

Article

Coral Oasis on Con Dao Islands: A Potential Refuge of Healthy Corals in the Offshore Waters of Vietnam?

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Abstract: Coral reefs of Vietnam are highly threatened by a combination of anthropogenic impacts and natural disturbances. As a result, preservation of the remaining reefs is a major governmental concern. Con Dao Islands, located in the coastal area of southern Vietnam in the South China Sea, still possess diverse and healthy coral communities. Coral surveys conducted in 2017–2020 on six sites within the marine protected area of Con Dao National Park revealed extensive coral cover (62.8–95.5%) and diversity (168 stony coral species). Coral communities were mostly dominated by Acroporidae followed by Poritidae and Fungiidae. Temporal dynamics over a 3-year period exhibited no significant decrease in the cover of dominant coral taxa, despite the severe thermal anomaly in 2019 and subsequent moderate coral bleaching, suggesting that the local corals may be successfully acclimating to the current level of thermal stress, although further study of coral adaptation in this region is warranted. High diversity and coral cover, together with the potential of resistance and resilience to repeated thermal stress in coral communities of the Con Dao Archipelago, highlights the need for authorities to pay special attention to this area and to expand conservational efforts to preserve this unique natural site.

Keywords: coral reefs; thermal anomalies; acclimation



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1. Introduction

Coral reefs are one of the most diverse and productive ecosystems in the world. Currently, coral reefs face a wide variety of global and local threats, including warming of the sea surface temperature (SST), ocean acidification, coral diseases, outbreaks of coral predators, coastal development, agricultural runoff, pollution, overfishing, destructive fishing and coral mining [1–3]. The global coverage of living coral has declined by half since the 1950s [3,4], and the present rate and scale is such that coral loss may be total by 2050 [5–7]. The coral reefs of Vietnam are highly threatened, with only 1% being considered healthy, and coral cover ranging from 50% to 75% [2,3,8]. A few fringing coral reefs in the coastal provinces of south-central Vietnam have remained relatively healthy, such as those in Nha Trang Bay in Khanh Hoa Province [9] and in the coastal area of Nui Chua National Park in Ninh Thuan Province [10]. Chronic anthropogenic disturbances and a severe outbreak of corallivorous crown-of-thorns starfish *Acanthaster* sp. (COTS) led the reefs in Nha Trang Bay to collapse in 2019 [11], while a long-term COTS outbreak and thermally induced coral bleaching in 2019 resulted in a dramatic coral decline in Nui Chua National Park [12]. Thus, only remote island areas, such as the Con Dao National Park established on Con Dao Islands (southern Vietnam) and some reefs within the Spratly Archipelago in the southern South China Sea still harbor healthy coral communities with high biodiversity [13–15].

The Con Dao Islands are located in the South China Sea, 185 km southeast from the city of Vung Tau of Ba Ria-Vung Tau Province in southern Vietnam. The Con Dao National Park

(CDNP) was designated in 1993 by the Ba Ria-Vung Tau Provincial People's Committee, comprising an overall area of 150 km² with 60 km² dedicated to special use forest and a 90 km² marine area [16]. The CDNP was declared by Ramsar Wetland to support high biodiversity due to its shallow marine waters and wetland areas, 18 km² of coral reefs, 10.4 km² of seagrass beds and 0.4 km² of mangrove forests [17]. The CDNP's coral reefs are highly diverse with over 370 coral species and over 200 coral fish species [17,18]. In addition, the waters of the CDNP provide nursing and nesting sites for about 90% of Vietnam's sea turtle population, and its sea grass meadows support a small population of the critically endangered marine mammal dugong *Dugong dugon*, numbering around 9–12 individuals [19]. The surveys conducted by Nha Trang Institute of Oceanography have shown the presence of 1323 species of marine fauna and flora, including 44 species listed in the Red Data Book of Vietnam [20]. Thus, the Con Dao Archipelago can be considered a biodiversity hotspot of South East Asia with close similarity of Con Dao's coral composition to the Spratly Islands area, whereas coral species richness (~400 species) is comparable with Brunei, Malaysia and Palawan, i.e., areas neighboring or included in the Coral Triangle [21]. However, scant data have been published on the ecological status of coral reefs within CDNP and on their resistance and resilience under current global and local threats.

Extensive coral bleaching and large-scale mortality result from heat shocks induced by SST anomalies closely related to El Niño Southern Oscillation (ENSO) events [22,23]. In the coastal waters of Vietnam, the ENSO strongly impacts fluctuations of SST and primary production of phytoplankton, although these fluctuations are significantly varied due to the annual development of regional Vietnamese upwelling in the narrow offshore shelf of south-central Vietnam [24–26]. Moreover, the intensity of ENSO events is expected to increase in the seas of South East Asia, including Vietnam, and NOAA Optimum Interpolation SST records testify that during ENSO periods the SST in this region is higher than in other areas [27,28]. Finally, there has been a global fourfold increase in the frequency of extreme ENSO events, from one event occurring every 60 years in the last century until the late 1980s, to one event every 15 years in the present day [29], which has inevitably aggravated the worldwide coral reef decline.

To date, only four publications have highlighted coral bleaching events related to the ENSO in the CDNP in 1998 and 2005 [30,31] and in 2019 during one of the most severe thermal anomalies [32,33]. Results of the coral surveys conducted by CDNP staff yearly at permanent locations using the rapid ReefCheck protocol remain inaccessible to the public. Some data on two coral bleaching events in 2010 and 2016 are presented in local media [34,35]. Nevertheless, the surveys carried out by CDNP staff showed that, up to 2015, both coral and seagrass coverage were stable. Densities of top predators (groupers and spiny lobsters) decreased, whereas moray eels and humphead wrasses had disappeared by 2015 due to fishing activity [19]. Our first coral survey conducted within the CDNP in 2017 confirmed high coral cover in local coral communities mostly dominated by acroporids [14]. Repeated surveys were performed in 2019 and 2020 on the selected target sites. The aim of this study was to estimate temporal dynamics in coral communities of the CDNP over a 3-year period and to track the possible response of local reef-building corals to the severe thermal stress that occurred in 2019.

2. Material and Methods

2.1. Study Area and Environmental Features

Con Dao Archipelago consists of 16 islands situated in the South China Sea on the wide shelf of southern Vietnam (Figure 1). The marine protected area of the CDNP comprises 14,000 ha and includes 1800 ha of coral reefs [20]. There are no permanent sources of fresh water on any of the islands in the Con Dao Archipelago. Thus, the impact of terrestrial run-off on marine ecosystems is negligible.

