

Article

The Probability of an Unrecoverable Coral Community in Dongsha Atoll Marine National Park Due to Recurrent Disturbances

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Abstract: In recent decades, coral reefs worldwide have been impacted annually by climate change and anthropogenic impacts. Marine parks are utilized to protect coral reef ecosystems and to ensure it is in sustainable use. In the present study, a 15-year change in coverage and composition of a hard coral community at Dongsha Atoll Marine National Park (DAMNP) was examined from 2005 to 2019. The reef has experienced several disturbances, including 11 typhoons and six coral bleaching events. A 34.39% decline in coral coverage had been recorded over the past 15 years in response to multiple and recurrent natural disturbances. The coral communities and functional ecology of the Dongsha Atoll changed during this period. The average dissimilarities in coral communities ranged from 55.38 to 59.02%. The dramatic decrease in the abundance of branching corals in addition to a slight increase in massive and encrusting corals suggest the habitat has simplified. The degraded coral reef communities represent a low resilience ecosystem, even though the DAMNP has been established. Without effective management, the coral reef ecosystem of the Dongsha Atoll may not persist due to repeated impacts from recurrent disturbances.

Keywords: marine park; coral community; Dongsha Atoll; climate change

1. Introduction

Coral reefs, the tropical rainforests of the sea, are one of the most productive ecosystems on Earth, providing important services to fisheries, coastal protection, medicines, and tourism [1]. However, the numbers of annual disturbances (typhoons, flood plumes, and climate change) and anthropogenic impacts (overfishing, pollution, sedimentation, and coastal development) on reefs have increased rapidly in recent decades, causing strains on coral reefs around the world [2–5]. It was predicted that most coral reef ecosystems will suffer from severe bleaching events every year, and the impact level will exceed the extent of the 1998 bleaching event by the year 2040 [2]. It is estimated that 15% of the worldwide coral reefs are already severely degraded and the remainder, approximately 20% of the world's coral reefs, will be under threat of loss within the next 20 to 40 years if there is no effective solution [5]. Therefore, it appears these degraded coral reef ecosystems suffered from escalating pressures at a global scale, which have led to an intense discussion on the strategies to conserve the biodiversity, enhance the resilience, and maintain the ecosystem processes in these habitats [3,4,6,7].

Marine Protected Areas (MPAs) are a section of the ocean where a government has placed limits on human activities. A Marine Park (MP), or a Nation Park (NP), is a type of MPA, meaning they include zoning plans to permit various human activities [8,9]. It is sometimes protected for recreational use, but is usually a set-aside for conservation [8,9]. Establishing an effective MP is a practical approach,

with consensus from conservation biologists, to better manage and conserve marine systems and coral reef ecosystems [6,8–13]. Even though there are extensive research evidence that proves the benefits of using an MP to manage and conserve marine biodiversity, some failure examples from mitigating the natural and anthropogenic disturbances have caused extensive debates on its effectiveness [8,9,14–18].

A well-developed coral reef structure across a multi-dimensional space and with a high coral coverage was found in the Dongsha Atoll (DA). With rich fishery resources, it has traditionally been recognized as an important fishing ground for many countries, such as China, Hong Kong, Taiwan, and Vietnam [19]. It has been the major reef in the northern South China Sea, thus playing an important role in the main breeding and nursery grounds for numerous marine organisms [19,20]. In 2007, the government of Taiwan designated it as a marine national park (hereafter, DAMNP) based on the concerns for sustainable fisheries management and to mitigate the effects of potential environmental impacts. Until now, it is still a protected area and is yet to be opened to tourists. However, despite having established the DAMNP, the Dongsha reef has suffered from natural and anthropogenic disturbances, including typhoons [21], coral bleaching events [22–24], illegal fishing (poisons and explosives) and overfishing [25–27], the proliferation of macroalgae [28], outbreaks of the coral predator *Acanthaster planci* Linnaeus 1758 (crown-of-thorns starfish) [29], and coral diseases or parasites [30]. These disturbances have continued to degrade the coral-dominated assemblages in the DAMNP waters. The reason behind the challenge in establishing a more appropriate and effective management for the DA is the current lack of understanding the changes in coral communities from disturbances.

In the present study, changes in coral coverage and composition at DAMNP were analyzed based on the surveys conducted from 2005 to 2019. We were particularly interested in whether recurrent disturbances played a major role in the state of coral communities (coral coverage, biodiversity, species composition, and ecological functions), especially in three different periods: before DAMNP establishment (in 2006), the period of the following five years (2006 to 2012), and the period of the following twelve years (2006 to 2019).

2. Materials and Methods

2.1. Study Site

Dongsha Atoll (DA) is located at 20°40′43″ N and 116°42′54″ E, and is the largest and the first developed, northernmost atoll in the South China Sea (SCS). It has formed a perfect ring-shaped reef with well-developed coral reefs, supporting highly diverse fauna and flora. It is about 340 km southeast of Hong Kong, 260 km south of Shantou off the Chinese mainland, and 450 km southwest of Taiwan (Figure 1). The atoll is approximately 25 km wide in diameter, and its reef table that emerges above water during low tides is approximately 46 km in length and 2 km in width. The inner-reef and lagoon covers more than 600 km², and the maximum depth is approximately 23.7 m [19,20].

2.2. The Historical State of the Dongsha Atoll (DA) Coral Community

2.2.1. Species Diversity of the Corals

Based on the results from extensive biological surveys conducted from 1975 to 2019, a total of 384 species of Cnidaria has been recorded in DA, including 257 species in 56 genera of the Scleractinia family, 118 species in 30 genera of the Alcyonacea family, two species in two genera of Antipatharia family, one species in one genus of Helioporacea family, and six species in two genera of Anthoathecata family (Figure 2).

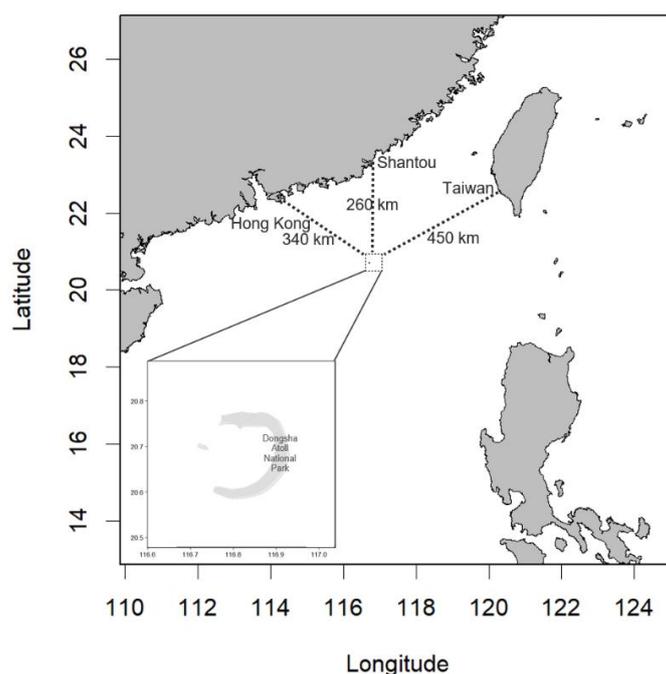


Figure 1. Map of Dongsha Atoll in the northern South China Sea.

