNeasy Plant Mini Kit, following the manufacturer's instructions with some modifications. The quality and concentration of the extracted DNA were assessed and adjusted using gel electrophoresis and NanoDrop 2000c (Thermo Fisher Scientific^{TM}).

To characterize the *Symbiodiniaceae* internal transcribed regions, both ITS-1 and ITS-2 regions were amplified employing the primer pair r18Sf(5′-CGCTCTTCCGATCTCTG GAAAGTTTCATGAACCTTAT3-′) and Sym28Sr-1st (5′-TGCTCTTCCGATCTGACCTTGTRTGACTTCATGCTA-3′). The first and second polymerase chain reactions (PCRs) were conducted in accordance with Jandang et al. (2022). The amplicon library, encompassing the second round of PCR products, was quantified with a Qubit 2.0 Fluorometer and the Agilent Bioanalyzer 2100 system. The final concentration of the DNA libraries was diluted to 8 pM and subsequently sequenced on an Illumina MiSeq platform.

Data processing and bioinformatics analysis

The quality control of the Illumina MiSeq platform output data was conducted in accordance with Shinzato et al. (2018). Quality trimming and adapter removal, as well as chimera filtering, were performed using Cutadapt and UCHIME2, respectively. Low-quality bases (Phred quality score <20) were trimmed using Cutadapt version 3.5 (Marcel, 2011), and high-quality sequences longer than 100 bp were retained for further analysis. ITS-2 gene sequences adjacent to the Sym28Sr primer were subjected to chimera filtering against the *Symbiodiniaceae* ITS-2 database (Shinzato et al., 2018) using the UCHIME2 algorithm (Edgar, 2016). For operational taxonomic unit (OTU) analysis, we used the *Symbiodiniaceae* ITS-2 database to prepare OTUs clustered at 97% sequence identity. Sequences that were trimmed and free from chimeras were aligned to the 97% identity clustering ITS-2 database to identify OTUs (Shinzato et al., 2018). The most abundant OTU sequence was selected for alignment using BLASTn. Reads that did not match *Symbiodiniaceae* and those of low quality were removed (Camacho et al., 2009) applying an e-value cutoff of 1e−100 and an alignment length cutoff of >100 bp. Subsequently, the number of sequences mapped to each OTU was counted. The raw sequence data were submitted to the BioProject archive under accession number PRJNA806638.

Statistical analysis

One-way ANOVA with *post-hoc* Tukey's test was utilized to assess differences in physical parameters (temperature and light intensity) among the study sites. Survival data of reared corals in each culture tank were analyzed using the non-parametric test (chi-square). Pairwise comparisons were performed using the log-rank test to compare the mean survival rates across different coral ages. The Shannon and Simpson indices were employed to describe and compare alpha diversity across samples from different groups (Simpson, 1949). Significant differences in the diversity index values between samples were evaluated using the Kruskal–Wallis test, followed by *post-hoc* Tukey HSD analysis. To assess beta diversity, *post-hoc* pairwise permutation multivariate analysis of variance (PERMANOVA) was conducted using pairwiseAdonis v.0.4. This analysis focused on the relative proportions of *Symbiodiniaceae* types in all samples. *Symbiodiniaceae* communities were compared using Bray–Curtis dissimilarity among samples from relative abundance data. These dissimilarity matrices were then employed to generate non-metric multidimensional scaling (NMDS) biplots and to test for differences between samples from each group using PERMANOVA with the phyloseq v. 1.36.0 and VEGAN packages v. 2.5-7.