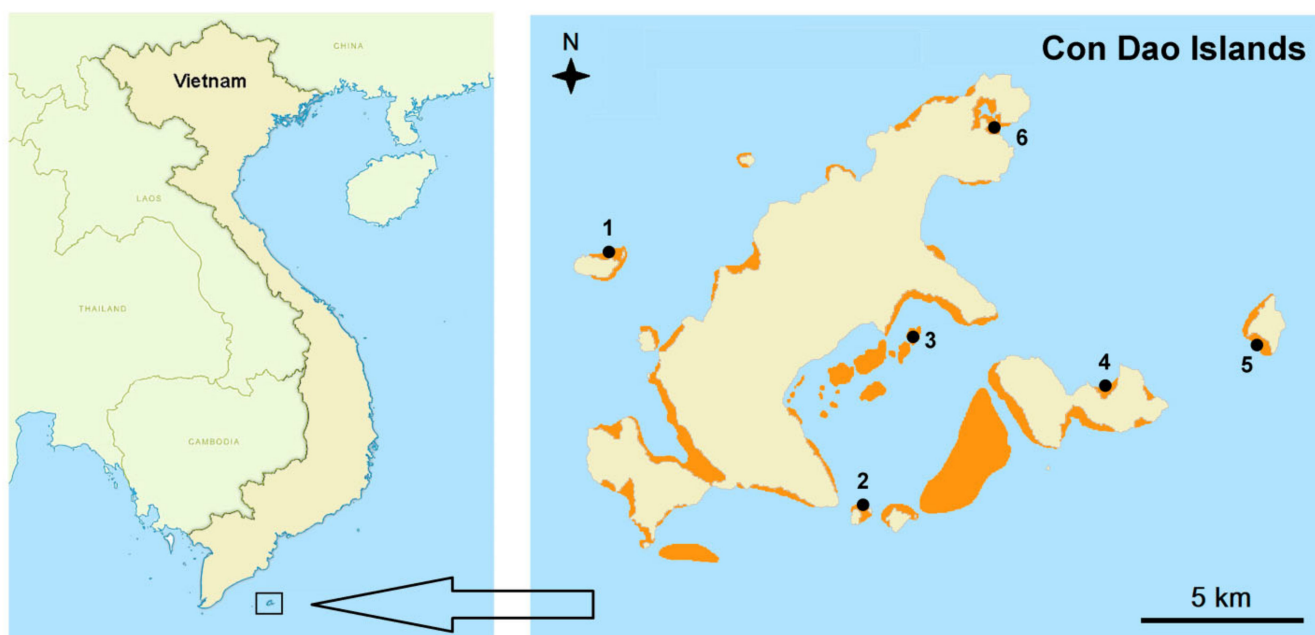


Figure 1. Location of Con Dao Islands and study sites (numbers). Coral reefs are shown in orange.

The CDNP is located in a tropical cyclone passage area in the Western Pacific; most cyclones arrive at the Vietnamese coast from northeast to southeast of the Western Pacific and move westward across the South China Sea [36]. Typhoon Linda in October 1997 was the strongest cyclone to hit southern Vietnam in the past 100 years, bringing unexpectedly significant damage to this area including Con Dao Archipelago [37]. However, according to long-term weather observations (<http://www.weather.unisys.com/hurricane>; accessed on 1 September 2022), there have been no cyclones and tropical storms with an intensity higher than a seven on the Beaufort scale (moderate gale) in the archipelago.

For the analysis of sea surface temperature (SST) dynamics during the study period (2017–2020), the data were derived from SST and degree heating weeks (DHWs) charts archived by the NOAA Coral Reef Watch [38] (<https://coralreefwatch.noaa.gov/product/5km/index.php>; accessed on 7 June 2022). In addition, two HOBO[®] temperature loggers (U22-001 model, Onset, Bourne, MA, USA) were deployed in April 2019 at 3 and 12 m of depth at target site 1 (Figure 1) at Hon Tre Lon Island, and the temperature was recorded four times a day for 11 months to track variations in near-bottom temperature over one year.

2.2. Sampling Design

The initial coral survey was performed in May 2017 on 6 sites within the marine protected area of the CDNP (Figure 1). Repeated surveys were conducted on the three selected target sites 1, 3 and 6, in April 2019 and February 2020. These target sites were selected because of their coral community composition dominated by Acroporidae, which is typical for an archipelago [13]. The base of fringing reefs at sites 1 and 6 were located at 12 and 10 m of depth, respectively. These reefs were surveyed in two horizons of the reef slope: 3–5 m and 9–12 m of depth. The inner semi-closed area of site 4 represented shallow coral shoals with a base at 4–6 m of depth, which were surrounded by a sandy plain. This site was surveyed at 2–4 m.

The phototranssect method was used to estimate the cover of stony corals, macroalgae, dead coral and rubble. At each site, four phototranssects, each 25 m long, were deployed in a line within the same depth horizon and separated by 10 m intervals. Each phototranssect consisted of 20 random photoquadrats with each photoquadrat covering 0.25 m² of sampling area. These same transects were used to estimate the abundance of COTS within a belt width of 4 m (with a total of four 4 × 25 m belt transects per site).

2.3. Data Analysis

The percentage cover of living stony corals (on a genus level with subdivision on the species level for the dominant genera), dead coral framework, coral rubble and macroalgae were estimated using CPCe software [39] with 25 randomly spaced points within each photoquadrat (with a total of 500 points per transect). The dead coral framework herein represents dead, unbroken coral colonies that retained their typical structure. The size (maximum diameter) of the largest adult colonies of table *Acropora* (mostly *A. hyacinthus*) and massive *Porites* (mostly *P. lobata* and *P. lutea*) was measured at each site for the assumptions on coral resistance.

The identification of coral taxa was based on the works of Veron [40] and Latypov [41] and verified with World Register of Marine Species (<https://www.marinespecies.org/aphia.php?p=taxdetails&id=1363>; accessed on 10 September 2022).

The susceptibility of coral taxa to bleaching associated with SST anomalies was identified following the generally accepted hierarchy of thermal susceptibility of Indo-Pacific reef-building corals [42–47]. To assess temporal variations in total coral cover and dominant coral taxa cover at three target sites (Table 1), one-way analysis of variance (ANOVA) was used. Prior to analysis, data were tested for homogeneity of variance (Cochran C-test) and log-transformed [$\log(x + 1)$]. Calculations were carried out using the software STATISTICA® 8.0 for Windows (StatSoft Inc. 2007).

Table 1. Subdivision of recorded stony coral taxa according to their thermal susceptibility. The occurrence of dominant genera in study sites is shown. Thermal susceptibility of coral genera is based on data from [42–47].