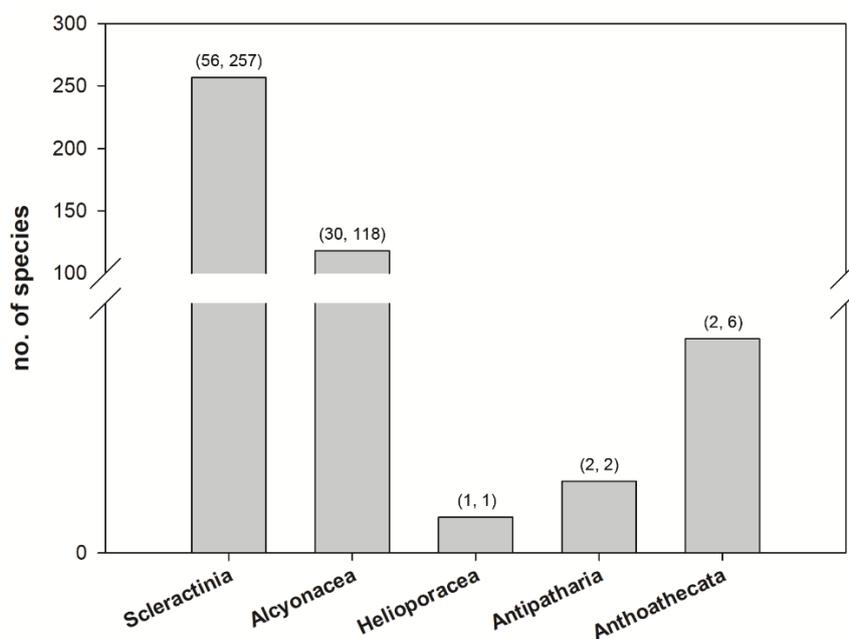


Figure 2. A total of 384 species of Cnidaria has been recorded by extensive biological surveys conducted from 1975 to 2019 in the Dongsha Atoll (DA). The numbers in the parentheses indicate the number of genera and species.

2.2.2. Coral Communities Prior to 1998: Before the Severe Coral Bleaching Event

The coral fauna in the DA has a close affinity with those from the Indo-West Pacific province, southern Taiwan, and Taiping Island [19]. According to Dai et al. [21], a high biodiversity (a total of 137 coral species) was recorded, and there was approximately over 50% of the average coral coverage (higher than 80% in some locations). At that time, well-developed coral communities occurred both in the outer and inner reefs. The coral communities were dominated by scleractinians, and *Acropora* spp. and *Porites* spp. were the most abundant and widespread corals in Dongsha [19,21,31,32].

2.2.3. Coral Communities from 1998–2007: Prior to the Establishment of Dongsha Atoll Marine National Park (DAMNP)

After the exceptional high seawater surface temperatures and a severe coral bleaching event observed in 1998, a significant decline in the coral coverage and biodiversity occurred from several biological surveys [22–24]. The live coral coverage (LCC) ranged from <1 to 6% and roughly around 23% in the outer reef and lagoon, respectively. In total, over 90% of the reefs and inhabitants were killed and replaced by filamentous algae or macroalgae [19]. Moreover, a dramatic degradation of coral reefs might be also caused by overfishing and destructive fishing practices, such as the overuse of poisons and explosions from illegal fishing, resulting in a dramatic decline in the coral species richness to the point that 60–90% of the corals died [25,26]. In terms of species composition of scleractinians, the coral species belonging to the Merulinidae and Fungiidae were dominant and the foliaceous corals (*Echinopora gemmacea*, *Echinopora lamellose*, and *Echinopora aspera*) were abundant in the inner reef [19,33].

2.2.4. Coral Communities from 2007–2012: The Protected Period

Field surveys conducted in 2012 revealed that the highest coral coverage (about 80%) was recorded from the outer reef, while the LCC of the inner reef was highly variable, ranging from 10.5% to 71.5% [34]. During the study period, no mass coral bleaching event occurred, but only a few individuals of *Acanthaster planci* were found. According to Gomez et al. [35] and Connell et al. [36], an LCC between 51 and 75% indicates a positive status. Thus, the coral coverage at most sites was higher than 50% in 2012, indicating that the reef environment was suitable for coral growth. However, the study pointed out that the DAMNP was under the threat of high fishing pressure in 2012 since the number and size of fishes and benthic invertebrates were low, particularly for the commercial ones [34].

2.3. Statistical Analysis

The data of the ecological surveys on the temporal variation of coral coverage (hard and soft corals) from previous studies were conducted using the Reef Check protocol from 2005 to 2017 [28,33,34,37–42]. In this study, coral coverage and communities of DA were re-surveyed in 2019 to reveal its recent state. A hierarchical survey design that included different sectors (the outer reef and the inner reef/lagoon) and sites were applied. Each sector included several sites where the water depth was approximately 10 m (Appendix A). In order to reveal the change in hard coral community structures, we analyzed the field survey data conducted before the establishment of the DAMNP in 2006, 5 years later in 2012, and 12 years later in 2019 (see Appendix A for details). During this 15-year study, eleven major typhoons and six coral bleaching events (Appendix B and Figure 3) affected the DA. Variations in the diversity indices were calculated with a multivariate analysis package (Primer 6.0) [43]. A non-metric multidimensional scaling (nMDS) ordination of the coral communities was conducted to reveal the grouping of the surveyed sites. Analysis of similarity (ANOSIM) was applied to separate different groupings from the nMDS and the Similarity Percentage (SIMPER) analysis was used to reveal the species that contributed to >90% of cumulative similarities within groups using a multivariate analysis package (Primer 6.0) [43]. In order to know whether the ecological functions of the coral community have been changed during this period, five coral growth forms (branching, encrusting, massive, foliaceous, and others) were referred to various functional groups. The structural variations of the functional groups among the sampling periods were explored using a principal components analysis (PCA, Primer 6.0).

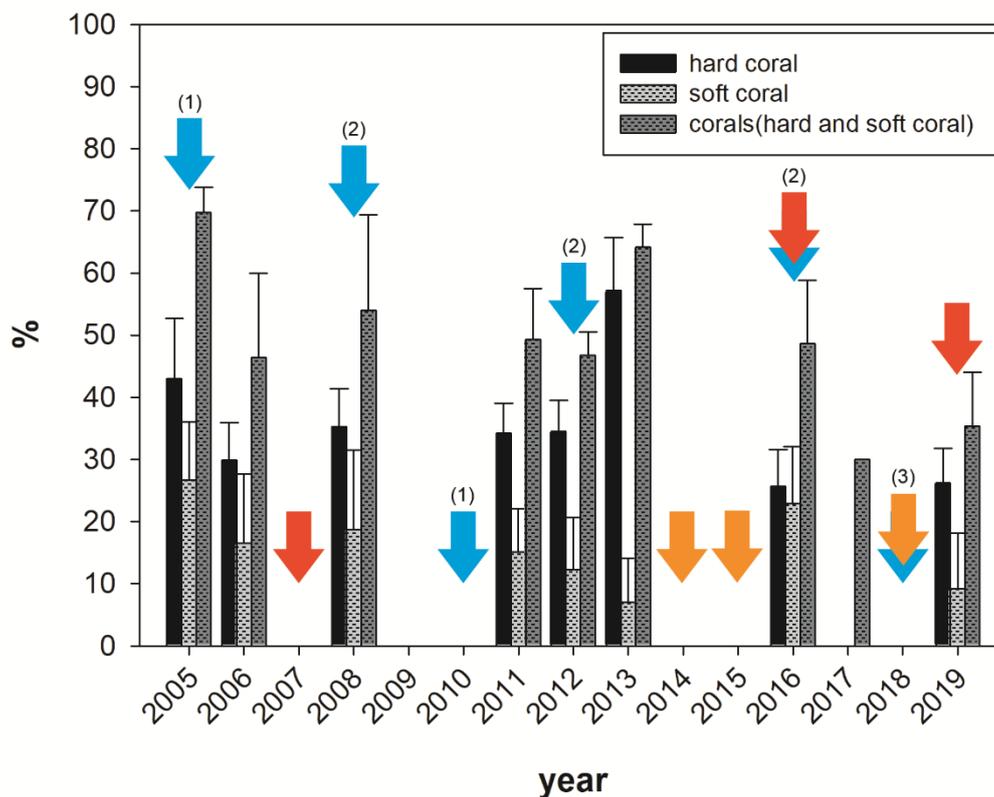


Figure 3. Temporal dynamics of the corals (hard and soft corals) in the Dongsha Atoll from 2005 to 2019. Eleven typhoons (blue color) and six bleaching events (orange: level 1; red: level 2) occurred in this period. The number in the parentheses indicates the number of typhoons.