Results

Physical factors from three study sites

The annual average sea surface temperature (SST) at TMI (2016), HNB (2018), and SSI (2016–2017) were 30.39 ± 0.28°C, 29.94 ± 0.33°C, and 28.66 ± 0.33°C, respectively. The average temperature at the coral hatchery (SSI) was significantly lower than that of the natural reefs (TMI and HNB) ($p < 0.05$). However, during the summer, the temperature at all sites was approximately 0.92°C higher than the annual average. Although the monthly average SST at the study sites was within the ecological limits for coral reefs, coral bleaching still occurred in some colonies during the summer across all sites. The Samae San Island (coral hatchery) experienced the lowest seawater temperature (29.62°C) during the summer compared with the other sites. Conversely, SSI's maximum daily average temperature reached 33.13°C in June 2016 (Figure 3). Large fluctuations in daily temperature and light intensity were also observed at SSI, with the maximum daily amplitude being 5.41 ± 0.29°C and 45.77 ± 1.75 µmol m^{-2} s^{-1}, respectively. Consequently, corals reared in the hatchery were subjected to high variability in environmental conditions, which sometimes exceeded the bleaching threshold, potentially leading to a low survival rate, especially during the summer.

The average light intensity differed significantly between the coral hatchery (SSI) and natural environments (TMI and HNB) ($p < 0.05$). An unusually low light intensity was recorded at SSI, 18.76 ± 1.92 µmol m^{-2} s^{-1}, whereas the ambient light intensity in the natural reef was around 50 µmol m^{-2} s^{-1} in the Gulf of Thailand. Given that the coral hatchery operates as an indoor system, a shade structure was constructed to protect against sunlight,

FIGURE 3
Average temperature and light intensity in TMI, HNB, and SSI. The bar graph illustrates the average temperature, while the dashed line depicts the light intensity at each study site (p < 0.05).

resulting in irregularly low light levels in the coral culture tanks. On the contrary, the average light intensities at TMI and HNB were 78.85 ± 12.5 µmol m^{-2} s^{-1} and 74.85 ± 5.01 µmol m^{-2} s^{-1}, respectively, which were higher than the annual average light intensity typically found in coral reefs in the upper Gulf of Thailand.

Fertilization and survivorship

The mean fertilization rate of *A. humilis* was 98.48 ± 0.34%. The fertilized embryos began cell division 1 h after fertilization and assumed a flat shape akin to a red blood cell after 8 h. Embryos that were abnormally shaped or round were considered unfertilized. The coral embryos then progressed to larvae (swimming stage) and settled on the artificial substrate within 4–5 days. These newly settled corals developed into primary polyps (no zooxanthellae cells were observable to the naked eye). The primary polyps budded and encrusted on the artificial substrate.

Survival rates were monitored every 3 months, revealing a gradual decline in the number of settled corals during the first 3 months, averaging around 9.46%. Notably, coral mortality was significantly higher at the 0–3-month-old stage (24.12%, p < 0.001) compared with other stages (Figure 4, Supplementary 1), especially during summer when temperatures reached 30.16°C. Overall, approximately 45% of juvenile corals across all culture tanks survived under hatchery conditions at ages 6–18 months.

For transplanted corals, a high mortality rate was observed within the first few months post-transplantation. At the conclusion of the 9-month experimental period at HNB, the overall survival rate of 1.5-year-old transplanted corals was 20%.