Dominant Coral Genera (Species Number)	Main Representatives of Dominant Genera	Site # with the Cover of Coral Taxa			Thermal Susceptibility of Genus
		>5%	>10%	>20%	
<i>Acropora</i> (32)	<i>A. austera</i>	1			Susceptible
	<i>A. intermedia</i>	3	5	1	
	<i>A. hyacinthus</i>		2, 5, 6	1, 3	
	<i>A. latistella</i>	6			
	<i>A. millepora</i>	2, 4			
	<i>A. muricata</i>	2, 3	1, 6		
<i>Montipora</i> (16)	<i>A. robusta</i>	2	1	5	Susceptible
	<i>M. aequituberculata</i>	1		6	
<i>Galaxea</i> (1)	<i>G. fascicularis</i>	1			Resistant
<i>Pachyseris</i> (2)	<i>P. speciosa</i>		1		Resistant
	<i>P. lobata</i>				Resistant (massive); Susceptible (branching)
<i>Porites</i> (8)	<i>P. rus</i>	2, 4			Resistant
		1, 4, 6			
<i>Lobophyllia</i> (6)	<i>Lobophyllia recta</i>	2, 4			Resistant
<i>Fungia</i> (5)	<i>Fungia fungites</i>	6			Resistant

Table 1. Cont.

Dominant Coral Genera (Species Number)	Main Representatives of Dominant Genera	Site # with the Cover of Coral Taxa			Thermal Susceptibility of Genus
		>5%	>10%	>20%	
Other recorded coral genera					
	<i>Acanthastrea</i> (1)				Resistant
	<i>Astreopora</i> (2)				Resistant
	<i>Astrea</i> (2)				Resistant
	<i>Caulastrea</i> (1)				Resistant
	<i>Coscinaraea</i> (1)				Resistant
	<i>Ctenactis</i> (1)				Resistant
	<i>Cycloseris</i> (2)				Resistant
	<i>Cyphastrea</i> (2)				Resistant
	<i>Dendrophyllia</i> (1)				Resistant
	<i>Diploastrea</i> (1)				Resistant
	<i>Dipsastraea</i> (10)				Resistant
	<i>Echinopora</i> (2)				Resistant
	<i>Echinophyllia</i> (3)				Resistant
	<i>Euphyllia</i> (2)				Resistant
	<i>Favites</i> (6)				Susceptible
	<i>Gardineroseris</i> (1)				Resistant
	<i>Goniastrea</i> (6)				Resistant
	<i>Goniopora</i> (2)				Resistant
	<i>Herpolitha</i> (1)				Resistant
	<i>Hydnophora</i> (3)				Resistant
	<i>Isopora</i> (2)				Susceptible
	<i>Leptastrea</i> (2)				Resistant
	<i>Leptoria</i> (1)				Susceptible
	<i>Leptoseris</i> (1)				Resistant
	<i>Lithophyllon</i> (1)				Resistant
	<i>Merulina</i> (1)				Resistant
	<i>Mycedium</i> (1)				Resistant
	<i>Oulastrea</i> (1)				Resistant
	<i>Oulophyllia</i> (1)				Resistant
	<i>Oxypora</i> (1)				Resistant
	<i>Pavona</i> (4)				Resistant
	<i>Pectinia</i> (2)				Susceptible
	<i>Physogyra</i> (1)				Susceptible
	<i>Platygyra</i> (4)				Resistant
	<i>Plerogyra</i> (1)				Susceptible
	<i>Plesiastrea</i> (1)				Susceptible
	<i>Pocillopora</i> (5)				Susceptible
	<i>Podabacia</i> (1)				Resistant
	<i>Psammocora</i> (4)				Resistant
	<i>Sandalolitha</i> (2)				Resistant
	<i>Seriatopora</i> (1)				Susceptible
	<i>Stylophora</i> (1)				Susceptible
	<i>Tubastrea</i> (2)				Resistant
	<i>Turbinaria</i> (3)				Resistant
	<i>Millepora</i> (2)				Susceptible
	<i>Heliopora</i> (1)				Resistant

3. Results

3.1. Sea Water Temperature Dynamics

Four-year remote sensing SST data for southern Vietnam (Figure 2) revealed that the coral bleaching threshold (CBT) was surpassed all four years of the study period (2017–2020), although only the episodes in 2019 and 2020 were sufficiently strong to result

in severe coral bleaching and mortality, as the DHWs exceeded NOAA’s Second Bleaching Alert Level (13 °C-week in 2019 and 10 °C-week in 2020, Figure 2). Coral bleaching in June 2019 varied between 20% and 50% of coral cover (CDNP staff personal communication). This temperature elevation event was also recorded by two temperature loggers installed at site 1 at 3 m and 12 m of depth. The temperature exceeded the CBT from the middle of April till the beginning of June 2019 and remained between 30.5 and 31.7 °C (Figure 3). The difference between the temperature at the two depths was insignificant (*t*-test, *t* = 0.45; *P* = 0.65) and remained within 0.5 °C (Figure 3). The total DHWs over a 12-week window reached 6 °C-week, which is half that of NOAA’s remotely obtained DHWs values for the larger area of southern Vietnam (Figure 2), as no values exceeding the CBT at Con Dao Islands were recorded in June. Nevertheless, 6 °C-week was adequate for the development of significant coral bleaching (NOAA’s First Bleaching Alert Level; $4 \leq \text{DHW} < 8$ °C-week). The coral survey in 2020 was performed in February prior to the onset of the increase in SST; therefore, the impact of this anomaly was not considered for the analysis.