3. Results

In 2019, a total of 257 species of scleractinian corals were recorded in the Dongsha Atoll (DA), and the top 20 species in abundance and five functional groups are listed in Table 1. The live coral coverage (LCC) dropped by 34.39%, ranging from 69.75% (hard corals: 43.00%; soft corals: 26.78%) in 2005 to 35.39% (hard corals: 26.23%; soft corals: 9.16%) in 2019 (Figure 3). The diversity indices of the coral communities at the surveyed sites are shown in Table 2. The highest species number (115 ± 15 and 139 ± 7), colony number (463 ± 67 and 508 ± 51), Shannon diversity index (6.36 ± 0.20 and 6.82 ± 0.07), and Evenness (0.96 ± 0.00) were recorded in 2006 and 2012, while those indices were the lowest in 2019.

The LCC of the DA has changed considerably over the 15-year period in response to multiple natural and anthropogenic disturbances. As in Figure 3, several changes can be identified and divided into several disturbance and inter-disturbance periods (also called the recovery period). In 2005, the LCC was about 69.75%, but in 2006, typhoon DAMREY caused a major decline in both soft and hard coral coverage, resulting in a sharp reduction to 46.38%. In 2007, a severe coral bleaching event occurred. Unfortunately, without an ecological survey, the conditions of the coral remain unknown. In 2008, two typhoons (named NURI and HAGUPIT) hit the DA, but the coral coverage was almost at the same level as that in 2006. From 2009 to 2013, only three typhoons hit, and they happened in 2010 (LIONROCK) and 2012 (TALIM and TEMBIN). It seems to have been a major recovery period for the DA corals, particularly the hard corals. The hard coral coverage (57.20%) in 2013 recovered to its original states and even higher than the percentage (43.00%) in 2005, although the soft corals might be removed by the typhoons. However, between 2014 and 2019, multiple disturbances, including five typhoons and several major bleaching events (both Level 1 and 2), led to a steady degradation of the coral assemblage.

Table 1. The hard coral species (the top 20 species in abundance) and five functional groups of corals recorded from the Dongsha Atoll from 2006 to 2019.

Coral Family	Species Name	Growth Form	2006	2012	2019
			Average ± SE	Average ± SE	Average ± SE
Acroporidae	<i>Montipora grisea</i>	encrusting	5.43 ± 1.53	2.00 ± 0.00	5.60 ± 3.11
	<i>Montipora informis</i>	encrusting	10.43 ± 1.56	8.00 ± 3.00	9.20 ± 2.94
Agariciidae	<i>Pavona varians</i>	encrusting	4.57 ± 0.43	2.00 ± 0.00	14.20 ± 0.80
Euphylliidae	<i>Galaxea fascicularis</i>	other	7.57 ± 1.21	2.00 ± 0.00	6.80 ± 1.80
Fungiidae	<i>Herpolitha limax</i>	other	2.00	0.00	0.00
Meruliniidae	<i>Leptastrea transversa</i>	massive	3.00 ± 0.63	3.50 ± 1.50	7.40 ± 1.47
	<i>Cyphastrea serailia</i>	massive	3.00 ± 0.63	3.50 ± 1.50	4.00 ± 1.92
	<i>Dipsastraea pallida</i>	massive	5.00 ± 0.00	3.50 ± 1.50	9.80 ± 1.20
	<i>Dipsastraea speciosa</i>	massive	7.57 ± 1.21	8.00 ± 3.00	6.20 ± 1.20
	<i>Echinopora gemmacea</i>	foliaceous	2.86 ± 0.55	2.00	4.80 ± 2.56
	<i>Echinopora lamellosa</i>	foliaceous	4.14 ± 1.26	5.00	3.80 ± 0.73
	<i>Favites abdita</i>	massive	9.29 ± 1.11	8.00 ± 3.00	11.80 ± 0.80
	<i>Favites halicora</i>	massive	5.00	6.50 ± 4.50	9.80 ± 1.20
	<i>Goniastrea edwardsi</i>	massive	2.86 ± 0.55	8.00 ± 3.00	3.20 ± 0.73
	<i>Goniastrea retiformis</i>	massive	2.43 ± 0.43	5.00 ± 0.00	10.60 ± 1.60
Pocilloporidae	<i>Pocillopora verrucosa</i>	branching	12.00 ± 1.81	3.50 ± 1.50	8.00 ± 1.90
Poritidae	<i>Porites cylindrica</i>	branching	6.00 ± 2.65	0.00	0.00
	<i>Porites lichen</i>	foliaceous	7.14 ± 1.42	8.00 ± 3.00	6.20 ± 1.20
	<i>Porites lobata</i>	massive	3.29 ± 0.61	8.00 ± 3.00	7.40 ± 1.47
	<i>Porites lutea</i>	massive	3.71 ± 0.61	3.50 ± 1.50	5.60 ± 1.47
Five Major Functional Groups of Corals					
		branching	103.44 ± 24.87	58.70 ± 7.52	59.07 ± 7.52
		encrusting	24.38 ± 4.53	33.50 ± 2.20	35.21 ± 6.50
		foliaceous	68.81 ± 11.45	83.90 ± 14.28	51.14 ± 8.28
		massive	161.00 ± 18.74	243.20 ± 23.46	203.29 ± 16.49
		other	32.69 ± 9.96	49.10 ± 14.82	40.43 ± 11.49

Scientific names are in italics.

Our results showed that the hard coral coverage dropped by 16.77%, declining from 43.00% in 2005 to 26.23% in 2019 (Figure 3). The reason behind the mass decline in hard coral coverage can be explained by the dramatic decrease in branching corals, which plunged from 103.44 ± 24.87 colonies in 2006 to 59.07 ± 7.52 in 2019. For example, from 2006 to 2019, *Pocillopora verrucosa* decreased to 33.33% (Table 1). A similar trend also occurred in other corals with foliaceous growth forms similarly sensitive to a high sea water temperature and the mechanical impacts brought by the typhoon disturbances. In contrast, the massive and encrusting corals only showed a slight variation in coverage and abundance (Table 1). *Favites halicora* and *Goniastrea retiformis* have increased significantly since 2006. Subsequently, *Pavona varians*, *Dipsastraea pallida*, and *Favites abdita* increased significantly after 2012. They remained the top five taxa in terms of abundance in 2019 and recently became the dominant species (Table 1).

The results of the non-metric multidimensional scaling (nMDS) did not show a clear grouping pattern at the surveyed sites between 2006, 2012, and 2019. However, the nMDS groupings among the outer- and inner-reef sectors showed a more site-oriented cluster (Figure 4). The results were also supported by the result from the analysis of similarity (ANOSIM), suggesting most sites among the different years ($p < 0.01$; Global R = 0.64) and sectors ($p < 0.01$; Global R = 0.49) were separated with significant differences. The results from the similarity percentage (SIMPER) showed that most of the abundant species contributed to more than 90% of the cumulative similarities and dissimilarities in 2006, 2012, and 2019 (only shows over 10% in Tables 3 and 4). The average similarities of the coral species at the surveyed sites ranged from 50.11 to 61.97%, while the average dissimilarities ranged from 55.38 to 59.02% (Tables 3 and 4). Among these coral species, *Porites lobata* (average abundance = 2.13–3.24 colonies; contribution = 1.95–4.03%) was the most abundant in the period of

this study. Other common species, including *Porites lutea* (2.06–3.15 colonies; contribute = 1.81–4.01%), *Goniastrea retiformis* (1.91 colonies; contribute = 2.04%), and *Favites abdita* (2.48 colonies; contribute = 1.36%), were also dominant. Nevertheless, most are encrusting and massive corals with a slower growth rate and recovery ability, except for *Montipora informis* (2.09 colonies; contribution = 1.66%).