Symbiodiniaceae diversity and community

A total of 2,115,916 high-quality sequences were obtained from 72 samples (approximately 29,387 reads per sample) after filtering and trimming. These sequencing data included wild parent, reared, and transplanted colonies of *A. humilis* (Supplementary 2). In total, 54 lineages were detected. These OTUs included three *Symbiodiniaceae* genera, namely, *Symbiodinium* (A3), *Cladocopium* (predominantly of Cspc_C3, C3w, C93type1, Cspf), and *Durusdinium* (predominantly of D1). The dominant *Symbiodiniaceae* in wild parent colonies were *Cladocopium* (Csps_C3 and C3W) and a minority of *Durusdinium* (D1), whereas juvenile coral under hatchery conditions vary depending on coral age. The 1-month-old corals showed similar *Symbiodiniaceae* diversity to their parent, but a higher proportion of *Durusdinium* was detected. Approximately 44.03% of 1-month-old colonies were associated with *Durusdinium* D1, followed by *Cladocopium* Csps_C3 (33.31%), C3w (16.55%), and 10 of minority strains. The *Symbiodinium* A3 was found in a particular colony of 3-month-old reared coral whereas most colonies were associated predominantly with *Durusdinium* D1 (80.18%). Surprisingly,
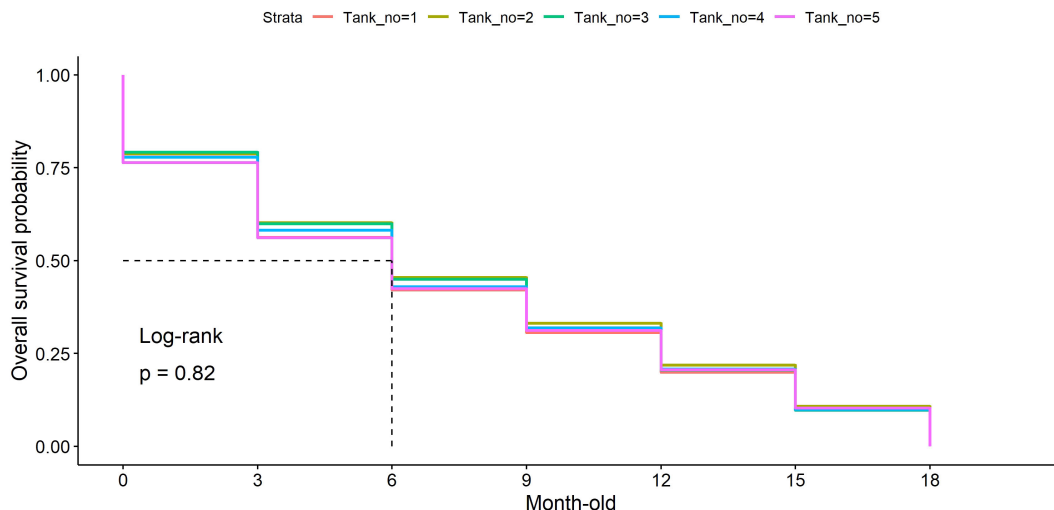
FIGURE 4
The survival rate of *Acropora humilis* under hatchery conditions. Each line color represents the survival rate observed in a different culture tank: orange (tank1, n = 174), olive green (tank2, n = 122), green (tank3, n = 215), blue (tank4, n = 112), and purple (tank5, n = 156). Values on the y-axis denote the overall survival probability of reared coral from the early stage to 18 months old, whereas the x-axis represents coral raising time.

reared corals were shown to be harbored with almost 100% of *Durusdinium* D1 at 3 months of age and maintain this stable proportion until the end of the experiment (18 months of age). On the contrary, the transplanted colonies of 18-month-old reared coral were shown to change their *Durusdinium* proportion and