Southern Vietnam

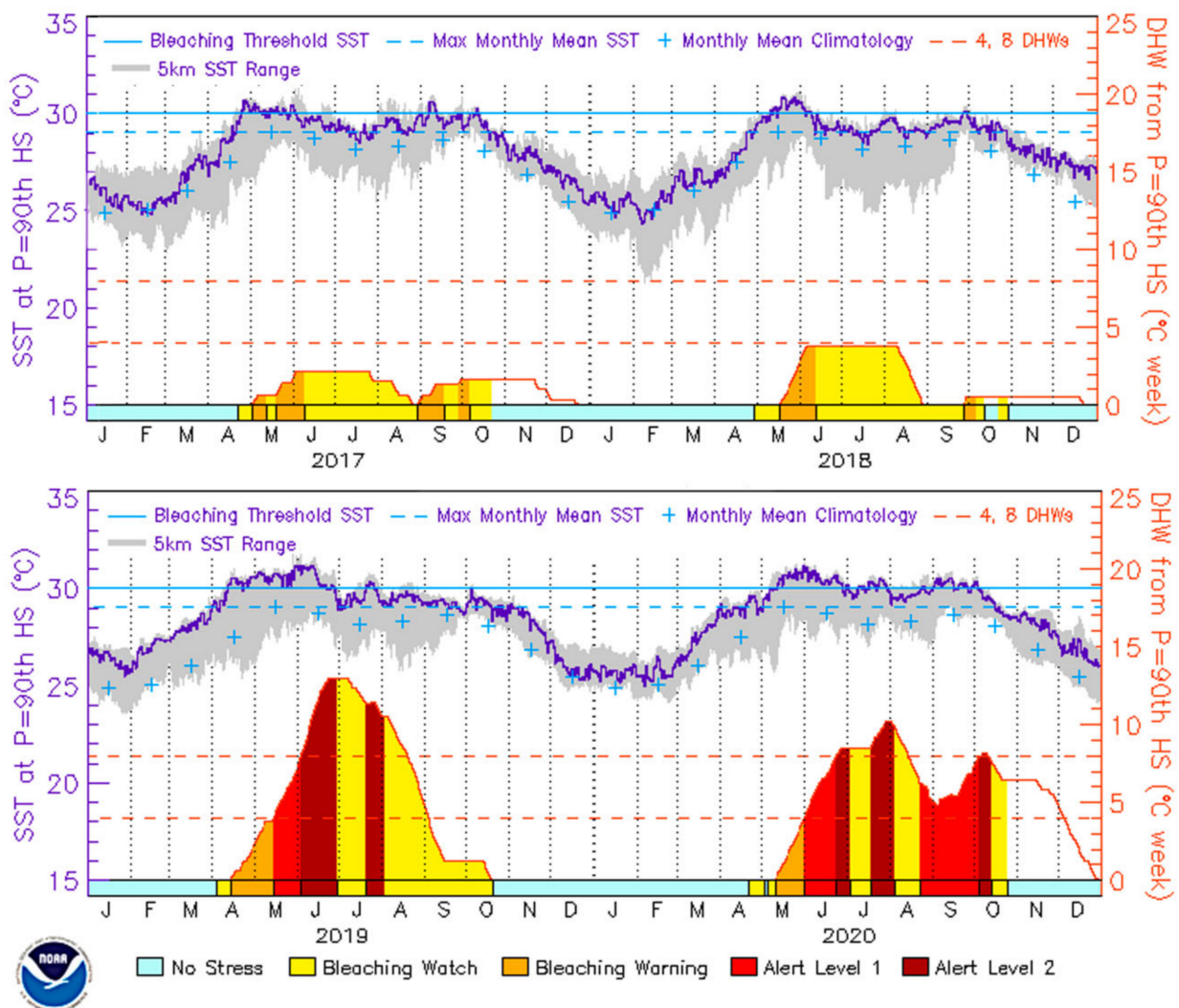


Figure 2. Sea surface temperature (SST) dynamics (°C) and degree heating weeks (DHWs, °C a week) offshore southern Vietnam (from 8°38' N to 13°45' N) in the study period (2017–2020) according to NOAA Coral Reef Watch time series data (https://coralreefwatch.noaa.gov/product/vs/timeseries/east_asia.php#southern_vietnam), last accessed 20 November 2022).

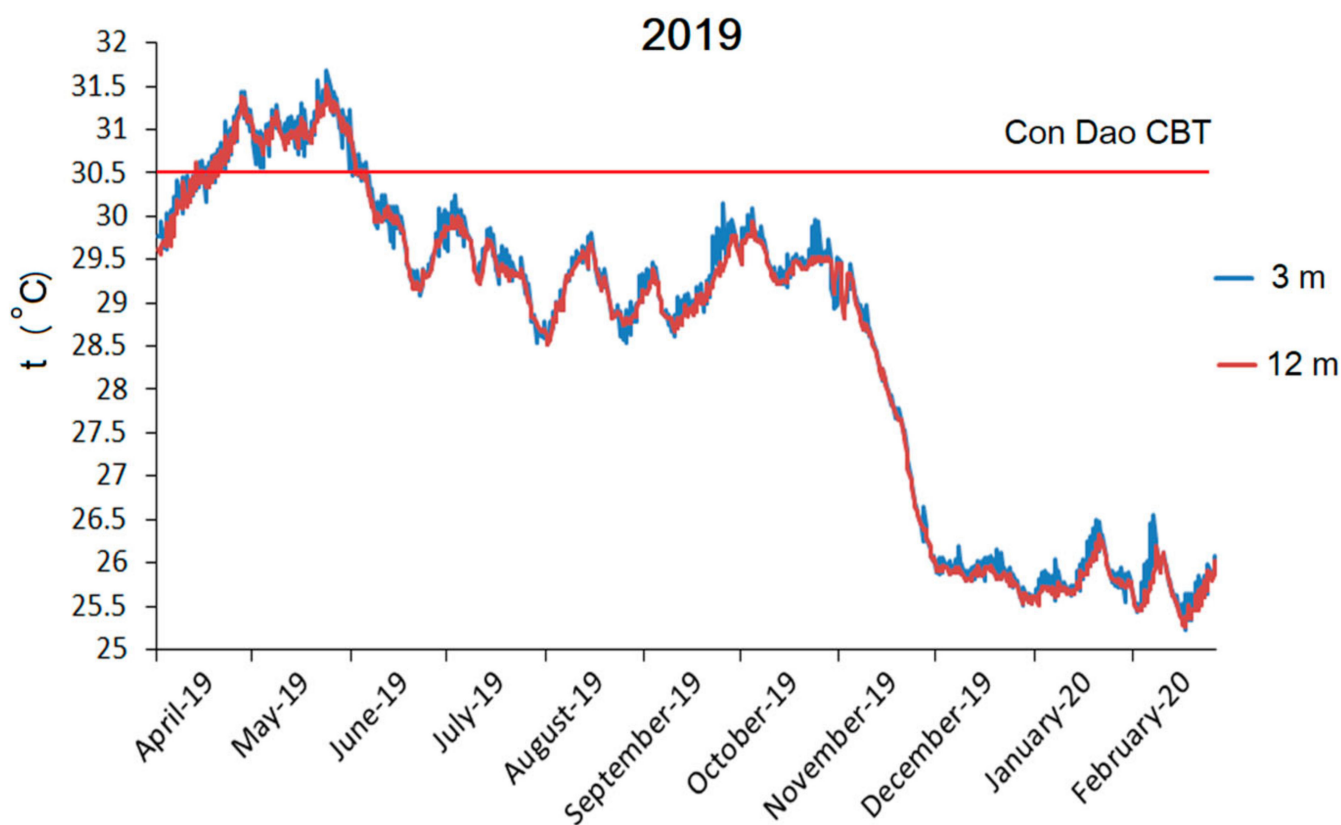


Figure 3. Temperature dynamics over 11 months at 3 m and 12 m of depth obtained by HOBO® u22-001 temperature loggers. The coral bleaching threshold (CBT) is shown by the red line. The CBT used here is based on NOAA Coral Reef Watch time series data for southern Vietnam and leveled to sea surface temperature (SST) 1 °C higher than the maximum monthly mean SST for this area. The year is pointed out next to the month: 19 mean 2019; 20 mean 2020.