Table 2. The biodiversity measures, including colony number (N), species number (S), Shannon diversity index (H'), and Evenness (E) in the studied sites of Dongsha in 2006, 2012, and 2019.

Locations (Year)	N	S	H'	E
06-1 (2006)	702	161	6.98	0.95
06-2 (2006)	687	164	7.00	0.95
06-3 (2006)	686	176	7.17	0.96
06-4 (2006)	704	188	7.26	0.96
06-5 (2006)	648	159	7.07	0.97
06-6 (2006)	663	152	6.96	0.96
06-7 (2006)	342	81	5.92	0.93
06-8 (2006)	209	55	5.49	0.95
06-9 (2006)	757	176	7.16	0.96
06-10 (2006)	828	186	7.19	0.95
06-11 (2006)	221	56	5.50	0.95
06-12 (2006)	378	73	5.88	0.95
06-13 (2006)	133	38	4.95	0.94
06-14 (2006)	192	51	5.44	0.96
06-A (2006)	162	81	6.34	1.00
06-B (2006)	88	44	5.46	1.00
Average ± SE	463 ± 67	115 ± 15	6.36 ± 0.20	0.96 ± 0.00
12-01 (2012)	625	138	6.72	0.94
12-04 (2012)	374	124	6.71	0.96
12-05 (2012)	814	161	7.04	0.96
12-08 (2012)	584	156	6.98	0.96
12-11 (2012)	280	104	6.49	0.97
12-12 (2012)	368	116	6.61	0.96
12-16 (2012)	512	154	6.94	0.95
12-17 (2012)	638	173	7.15	0.96
12-20 (2012)	487	138	6.85	0.96
12-23 (2012)	399	127	6.71	0.96
Average	508 ± 51	139 ± 7	6.82 ± 0.07	0.96 ± 0.00
12-1 (2019)	223	60	5.55	0.94
12-4 (2019)	609	102	6.34	0.95
12-5 (2019)	521	75	5.89	0.95
12-8 (2019)	574	103	6.32	0.95
12-11 (2019)	182	28	4.38	0.91
12-12 (2019)	251	57	5.51	0.94
12-16 (2019)	415	68	5.72	0.94
12-17 (2019)	524	100	6.28	0.95
12-20 (2019)	485	93	6.20	0.95
12-23 (2019)	520	100	6.30	0.95
19-01 (2019)	683	114	6.51	0.95
19-02 (2019)	462	89	6.13	0.95
19-03 (2019)	536	101	6.32	0.95
19-05 (2019)	351	68	5.75	0.94
Average	453 ± 40	83 ± 6	5.94 ± 0.15	0.94 ± 0.00

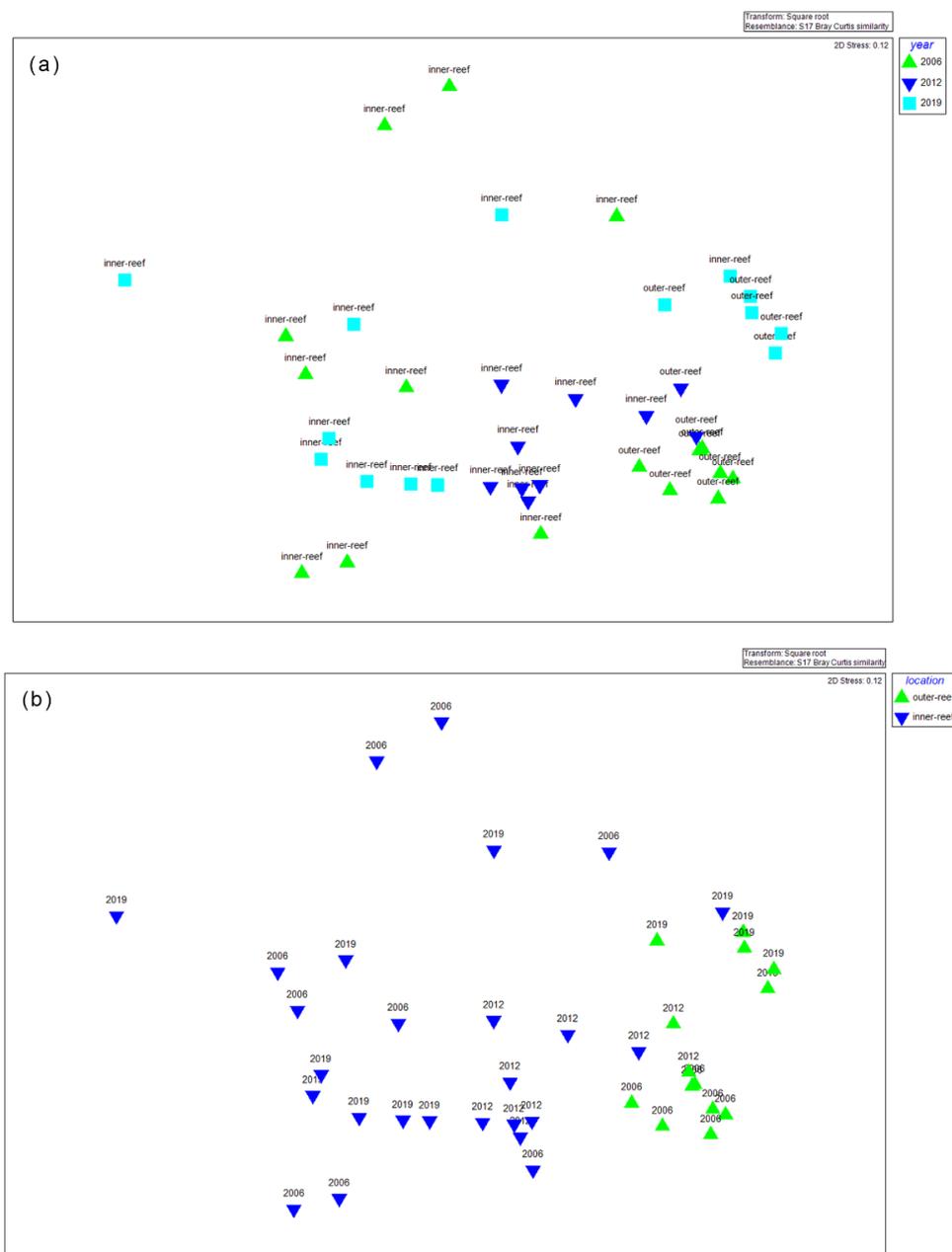


Figure 4. Multidimensional scaling (MDS) plot of the species composition and abundance of corals: (a) among various sampling periods (2006, 2012, and 2019); (b) among various locations (outer reef and inner reef).

Table 3. The average similarity of the coral species at the surveyed sites among 2006, 2012, and 2019. Only the corals with a more than 10% cum. contribution are listed.

	Average Abundance	Contribution (%)	Cum. Contribution (%)
	2006 average similarity: 54.11		
<i>Porites lobata</i>	2.13	2.27	2.27
<i>Porites lutea</i>	2.06	2.16	4.43
<i>Goniastrea retiformis</i>	1.91	2.04	6.47
<i>Goniopora djiboutiensis</i>	1.96	1.80	8.27
<i>Montipora informis</i>	2.09	1.66	9.93

Table 3. Cont.