gradual uptake new *Cladocopium* strains after 9 months (Figure 5A). Overall, the *Symbiodiniaceae* communities in parent, reared, and transplanted colonies were found to be significantly different. The results showed that the *Symbiodiniaceae* genus *Cladocopium* was the most common in parent colonies (98.54%),
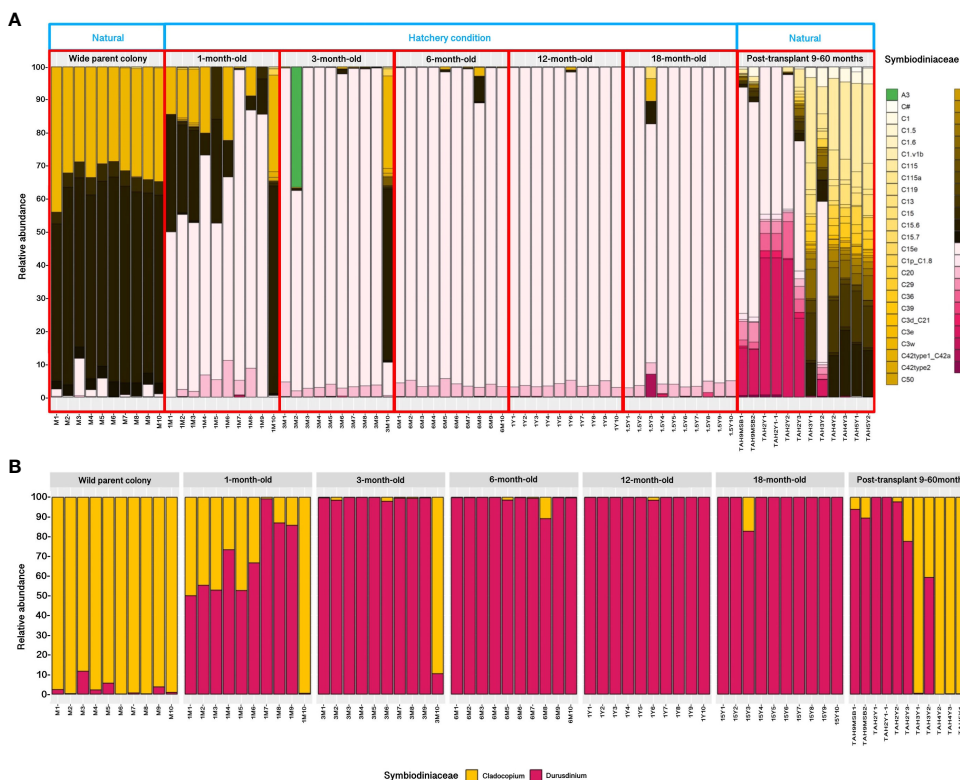

FIGURE 5
Relative abundance of *Symbiodiniaceae* communities in *Acropora humilis* from the wild parent, reared (different stages), and post-transplantation corals **(A)**. An overall *Symbiodiniaceae* proportion (*Cladocopium* and *Durusdinium*) from three distinct coral sources **(B)**.

whereas *Durusdinium* were in reared corals (95.13%) Additionally, the transplanted corals exhibited a comparable proportion of *Durusdinium* (59.51%) and *Cladocopium* (40.48%), respectively (Figure 5B).

The Shannon and Simpson diversity indices for *Symbiodiniaceae* suggested that transplanted corals possessed relatively high diversity, in contrast to the low diversity observed in reared corals (Kruskal–Wallis test, p < 0.0001). This finding indicates that transplanted corals tend to harbor *Symbiodiniaceae* communities with higher diversity than those in wild parent and reared coral colonies. In transplanted corals, multiple *Cladocopium* assemblages were present, differing from the wild parent colony, which predominantly hosted two strains (Cspc_C3 and C3W) (Figure 6). Non-metric multidimensional scaling also depicted the dissimilarity of *Symbiodiniaceae* communities, revealing a distinct pattern that varied significantly between communities associated with wild parent, reared, and transplanted corals (PERMANOVA, p-value = 0.001) (Figure 7).

Discussion

In this study, we observed a significant shift in the *Symbiodiniaceae* community composition from the early developmental to juvenile stages of *Acropora humilis* under hatchery conditions and following the transplantation of reared corals to a natural reef. Most early-stage reared corals (1-month-old) displayed *Symbiodiniaceae* genotypes similar to those of their wild parent colony, but with increased *Durusdinium* predominance. Furthermore, reared corals maintained a strong association with almost 100% *Durusdinium* from 3 to 18 months. Early life stages of *Acropora* spp. have been reported to harbor a broader range of *Symbiodiniaceae*, especially *Cladocopium*, *Durusdinium*, and *Symbiodinium*, under ambient conditions (Abrego et al., 2009; Yamashita et al., 2014; Quigley et al., 2017a; Yorifuji et al., 2017). However, the community of *Symbiodiniaceae* may vary regardless of the physical conditions, like with an increase in temperature (LaJeunesse et al., 2010; Gouezo et al., 2020; Naugle et al., 2021; Palacio-Castro et al., 2023). Juvenile *Acropora* corals exhibited a