3.2. Coral Communities

The initial surveys conducted in 2017 revealed thriving coral communities mostly dominated by Acroporidae with coral cover range from high to continuous (62.8–95.5%, mean $82.5 \pm 11.1\%$, Figure 4). In total, 168 species of reef-building corals from 54 genera, including non-scleractinian octocoral *Heliopora coerulea* and hydrocorals *Millepora dichotoma* and *M. platyphylla*, were recorded at six study sites (Table 1). The highest relative proportion of dead stony corals (30.6%) was recorded at site 3 in the semi-closed inner bay of Con Son Island, testifying to the moderate coral decline in this reef in the recent past. Both site 3 and site 2 revealed >5% coral rubble (Figure 5). Site 6 was the only site with an abundant macroalgae (9.2%) dominated by *Sargassum* sp. in the shallow zone (3–5 m) in the inner part of the bay. Among the seven selected dominant coral genera, the largest contributor in terms of cover and species richness was *Acropora* (Table 1).

Temporal dynamics in total stony coral cover, dead coral cover and the dominant coral genera cover at three target sites revealed no significant changes (ANOVA, $p > 0.05$ for all cases except for *Acropora* and stony coral cover mostly represented by *Acropora* in the shallow zone of site 6; Figure 6A–C, Table 2) and signs of coral decline following the severe thermal anomaly in 2019 (no significant increase in the cover of dead coral was recorded). The shallowest site 3, located in the semi-closed bay of Con Son Island, showed a decrease in stony coral cover (mostly represented by *Acropora*) (Figure 6B). In contrast, site 6 revealed a significant increase in *Acropora* and total stony coral cover in the shallow zone (ANOVA, Figure 6C, Table 2), whereas the abundance of *Sargassum* sp. significantly decreased between 2017 and 2019 (ANOVA, Figure 6C, Table 2). Table *Acropora* was mostly dominated by adult colonies in the size range of 150–250 cm in the largest diameter of a

colony at all three target sites, with the size of the largest colonies exceeding 300 cm. The largest colonies of massive *Porites* varied between 200 and 400 cm in diameter. Only one COTS individual was recorded in 2019 at site 3.