	Average Abundance	Contribution (%)	Cum. Contribution (%)
2012 average similarity: 61.97			
<i>Porites lobata</i>	3.21	1.95	1.95
<i>Porites lutea</i>	2.86	1.81	3.77
<i>Favites abdita</i>	2.48	1.36	5.12
<i>Favites russelli</i>	2.29	1.32	6.44
<i>Astreopora ocellata</i>	2.21	1.31	7.75
<i>Turbinaria mesenterina</i>	2.23	1.25	9.00
2019 average similarity: 50.11			
<i>Porites lobata</i>	3.24	4.03	4.03
<i>Porites lutea</i>	3.15	4.01	8.04

Scientific names are in italics.

Table 4. The average dissimilarity of the coral species of the coral communities at the surveyed sites among 2006, 2012, and 2019. Only the corals with a more than 10% cum. contribution are listed.

	Average Abundance (2006)	Average Abundance (2012)	Contribution (%)	Cum. Contribution (%)
average dissimilarity: 55.38				
<i>Favites russelli</i>	0.63	2.29	0.96	0.96
<i>Psammocora contigua</i>	0.40	1.87	0.93	1.89
<i>Astreopora ocellata</i>	0.76	2.21	0.89	2.78
<i>Turbinaria irregularis</i>	0.00	1.82	0.89	3.67
<i>Porites nigrescens</i>	0.44	1.78	0.84	4.50
<i>Pectinia paeonia</i>	0.42	1.78	0.81	5.31
<i>Hydnophora exesa</i>	1.03	1.74	0.78	6.09
<i>Favites halicora</i>	0.66	2.31	0.77	6.86
<i>Montipora spongodes</i>	0.00	1.60	0.74	7.60
<i>Echinopora lamellosa</i>	1.99	2.33	0.73	8.33
<i>Echinopora gemmacea</i>	1.77	1.47	0.71	9.04
<i>Goniopora columna</i>	0.77	1.53	0.69	9.73
	Average Abundance (2012)	Average Abundance (2019)	Contribute (%)	Cum. Contribute (%)
average dissimilarity: 55.92				
<i>Psammocora contigua</i>	1.87	0.36	0.83	0.83
<i>Astreopora ocellata</i>	2.21	0.40	0.83	1.66
<i>Gardineroseris planulata</i>	1.68	0.00	0.76	2.42
<i>Favites russelli</i>	2.29	0.77	0.75	3.17
<i>Favites flexuosa</i>	1.85	0.10	0.74	3.91
<i>Herpolitha limax</i>	1.53	1.50	0.72	4.63
<i>Pectinia paeonia</i>	1.78	0.51	0.71	5.34
<i>Symphyllia agaricia</i>	1.68	0.20	0.69	6.04
<i>Pavona decussata</i>	1.46	0.91	0.67	6.71
<i>Lithophyllon undulatum</i>	1.07	1.45	0.67	7.38
<i>Pavona venosa</i>	1.66	0.50	0.67	8.05
<i>Echinopora gemmacea</i>	1.47	1.51	0.67	8.72
<i>Coeloseris mayeri</i>	1.44	0.16	0.67	9.39

Table 4. Cont.

	Average Abundance (2006)	Average Abundance (2019)	Contribute (%)	Cum. Contribute (%)
average dissimilarity: 59.02				
<i>Porites nigrescens</i>	0.44	1.55	1.08	1.08
<i>Leptastrea transversa</i>	1.04	2.52	1.00	2.08
<i>Goniopora djiboutiensis</i>	1.96	0.20	0.95	3.03
<i>Acropora microphthalma</i>	0.89	1.13	0.93	3.97
<i>Favites halicora</i>	0.66	2.20	0.87	4.83
<i>Herpolitha limax</i>	1.16	1.50	0.84	5.67
<i>Fungia concinna</i>	0.49	1.45	0.83	6.51
<i>Pavona decussata</i>	1.30	0.91	0.81	7.31
<i>Montipora grisea</i>	1.31	1.95	0.80	8.11
<i>Lithophyllon undulatum</i>	1.26	1.45	0.79	8.90
<i>Leptastrea pruinosa</i>	1.08	2.19	0.78	9.68

Scientific names are in italics.

In terms of the variation in the functional groups of corals, various lifeforms of corals showed different tendencies in changing in abundance from 2006 to 2019 (Table 1, Figure 5). The results of the principal components analysis (PCA) revealed that a 2-D PCA was a good description of the structure, with PC1 and PC2 accounting for 78.4% and 21.6%, respectively (Figure 5). The branching coral showed a massive decrease while the number of encrusting and massive corals slightly increased (Table 1; Figure 5). The same trends also occurred if we divided the DA data into outer- and inner-reefs (Figures 6 and 7).

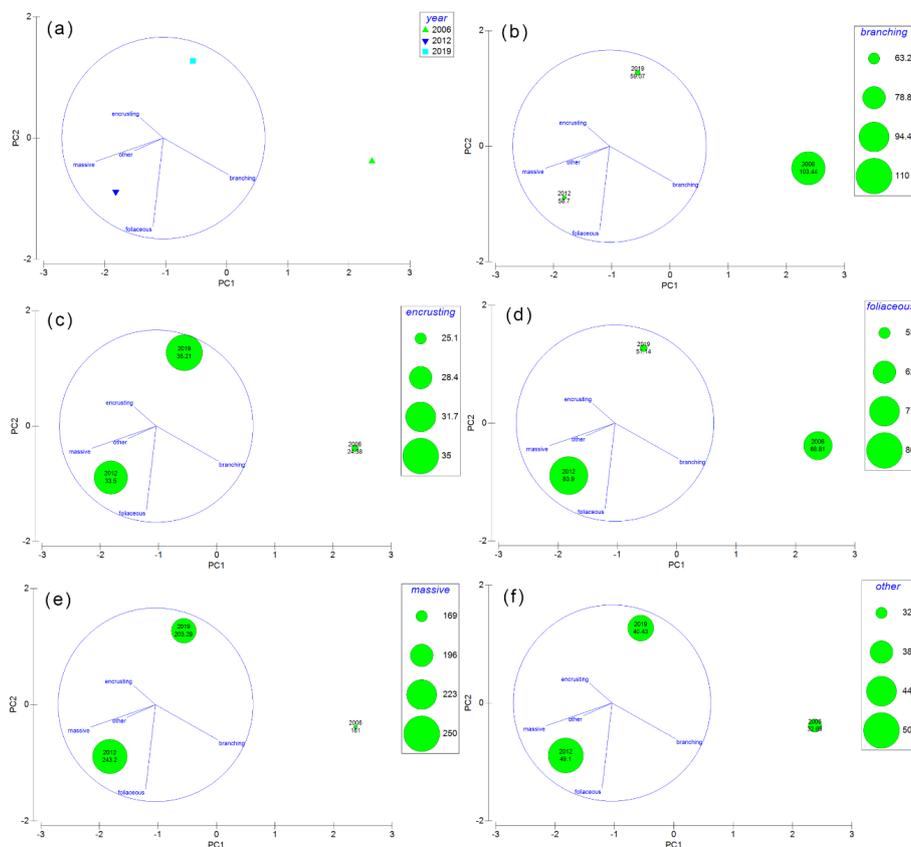


Figure 5. Principal component analysis (PCA) of the coral colonies from the Dongsha Atoll for three sampling periods (2006, 2012, and 2019): (a) hard corals; (b–f) the five functional categories of corals: branching, encrusting, foliaceous, massive, and others. PC1 accounted for 78.4% of the variability, and PC2 accounted for 21.6%. The size of the green circles indicates the number of coral colonies.