higher number of heat-tolerant symbionts under elevated temperatures (Yuyama et al., 2016). This study recorded the highest average temperature in June 2016 when reared corals were approximately 3 months old. Notably, coral survivorship significantly declined following the hottest month, whereas the surviving corals were predominantly associated with *Durusdinium*. Elevations in temperature may contribute to the preferential association of corals with *Durusdinium*, which has been demonstrated to confer its thermo-tolerance capacity to its host (Baker et al., 2004; Palacio-Castro et al., 2023). Hence, this may reflect the sustained exposure to higher temperatures in the culture tank, which could have aided the remaining juvenile corals in withstanding warmer conditions (Cárdenas-Alvarado et al., 2021; Palacio-Castro et al., 2023). In addition, condition of rearing in tanks with a limited volume (400 L/tank) and circulation rate of seawater in the culture tanks led to rapid temperature fluctuations, adversely affecting the survival rate of the corals. Moreover, light limitation in the coral hatchery emerged as another stressor that could disrupt the photosynthetic efficiency and metabolic interactions between coral and its symbionts (Matthews et al., 2017; Brunner et al., 2022). Environments with low light can increase cellular pigment concentration and alter coral performance; the corals may adapt by shifting their *Symbiodiniaceae* community composition (Ros et al., 2021; Russnak et al., 2021). Consequently, juvenile corals need to maintain a predominantly *Durusdinium* population, which may confer advantages in hostile environments (Abrego et al., 2009; Yuyama et al., 2012a).

While the dominance of thermo-tolerant symbionts such as *Durusdinium* can make corals more resilient to stressors, it might also lead to reduced calcification and growth rates compared with corals hosting the thermo-sensitive *Cladocopium* (Cunning et al., 2015; A. Jones & Berkelmans, 2010). Due to the lower transfer of photosynthate to the host, corals associated with *Durusdinium* exhibited a slower growth rate, particularly in environments limited by various factors such as light, food availability, water circulation, and biotic competition (Nakamura et al., 2011; Stat & Gates, 2011; Omori & Iwao, 2014; Gleason et al., 2018). Our reared corals had an average growth rate of 1.57 ± 0.14 year^{-1} (from ages 1–5 years) (unpublished data), whereas wild colonies of *Acropora* spp. can grow approximately three to four times faster. This
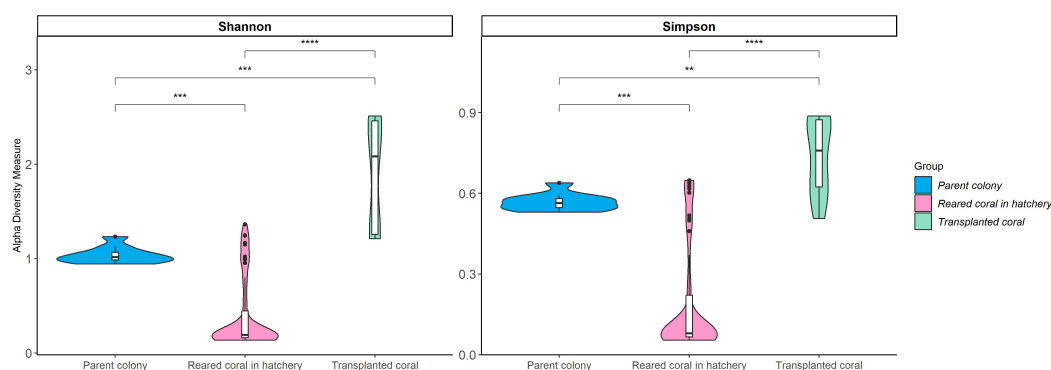