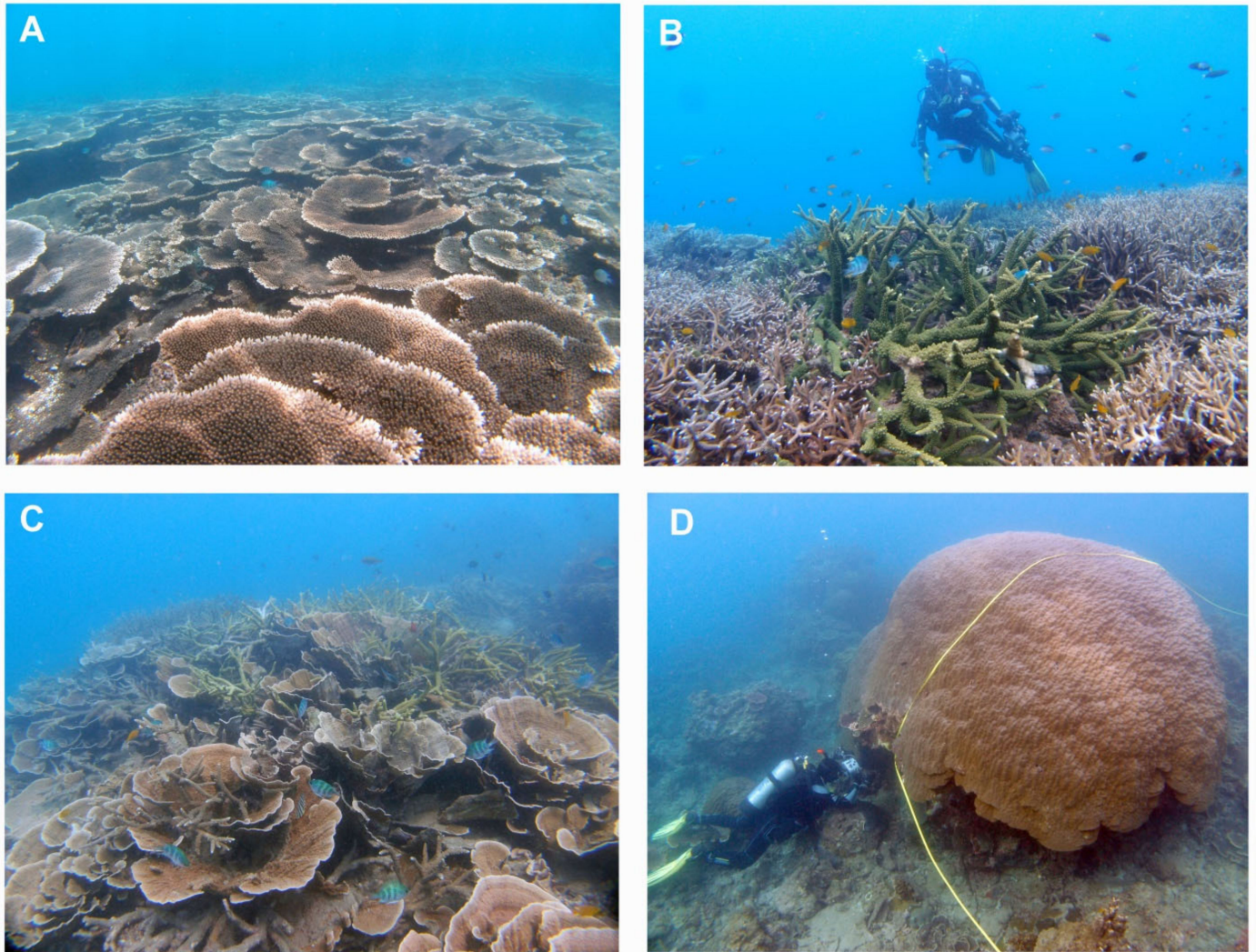


Figure 4. Dominant coral communities in the water area of Con Dao National Park. (A): multi-tiered stands of table *Acropora* (mostly *A. hyacinthus* and *A. cytherea*) in the upper reef slopes (2–5 m depth, sites 1–6); (B): branching *Acropora* (mostly *A. intermedia*, *A. muricata*, *A. grandis* and *A. robusta*) in the upper and middle reef slopes (3–7 m depth, sites 1–6); (C): assemblages of foliaceous *Montipora* (mostly *M. aequituberculata* and *M. hispida*) together with branching *Acropora* in the middle reef slopes (4–8 m depth, sites 1, 2, 4 and 6); (D): large heads of massive *Porites* (mostly *P. lobata* and *P. lutea*) in the lower reef slopes (7–12 m depth, sites 1, 4 and 6). (Photos taken by K.S. Tkachenko).

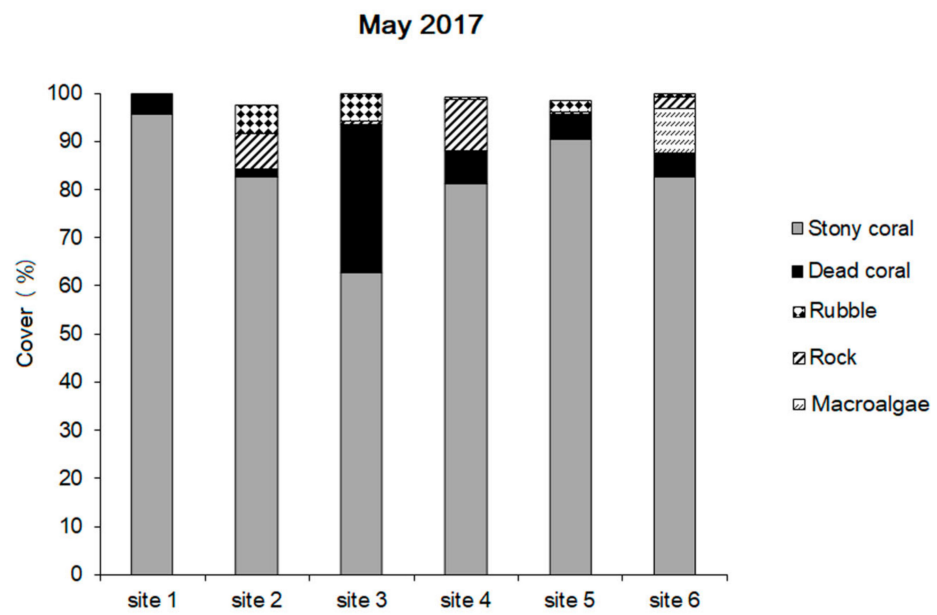


Figure 5. Distribution of the major benthic categories at 6 sites surveyed in May 2017.

Table 2. Results of one-way ANOVA for temporal differences in major categories and dominant taxa at three study sites.

		F	P
Site 1			
3–5 m depth	Stony coral	0.11	0.893
	Dead coral	0.42	0.669
	<i>Acropora</i>	2.15	0.172
9–12 m depth	Stony coral	1.77	0.224
	Dead coral	0.25	0.783
	<i>Montipora aequituberculata</i>	0.44	0.653
	<i>Porites rus</i>	0.56	0.585
	<i>Pachyseris speciosa</i>	0.12	0.882
	<i>Galaxea fascicularis</i>	0.35	0.708
Site 3			
3–5 m depth	Stony coral	0.41	0.673
	Dead coral	0.7	0.517
	<i>Acropora</i>	0.21	0.807
Site 6			
3–5 m depth	Stony coral	4.59	0.023
	Dead coral	1.40	0.293
	<i>Sargassum</i>	5.77	0.010
	<i>Acropora</i>	3.85	0.036
	<i>Montipora aequituberculata</i>	1.7	0.234
	9–12 m depth	Stony coral	0.57
Dead coral		1.13	0.362
<i>Acropora</i>		0.23	0.796
<i>Montipora aequituberculata</i>		0.16	0.847
<i>Fungia</i>		0.07	0.929
<i>Porites rus</i>		0.38	0.693