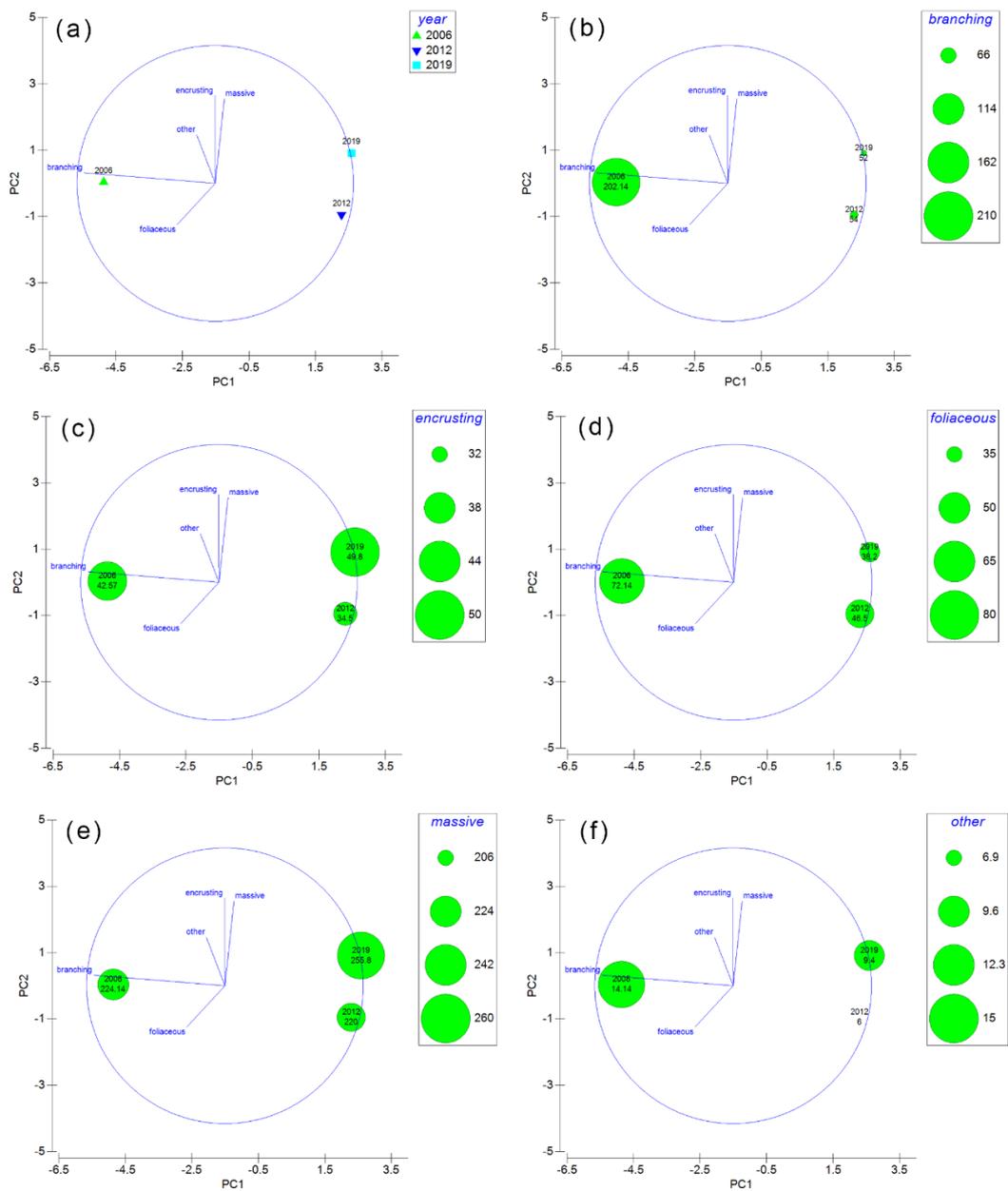


Figure 6. Principal component analysis (PCA) of the coral colonies from the outer reef of the Dongsha Atoll for three sampling periods (2006, 2012, and 2019): (a) hard corals; (b–f) the five functional categories of corals: branching, encrusting, foliaceous, massive, and others. PC1 accounted for 95.3% of the variability, and PC2 accounted for 4.7%. The size of the green circles indicates the number of coral colonies.

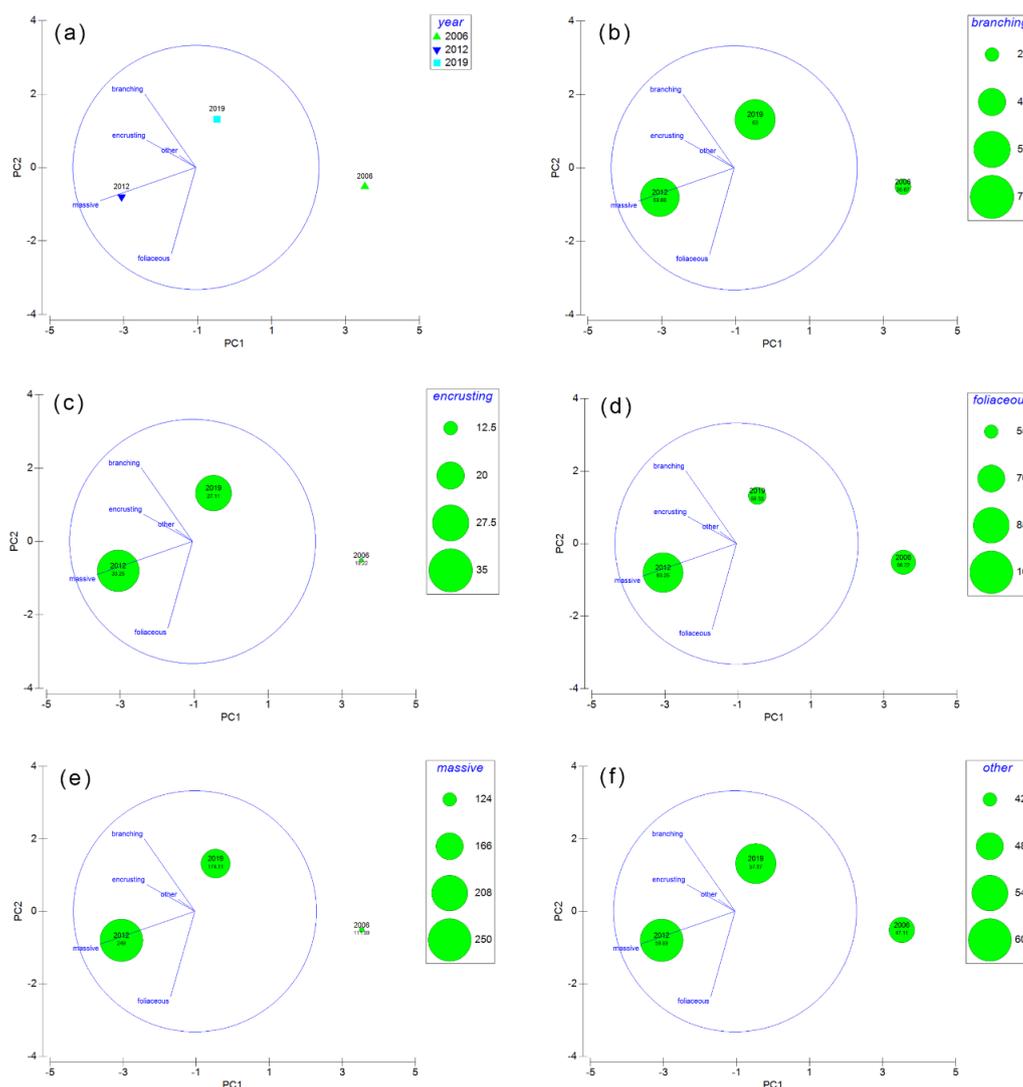


Figure 7. Principal component analysis (PCA) of the coral colonies from the inner reef of the Dongsha Atoll for three sampling periods (2006, 2012, and 2019): (a) hard corals; (b–f) the five functional categories of corals: branching, encrusting, foliaceous, massive, and others. PC1 accounted for 89.3% of the variability, and PC2 accounted for 10.7%. The size of the green circles indicates the number of coral colonies.