FIGURE 6
Alpha diversity indices (Shannon and Simpson) of *Symbiodiniaceae* community among *Acropora humilis* in different conditions. ** p < 0.01, *** p < 0.001 and **** p < 0.0001.
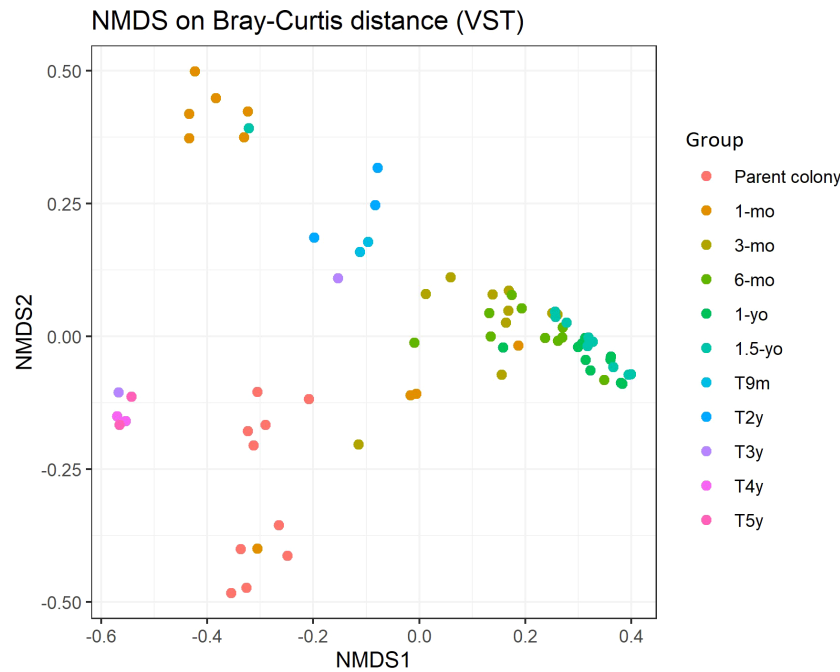
FIGURE 7
Non-metric multidimensional scaling (nMDS) plotting of the *Symbiodiniaceae* strain composition of *Acropora humilis* from different conditions and/or age based on Bray−Curtis dissimilarity indices.

discrepancy may correlate with the differences in *Symbiodiniaceae* types (Anderson et al., 2017; Ware et al., 2020; Weil et al., 2020).

Several studies have confirmed that juvenile *Acropora* exhibit greater flexibility than adult colonies due to higher *Symbiodiniaceae* assemblages (Little et al., 2004; Yamashita et al., 2014). Within the first 3 months of reared coral development, three genera of *Symbiodiniaceae* were observed, namely, *Cladocopium*, *Durusdinium*, and *Symbiodinium*. We also report the first presence of *Symbiodinium tridacnidorum* (A3) in Thai waters. Generally, *Acropora* larvae harboring *Symbiodinium* is common in many regions (Abrego et al., 2009; Yamashita et al., 2014; Quigley et al., 2017a). Most horizontally transmitting corals rely on free-living *Symbiodiniaceae* from surrounding environments, including seawater, some benthic organisms, and sediment (Hirose & Hidaka, 2006; Hirose et al., 2008; Sweet, 2014). *Symbiodinium* is recognized as an opportunistic symbiont as it has been found in corals that exhibit physiological vulnerabilities (e.g., coral disease, early developmental stages), whereas certain types can provide a degree of protection to the coral from high light stress (Suggett, 2008; LaJeunesse et al., 2010; LaJeunesse et al., 2015; Rouzé et al., 2016). Furthermore, the acquisition of *Symbiodiniaceae* cells in an azooxanthellate larva is exclusive with certain genera and exhibits an increasing level of selectivity later (Bay et al., 2011; Yamashita et al., 2014; Silverstein et al., 2015). *Acropora* larvae have demonstrated an active preference for *Cladocopium*, *Durusdinium*, and *Symbiodinium*, even when exposed to multiple types of *Symbiodiniaceae* during experiments (Adams et al., 2009; Mieog et al., 2009). Thus, during this stage, corals uniquely accommodate a particular group of *Symbiodiniaceae* to meet their energy needs (Gordon & Leggat, 2010; Suzuki et al., 2013; Hillyer