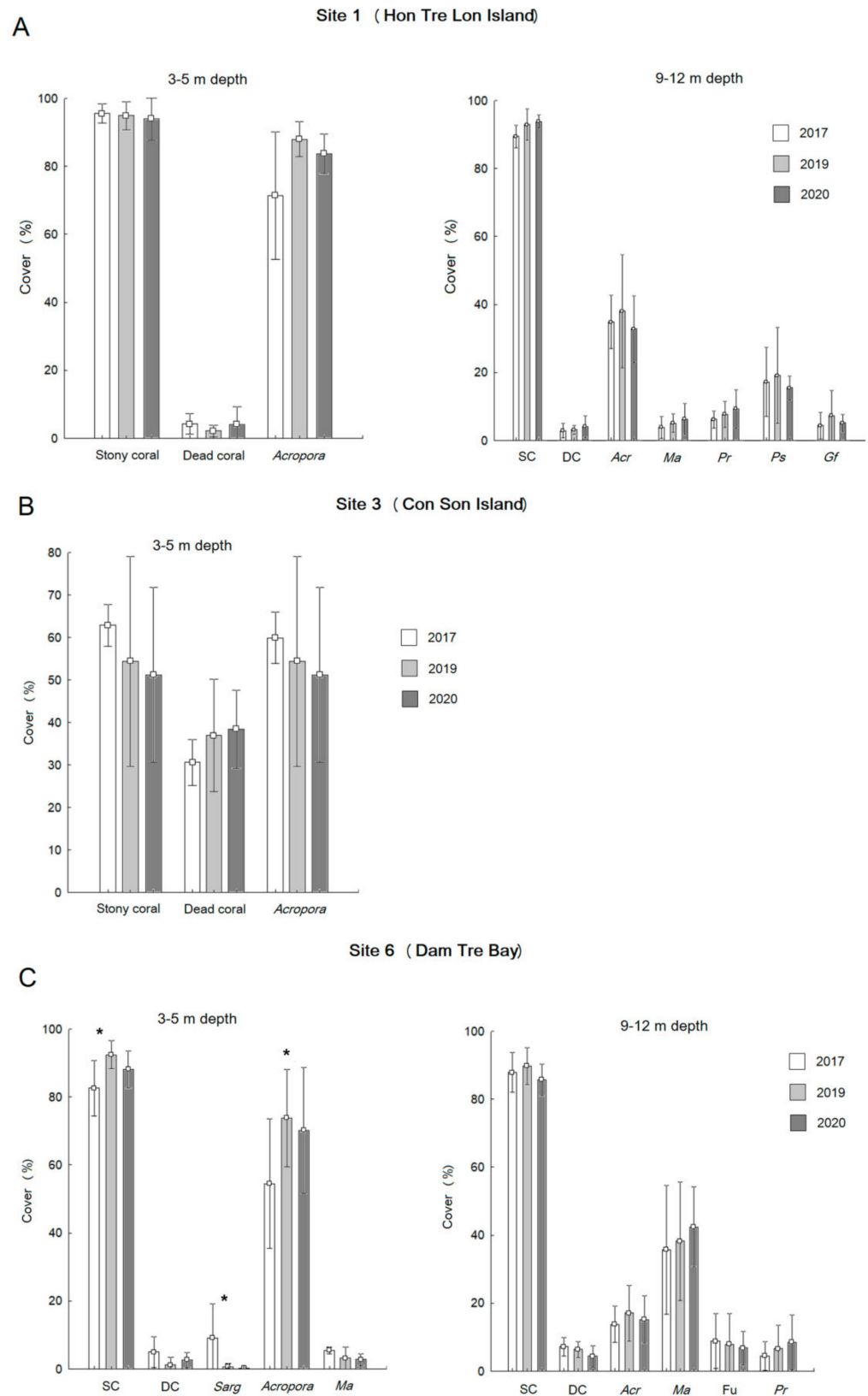


Figure 6. Temporal variations over the 3-year period in covers (\pm SD) of stony coral, dead coral and dominant coral taxa (by cover > 5% in at least one of 3 years of observations) at three target sites ((A–C), sites 1, 3 and 6). SC: stony coral; DC: dead coral; Acr: *Acropora* spp.; Sarg: *Sargassum* sp.; Ma: *Montipora aequituberculata*; Pr: *Porites rus*; Ps: *Pachyseris speciosa*; Gf: *Galaxea fascicularis*; Fu: Fungiidae. Significant differences (ANOVA, $p < 0.05$) are marked by asterisks.

4. Discussion

The present results show signs of coral acclimation to thermal stress in the coral communities of Con Dao Islands. An assessment of a coral bleaching event in the CDNP in June 2019 at five study sites using the ReefCheck protocol revealed high cover of live stony corals (mean $65.6 \pm 18\%$), of which only one-quarter ($25 \pm 11.1\%$) were bleached to a different extent [32]. Moreover, out of all the dominant coral taxa in the CDNP, thermally susceptible *Acropora* and *Montipora* exhibited only 2.6% and 11% bleached coverage, respectively, whereas thermally resistant massive *Porites* showed 50% bleached coverage [32,33]. The previous severe thermal anomaly in 2010 was equivalent to that in 2019 (the DHWs of $13\text{ }^{\circ}\text{C}\text{-week}$ in 2010 reached NOAA's Second Bleaching Alert Level), and coral bleaching in the CDNP was more pronounced (mean cover of bleached coral was $43.3 \pm 21.1\%$), although the pattern of coral bleaching was similar to that in 2019 with the largest and smallest proportions of bleached corals being Poritidae and Acroporidae, respectively [34]. The first recorded coral bleaching event at the Con Dao Islands in October 1998 resulted in 37.8% of the stony coral colonies being bleached [30]. The subsequent ENSO-related thermal anomalies in this area in 2005, 2010 and 2016 demonstrated a similar reverse hierarchy of coral bleaching; thermally susceptible Acroporidae were bleached much less severely than thermally resistant Poritidae [31,34,35]. Published data for 1998 and 2019 [30,32] coral bleaching events allowed us to graphically show this continued pattern of decreased bleaching in 2019 for some dominant coral genera (Figure 7).

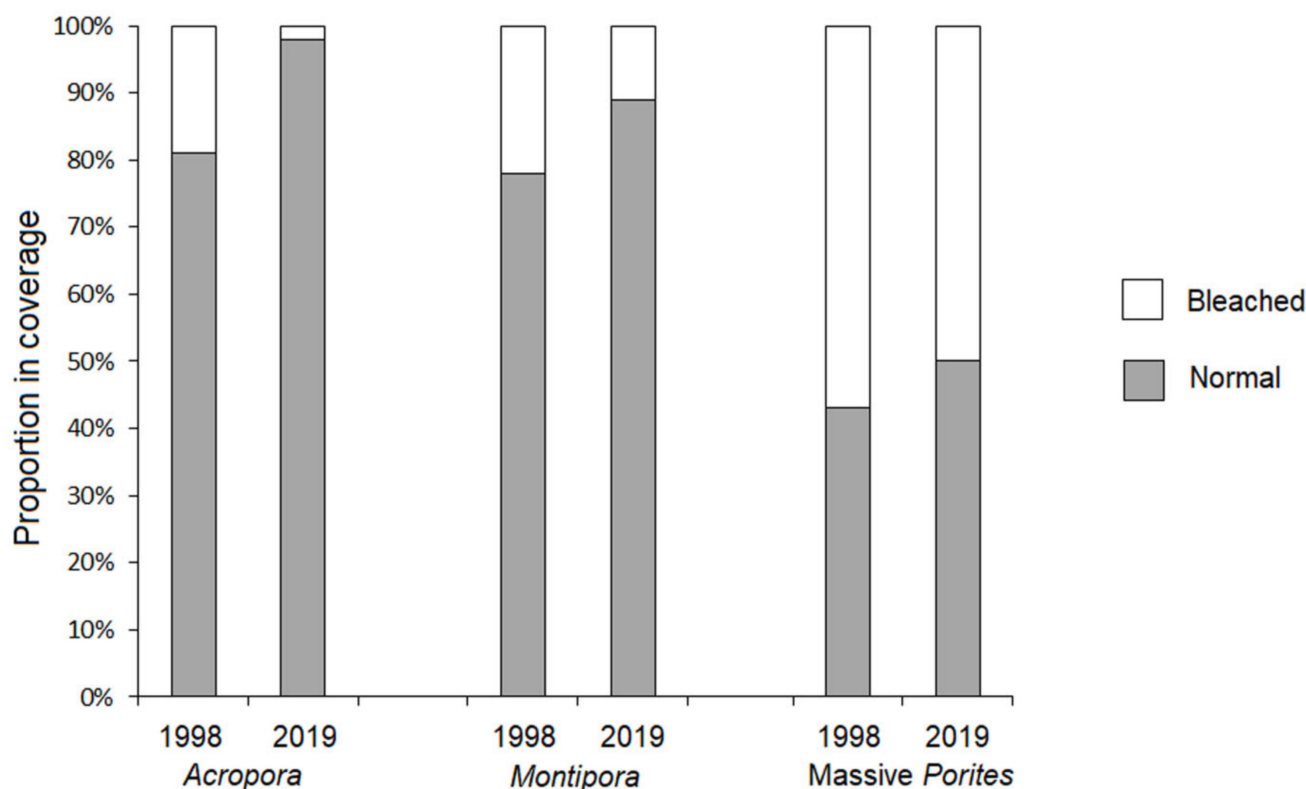


Figure 7. Variations in proportion of bleached vs. normal coral colonies of the dominant coral taxa of the CDNP during 1998 and 2019 ENSO-related thermal anomalies (based on data presented in [30,32]).