4. Discussion

Historically, the Dongsha Atoll (DA) was a well-developed reef, crossing a multi-dimensional space and with a high coral coverage. The environmental factors in the outer reef were favorable for coral growth, especially when the seawater temperature was higher [44]. Consequently, most coral species in the outer reef displayed diverse growth forms and large coral colonies. On the contrary, the coral communities in the inner reef seemed to be in an inferior condition even though some high coverages of the live corals and large coral colonies could still be found. Higher sedimentation rates, as well as the organic contents combined with greater SST fluctuations were the possible factors that restricted the distribution and development of the corals, and they might have shaped the coral communities in the inner reef [19]. When the turbidity level was high, the coral colonies were sometimes covered by heavy sedimentation, which was a common cause of some coral mortalities. The main coral species found at the sites were stress-tolerant, sediment-tolerant, or ruderal species, such as species of Poritidae, Meruliniidae, and Acroporiidae [19,20,34]. However, we found that, within only 15 years, both the outer and inner reefs have suffered from dramatic changes in live coral coverage

(LCC), and so too the coral communities, even though it has already been protected by the Dongsha Atoll Marine National Park (DAMNP).

Coral coverage is used as an index for comparisons between different treatments as well as for temporal and spatial variations in the coral ecosystems [35,36]. Comparing with the results from previous studies revealed that the recurrent disturbances may contribute to coral community degradation. After the 1998 mass bleaching event, the LCC reduced to about 6% in the lagoon, 23% in the outer reef, and then went through a stable recovery phase until 2005, in which the LCC was around 70%. However, when the coral community was under significant degradation in 2006, the species composition of the corals did not change significantly, and the dominant coral species were branching corals, such as *Acropora* and *Pocillopora*. From 2006 to 2018, the LCC never regained or exceeded the previous level. However, the LCC in 2008 and 2013 were higher than 50% (indicating the coral communities were still in good conditions) [35,36]. From 2016 to 2019, the recovery pattern changed again (probably from 2014, but with no supporting data). In 2019, the state of the coral assemblage was at its worst (26.23% for hard corals, 9.16% for soft corals) and the coral species composition and ecological function were thus changed due to a dramatic reduction in branching-form corals (Figures 5–7; Table 1). The *Acropora* was not abundant in the assemblage in 2019, and it was extirpated locally up to today (Table 1).

There were differences in the coral community indices among three periods in this study (Table 1). All coral community indices declined in 2019. Additionally, the coral species composition in 2019 was already changed. In total, 73 scleractinian corals were unfound in this study [45] and the dominant coral species were mainly stress-tolerant species, such as species belonging to Poritidae and Merulinidae (Table 1; $p < 0.05$). In terms of the coral functional groups, the common coral growth forms were classed into five types: branching, encrusting, massive, foliaceous, and others in this study. Various coral lifeforms might have different adaptability towards physical environments and are also particularly vulnerable to a specific disturbance. Branching corals, especially *Acropora* and *Pocillopora* species, exhibit a high growth rate, but they are more susceptible to physical damages and cannot withstand the high current impact [45]. Although a few colonies of branching corals appeared in 2019 (Table 1), it is believed that the fast-growing branching corals can recolonize faster in unoccupied spaces created by disturbances. The foliaceous corals frequently appeared in the outer and inner reefs since they might have a stronger tolerance to higher seawater temperature, turbidity, and sedimentation, although they do seem to show a relatively moderate growth rate compared to branching corals (Table 1). For the slow-growing massive corals, they are usually found in the inner reefs, a more confined area with high suspended sediment loads. The massive or encrusting corals are resistant to a high seawater temperature, turbidity, sedimentation, and typhoon damages, since they possess more powerful mechanisms to remove sediment and can fight against mechanical breaks [46–50]. These stress-tolerant species are usually found as abundant in all communities, but they are only dominant in a high-stress environment where other coral lifeforms are mostly excluded [49,51,52]. On the other hand, the slow-growing massive corals have a lower spatial complexity and provide poorer fish habitat regarding supporting reef fish diversity. Recently, this has indeed become a common situation in the DA. The abundance of fishes and benthic invertebrates, especially those with commercial value, were low in most sites, suggesting that (1) the habitats were simplified; and (2) the DA was still under the threat of high fishing pressure [19,34,39,40,45]. The results from our SIMPER analysis also support this idea. It showed that the top six dominant species contributing to >80% were the encrusting and massive species in 2019, indicating the coral community was in a degraded state, and the original state or ecological function has been changed even though the DAMNP has already been established for five years (in 2012) and 12 years (in 2019).

It has been suggested that the crown-of-thorns starfish (COTS), a high sea surface temperature (SST), or coral bleaching and typhoons could serve as large-scale disturbances and thus exert considerable impact on coral reef ecosystems [46,53–55]. During the period of this study, the dramatic changes on the coral communities in the DA coincided with high seawater temperatures and typhoon

events, suggesting that they were the vital ecological parameters for the local reef community. Coral bleaching caused by high SST has traditionally been regarded as the most important factor to affect coral distribution, growth, fecundity, mortality, and the occurrence of disease or parasites [56–59]. Typhoons also had a considerable impact on the extensive changes in the coral reefs, and the coral damages caused by the typhoon waves could be very serious [36,60–63], especially on the reefs dominated by branching and tabulate corals [64–66]. Such extensive changes in reefs might also affect fish densities and coral-associated fish assemblages [67–70]. From our field observation, the density of parrotfish at some diving sites in the DA was preserved at a high level in 2019 [45]. Our result was partially similar to Russ et al. [71], suggesting that the density of parrotfish might increase after a hard coral loss caused by typhoon or bleaching events. The crown-of-thorns starfish is a voracious predator of live coral and has been recorded several times in the DAMNP waters [29,34]. However, the COTS rarely appeared nor reached the level of a population outbreak; indeed, the first case of a COTS outbreak was only recently reported at the DA [29]. There is no doubt that many physical and biological factors have influenced the spatial and temporal variation of the DA coral reefs. Nevertheless, overfishing and destructive fishing have played a significant role in reef degradation [19,27,34].

The result from a modeling study used to assess coral community persistence and resilience under different disturbance frequencies showed that shorter intervals between disturbances (every two years) would lead to a community that supported only a low level of soft coral, which the hard coral did not seem to benefit from [72]. Besides, in their report, two main points were also pointed out: (1) an eight-year disturbance frequency is suitable for coral recovery; (2) a longer interval between two disturbances (up to 16 years) may result in the monopolization of the fastest-growing corals. In the case of coral communities in the DA, we saw that the environment was no longer beneficial for hard corals due to shorter intervals between disturbances. The recurrent disturbances caused by natural disturbances and anthropogenic impacts may have a critical effect on shaping the structure and function of coral reef communities [73]. The surveys conducted from 2005 to 2019 showed that high proportions of the substrates were occupied by macroalgae, turf algae, or sediments. Algal communities would certainly undergo a rapid transition after disturbances [60,74–77]. The algae would not only reduce the survivability of corals but also inhibit the settlement of coral recruits and, finally, decrease the recovery potential of the coral communities [36,74,76,78]. From previous studies, we can see a low coral coverage and relatively high macroalgae coverage in the inner reefs, which suggests that the communities were in the process of phase-shifting from a coral-dominant to seaweed-dominant ecosystem, and this represents a low resilience ecosystem [27,28,79]. From our present study, we also found a dramatic change where the dominant coral type in the DA has suddenly changed from branching corals to massive or encrusting corals, within merely 5 to 10 years.