et al., 2017) or, as *Acropora* spp. in the Gulf of Thailand (GoT) spawn in early summer, the hosting of multiple *Symbiodiniaceae* genera/types in new recruits may be advantageous for coping with the rising temperatures of the upcoming summer (Yuyama et al., 2016). Juvenile *Acropora humilis* (18 months old under *ex-situ* conditions) in this study did not exhibit the same *Symbiodiniaceae* proportions as that of their parent colony, aligning with previous reports by Abrego et al. (2009) and Mieog et al. (2009). These juvenile corals maintained a stable association with *Durusdinium* from 6 to 18 months old under hatchery conditions and even after 3 years post-transplantation to a natural reef.

Utilizing juveniles from sexually propagated corals is a viable approach for active coral restoration because they can provide greater genetic diversity compared with asexual fragmentation, thereby offering potentially higher genetic resilience in response to environmental threats (Baums, 2008; Omori & Iwao, 2014; van Oppen et al., 2017; Baums et al., 2019). The success of coral transplantation is contingent upon physical and ecological factors (Baums et al., 2019; Ladd et al., 2019). Generally, reared corals aged 1–2 years are deemed suitable for transplantation due to their higher survival rates (Omori et al., 2008). A wide range of survival rates after coral transplantation has been observed, approximately 3%–89%, depending on the size, species, and location (Omori et al., 2008; Villanueva et al., 2012; Chamberland et al., 2015; Ligson et al., 2020). When we transplanted 1.5-year-old reared corals to a natural reef, only 20% survived after 9 months. Smaller colonies or younger corals may not survive under such conditions due to disturbances such as increased sedimentation, light intensity, and temperature fluctuations (Raymundo & Maypa, 2004; Tuttle & Donahue, 2022). Therefore, exploring the

heightened flexibility demonstrated during early stages is recommended to increase the success of acclimation under unfamiliar conditions at out-planting sites. Identically, examining the tipping point of flexibility in *Acropora* throughout its ontogenic cycle would be useful for specifically identifying the oldest and most robust stages at which the corals retain their flexible *Symbiodiniaceae*-conferred traits.

Additionally, the upper Gulf of Thailand is influenced by major and minor rivers, resulting in significant water and sediment discharge into the area (Zhang et al., 2022). High levels of suspended sediment can reduce photosynthesis and respiration in corals, leading to high mortality rates (Erftemeijer et al., 2012; Tuttle & Donahue, 2022). Furthermore, recent studies have suggested that reared juvenile corals tend not to shift their *Symbiodiniaceae* communities during the first 2 years after transplantation to a natural reef. This resistance to change may be linked to the high mortality rate of corals, as the interaction between corals and their symbiont communities might impact the corals' resistance/resilience abilities when environmental conditions alter (Bairos-Novak et al., 2021; De Souza et al., 2022).