Our study revealed no significant post-bleaching response of the dominant Acroporidae and Poritidae species to thermal stress in 2019 and a stable, healthy state of coral communities in general. In addition, the size of the largest table *Acropora* colonies observed at target sites 'indicates' the resistance to thermal stress events. Given that colonies of table *Acropora* larger than 15 cm stabilize their radial extension at a nearly constant rate of $\sim 10\text{ cm}\cdot\text{year}^{-1}$ [48,49], the largest colonies ($>300\text{ cm}$ in diameter) observed in the present

study had been developing for ~30 years and had survived all significant thermal anomalies in this area over the last three decades. In addition, the largest colonies of thermally resistant massive *Porites* (200–400 cm in diameter) at sites 1 and 6 exhibited high rates of survivorship during heat stresses for at least the last two centuries given their radial extension rate of ~1 cm·year⁻¹ [50] and respective age of 200+ years. Differences in the proportions of dead coral (mostly Acroporidae) and coral rubble between the shallow and semi-closed site 3 and more open and deeper study sites could be due to the shallowness and higher irradiance (and UV radiation) of site 3 and its lower rate of water exchange, which contributes to higher coral bleaching and mortality.

Studies have reported that the thermal acclimation of corals in environments with naturally higher thermal fluctuations may lead to a higher tolerance of corals and to significant differences in the bleaching response among different locations during thermal anomalies [43,51–53]. Pre-exposure to high sublethal temperatures may increase the thermal tolerance of reef-building corals, and thus, corals in the outer reefs and deeper waters as well as corals in high-latitude reefs may become more susceptible to bleaching relative to their conspecifics from inner and shallower reefs and lagoon habitats [43,54]. Depending both on the location and the severity of the past sublethal coral bleaching events, such thermal acclimation may totally reverse the “susceptibility” of coral taxa and cause a shift in the widely accepted hierarchy of coral bleaching responses. Consequently, after exposure to rises in SST, the thermally resistant poritids become less resistant to bleaching than thermally susceptible acroporids, as was shown for Malaysian reefs [53]. A similar shift may have occurred in the coral communities off the Con Dao Islands. Nevertheless, adaptations to heat stress are location-dependent, and prior thermal exposures do not guarantee acclimation, as was demonstrated by the coral communities of the Great Barrier Reef, where prior thermal stress exposures in 1998 and 2002 did not diminish the severity of coral bleaching in 2016 [55]. Even stress-resistant corals from thermally extreme reefs in northwest Australia were unable to increase their bleaching threshold after 6 months of acclimation to +1 °C warming [56]. In addition, downscaling linear models of seasonal and inter-annual SST variability in the tropics showed that climate change will overwhelm thermal refugia for reef-building corals, stipulated by oceanographic features such as upwelling, strong ocean currents, etc., from 84% of coral reef pixels under the present-day climate to 0.2% at 1.5 °C, and 0% at 2 °C of global warming [57]. Coral reefs located in environments with high temporal SST variability and high historical thermal exposure such as those of Con Dao Archipelago are used to identify coral reef refugia as these reefs have been able to acclimate/adapt to thermal stress [58,59]. In the light of current trends in climate change, reefs exposed to highly variable temperature environment may be better able to facilitate the recovery of the low variability thermal refugia once they become exposed to thermal stress by supplying more thermally resistant larval recruits [57]. Increasing the vulnerability of corals to ocean warming provides a rationale for human-assisted larval translocation to restore degraded reefs in cooler areas (higher latitude or upwelling areas) with corals from thermally extreme reefs [56].

Thermal tolerance and reductions in bleaching response occur due to several physiological and morphological features of corals. The following allochthonic and hereditary characteristics are shown to contribute to coral survival and acclimation the most: (1) the dominance of heat-resistant genotypes of symbiotic algae (dinoflagellates) in coral tissue; (2) a higher density of symbiotic algae in coral tissue; (3) the possession of massive growth forms with larger corallites and the ability to retract coral polyps deeper into a corallite during thermal stress; (4) a higher coral tissue biomass and thickness; (5) the ability for alternative heterotrophic nutrition during the bleaching period; and (6) the ability to produce protective proteins, amino acids, and antioxidants mitigating the impact of thermal shock and UV radiation [60–66]. The density of symbiotic dinoflagellates, the Chl *a* content and the tissue biomass in the five dominant scleractinian genera of the South China Sea (*Acropora*, *Montipora*, *Pavona*, *Porites*, and *Dipsastraea*) are shown to significantly vary along the latitudinal gradient from north to south within the South China Sea, and the

lowest values of these parameters were attributed to its southern part (the area of Spratly Islands) [67]. Qin et al. [67] believed that such a difference is likely due to the peculiarities of the long-term thermal history in the region and possibly higher UV radiation induced by higher water transparency in this remote area of the South China Sea. Further research into the biological underpinnings of coral survivorship in the Con Dao Islands is recommended to better understand the way these communities are responding to climate change.

In the light of presented data, the CDNP represents an oasis of healthy coral reefs with high biodiversity and potential for adaptation and acclimation to the globally changing environment. The government of Vietnam and authority of Ba Ria-Vung Tau Province should pay special attention to this unique area and contribute to the development of its sustainable management. Effective preservation is only possible under the condition that fishing activity in the water area of the CDNP is totally banned. In addition, only carefully verified ecological and educational tourism in this area should be permitted, without the massive construction of touristic resorts and hotels and concomitant aquaculture development that was seen in Nha Trang Bay, which resulted in significant coral degradation [9]. In the face of escalating cumulative local and global threats, the fate of the regionally significant CDNP coral reef ecosystems depends on responsible and sustainable management.

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