Recently, the accelerating rates of coral loss in the DA have increased the need for effective management that can improve ecosystem resilience. In the independent island reefs, local fisheries' management actions can increase the resilience of coral reef ecosystems and thus improve their recovery potential from major disturbances [80,81]. Limiting the algal abundance can also improve the capacity of coral reefs to remain coral-dominant [82]. In the short-term, we suggest protecting the herbivorous fish that graze on macroalgae since this may contribute to faster coral recovery [80]. Protection from fishing and reducing impacts for five years following a disturbance might also speed up the recovery rate [9]. In the long-term, an ecosystem-based management approach will be successful if the ecosystem's function and structure driving process is known and managed. In the future, more research will be needed for a more comprehensive understanding of the DA ecosystem. The recovery and dynamics of coral communities following the disturbances also need to be continually monitored. Long-term monitoring and research projects with fixed monitoring sites are essential to understand ecological changes. The marine ecosystem baseline and ecosystem valuation should be ascertained as soon as possible in order to support future management actions of the DAMNP. Moreover, adequate management or planning that is in accordance with the actual situation of the marine resources are also needed. The revision of laws and effective management have to be planned

and discussed by governmental administrations. There are numerous things to be done: the laws need to be revised, the environmental penalties have to be raised, and the regulations need to be enforced so we can better prevent human harm to the environment. Otherwise, the DA coral reef ecosystem would be unrecoverable in the future.

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Appendix A

Table A1. Information of the survey locations conducted in 2006 (before the Dongsha Atoll Marine National Park was established), 2012 (established for 5 years), and 2019 (established for 12 years).

Name of Locations	Sector	Date	Longitude and Latitude		Depth	Reference
06-1	outer reef	2006/7/21	20°35'10.00" N	116°47'50.40" E	10–15 m	Jeng 2006 [38]
06-2	outer reef	2006/7/21	20°35'23.60" N	116°49'22.40" E	10–15 m	Jeng 2006 [38]
06-3	outer reef	2006/7/22	20°46'51.20" N	116°48'28.10" E	11–14 m	Jeng 2006 [38]
06-4	outer reef	2006/7/22	20°46'48.30" N	116°51'40.60" E	10–12 m	Jeng 2006 [38]
06-5	outer reef	2006/7/23	20°42'58.40" N	116°42'14.30" E	12–16 m	Jeng 2006 [38]
06-6	inner reef	2006/7/23	20°42'09.70" N	116°52'02.40" E	13–14 m	Jeng 2006 [38]
06-7	inner reef	2006/8/26	20°42'12.40" N	116°48'17.20" E	5–11 m	Jeng 2006 [38]
06-8	inner reef	2006/8/26	20°39'56.90" N	116°47'57.50" E	14–15 m	Jeng 2006 [38]
06-9	outer reef	2006/8/27	20°40'29.80" N	116°55'25.80" E	10–12 m	Jeng 2006 [38]
06-10	outer reef	2006/8/27	20°44'31.60" N	116°54'46.30" E	12–18 m	Jeng 2006 [38]
06-11	inner reef	2006/8/29	20°41'54.70" N	116°46'51.10" E	17–23 m	Jeng 2006 [38]
06-12	inner reef	2006/8/30	20°41'42.50" N	116°44'46.60" E	4–6 m	Jeng 2006 [38]
06-13	inner reef	2006/9/25	20°43'10.50" N	116°44'13.30" E	4–5 m	Jeng 2006 [38]
06-14	inner reef	2006/9/27	20°40'00.80" N	116°46'01.10" E	6–8 m	Jeng 2006 [38]
06-A	inner reef	2006/8/28	20°42'48.20" N	116°42'20.50" E	3–6 m	Jeng 2006 [38]
06-B	inner reef	2006/8/29	20°43'10.50" N	116°44'12.70" E	4–6 m	Jeng 2006 [38]
12-01	inner reef	2012.04.27	20°41'47.73" N	116°44'49.32" E	6–11 m	Dai 2012 [34]
12-04	inner reef	2012.04.30	20°39'29.26" N	116°45'33.84" E	9 m	Dai 2012 [34]
12-05	inner reef	2012.05.01	20°41'46.07" N	116°47'05.24" E	6–12 m	Dai 2012 [34]
12-08	outer reef	2012.06.08	20°46'47.47" N	116°48'25.28" E	7–10 m	Dai 2012 [34]
12-11	inner reef	2012.07.15	20°41'13.20" N	116°49'55.61" E	7–13 m	Dai 2012 [34]
12-12	inner reef	2012.07.16	20°43'16.31" N	116°44'09.24" E	4–5 m	Dai 2012 [34]
12-16	inner reef	2012.09.07	20°44'32.69" N	116°51'54.38" E	7–10 m	Dai 2012 [34]
12-17	inner reef	2012.09.09	20°38'30.36" N	116°49'30.90" E	8–12 m	Dai 2012 [34]
12-20	inner reef	2012.09.10	20°42'20.35" N	116°42'04.82" E	5–6 m	Dai 2012 [34]
12-23	outer reef	2012.09.12	20°38'24.95" N	116°42'00.65" E	14–16 m	Dai 2012 [34]

Table A1. Cont.

Name of Locations	Sector	Date	Longitude and Latitude		Depth	Reference
12-01	inner reef	2019/8/31	20°41'47.72" N	116°44'49.31" E	7–8.5 m	This study
12-04	inner reef	2019/4/23	20°39'29.24" N	116°45'33.84" E	8–10 m	This study
12-05	inner reef	2019/4/17	20°41'46.06" N	116°47'05.23" E	7–11 m	This study
12-08	outer reef	2019/4/19	20°46'47.46" N	116°48'25.27" E	9–11 m	This study
12-11	inner reef	2019/4/17	20°41'13.19" N	116°49'55.60" E	12–14 m	This study
12-12	inner reef	2019/8/31	20°43'16.30" N	116°44'09.24" E	4–5 m	This study
12-16	inner reef	2019/8/30	20°44'32.68" N	116°51'54.37" E	5–7 m	This study
12-17	inner reef	2019/8/30	20°38'30.36" N	116°49'30.89" E	6.5–8.5 m	This study
12-20	inner reef	2019/4/23	20°42'20.34" N	116°42'04.81" E	5–6 m	This study
12-23	outer reef	2019/4/21	20°38'24.94" N	116°42'00.64" E	13–15 m	This study
19-01	outer reef	2019/4/19	20°46'42.00" N	116°53'08.22" E	9–10 m	This study
19-02	outer reef	2019/4/22	20°38'55.97" N	116°54'51.29" E	9.7–10.5 m	This study
19-03	outer reef	2019/4/21	20°35'26.28" N	116°49'36.54" E	9–11 m	This study
19-05	inner reef	2019/8/30	20°43'34.43" N	116°51'39.17" E	6–8 m	This study

Appendix B

Table A2. Information of the 11 typhoons (based on a 50 km radius) that passed through the Dongsha area from 2005 to 2019.

Number	Date	Name	Maximum Wind (knots)	Average Speed	Min Pressure (hPa)
1	2005/09	DAMREY	80	14.7 (km/h) 351 (km/d)	955
2	2008/08	NURI	75	20.7 (km/h) 495 (km/d)	955
3	2008/09	HAGUPIT	90	23.6 (km/h) 565 (km/d)	935
4	2010/08	LIONROCK	50	9.9 (km/h) 238 (km/d)	985
5	2012/06	TALIM	50	15.8 (km/h) 378 (km/d)	985
6	2012/08	TEMBIN	80	14.7 (km/h) 353 (km/d)	950
7	2016/10	AERE	60	10.2 (km/h) 245 (km/d)	975
8	2016/10	HAIMA	115	23.7 (km/h) 569 (km/d)	900
9	2018/09	MANGKHUT	110	28.0 (km/h) 671 (km/d)	905
10	2018/09	BARIJAT	40	18.0 (km/h) 431 (km/d)	998
11	2018/11	YUTU	115	17.8 (km/h) 427 (km/d)	900

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