The juvenile *Acropora* corals harbored a different *Symbiodiniaceae* community compared with parental colonies (Abrego et al., 2009; Yorifuji et al., 2017). However, juvenile *Acropora* corals hosted predominantly *Durusdinium* starting at 3 months and began to shift their symbiont to *Cladocopium* at approximately 3.5 years of age in this study, aligning with a previous report by Abrego et al. (2009). The timing of the change in relative abundance of *Symbiodiniaceae* in juvenile *Acropora* to resemble that of the local adult colony is dependent on coral species and environmental conditions (Gómez-Cabrera et al., 2008; Abrego et al., 2009). Although our corals were entirely associated with several *Cladocopium* assemblages after 4 years of transplantation, none of the reared corals exhibited a *Symbiodiniaceae* structure similar to the parent colony, which mainly harbored types Cspc_C3 and C3W. Several possible explanations exist for juvenile corals hosting different types of *Symbiodiniaceae* compared with those found in field surveys of *A. humilis*: (1) reared corals may experience prolonged stress under *ex-situ* conditions, and even after transplantation to a new environment, they may require more time to acclimatize (Sampayo et al., 2016; DeCarlo, 2020); (2) harboring a greater diversity of *Cladocopium* than the parent colony could be advantageous for juveniles to cope with local stressors; (Abrego et al., 2012; Yorifuji et al., 2017); and (3) the locally available *Symbiodiniaceae* communities at the out-planting sites might be distinct from those at the parental field location. Such outcomes enable corals to acquire novel *Symbiodiniaceae* types from their surrounding environment (Boulotte et al., 2016; Scharfenstein et al., 2022).

Wild adult colonies of *Acropora humilis* are strongly associated with *Cladocopium* (Cspc_C3 and C3W in this study). *Cladocopium* is considered a generalist symbiont, commonly found in Indo-Pacific corals, with several lineages detected (Gong et al., 2018; Chen et al., 2019; Jandang et al., 2022). Corals hosting *Cladocopium* have often shown faster growth, potentially indicating a greater transfer of photosynthetically fixed carbon to their host (Cantin et al., 2009; Cunning et al., 2015). Coral sexual maturity is size-dependent; some faster-growing staghorn corals can reach maturity at around 2–4

years of age (Ligson & Cabaitan, 2021; Suzuki, 2021). Therefore, the time it takes for corals harboring *Cladocopium* to reach full mature size and produce offspring may be shorter, allowing them to increase their population faster than some massive corals (Van Oppen & Medina, 2020). Although stable *Symbiodiniaceae* lineages are present in most adult corals under ambient conditions, some corals may rapidly change their symbiont population when exposed to high seawater temperatures (Silverstein et al., 2015; Palacio-Castro et al., 2023). Such a situation is referred to as the adaptive bleaching hypothesis, occurring when corals experience bleaching events to increase heat tolerance and survive in warmer oceans (Jones et al., 2008; Howells et al., 2013; Baird et al., 2021). In this context, corals may grow slower than in non-stressful conditions due to the increased predominance of heat-evolved symbionts (Cunning et al., 2015). However, after acclimatization (shuffling or switching), corals have been shown to transition back to their pre-bleaching symbiont communities if the environment returns to optimal conditions (Coffroth et al., 2010; Kao et al., 2018).

To the best of our knowledge, this study is the first to examine the coral–*Symbiodiniaceae* association in *A. humilis* from wild and cultured colonies. In summary, we documented the distinct *Symbiodiniaceae* communities among wild parents, reared, and post-transplanted corals. Our reared juvenile corals exhibited the flexibility of their *Symbiodiniaceae* partners when changing environments. However, not all corals successfully survive varying environmental conditions; some do not acclimate and eventually perish. Despite the ability of corals to shift their *Symbiodiniaceae* community under stress conditions, coral survival during reef restoration in this area also depends on the initial juvenile size and the physical conditions of the transplantation site. Furthermore, extensive collections of coral species and free-living *Symbiodiniaceae* from the surrounding environment can enhance our understanding of coral and *Symbiodiniaceae* associations, as well as the ability of corals to acclimate to climate change.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: BioProject, PRJNA806638.

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

SJ and SC conceived the study and drafted the manuscript. SJ, YY, and CS carried out the molecular biology experiment and statistical analysis. JS and VV executed the experiments and collected samples. VV and SC coordinated the study and were involved in manuscript revising. All authors gave the final approval for publication.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2024.1138021/full#supplementary-material

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