RESEARCH ARTICLE
doi: 10.2306/scienceasia1513-1874.2025.005

*ScienceAsia* 51 (1): 2025: ID 2025005: **1–8**

# Herbivory influences coral-algal abundance and dynamics in different degrees of coral bleaching on a tropical subtidal reef community

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*Received 3 Jun 2024, Accepted 22 Oct 2024*
*Available online 15 Feb 2025*

**ABSTRACT**: Effect of herbivory on coral-algal community dynamics was experimentally investigated at the tropical subtidal reef crest using cages (uncaged and fully caged treatments) in different degrees of coral bleaching (healthy, bleached, and severely bleached). Cover, recruitment, and succession of coral and algae were monitored. In this study, twenty-three algal species were encountered, comprising three dominant groups: red turf algae, *Padina* sp., and *Lobophora variegata*. Red turf algae were dominant and persisted in bleached and severely bleached plots for a year. The results showed that herbivory had significant effects on the cover of algae and might contribute to differences in algal composition and abundance. There was significant difference in percent cover of *Padina* between caged and uncaged plots. The foliose form of *Padina* was dominant inside the cages while the *Vaughaniella* stage of *Padina* developed high percent covers on uncaged patches. It might be because *Padina* inside the cages had less grazing pressure from territorial damselfishes and other herbivorous fishes than thalli outside the cages. Therefore, the foliose form of *Padina* had greater cover in full cages than open cages. As expected, the percent cover of coral in the caged plots was lower than in uncaged plots. Coral juveniles settled in the severely bleached plots within one month and then disappeared. From this study, herbivory likely plays important roles in coral-algal abundance; however, the impact of herbivory varies according to degrees of coral bleaching that might also directly or indirectly influence coral-algal community dynamics and coral recovery.

**KEYWORDS**: algal succession, coral bleaching, disturbance, overfishing, turf algae

## INTRODUCTION

Coral reefs are one of the most important marine ecosystems providing ecosystem services that comprise fisheries, food-security, recreation, tourism, and coastal protection [1], but, worldwide, coral reefs are vulnerable. Around 50% of reefs have become degraded due to natural and anthropogenic disturbances such as ocean warming and acidification, pollution, careless tourism, sediment run-off, and coral bleaching [2–5]. The degradation of coral reefs has resulted in biodiversity loss, coral mortality, and the increasing occurrence of phase shifts from coral- to macroalgal-dominated reefs [3, 6, 7]. These disturbances can influence reef community dynamics, reducing coral-algal abundance, species richness, complexity, and species composition [8, 9].

The phenomenon of coral bleaching was reported as a major cause of coral reef degradation [3, 9, 10]. Mass bleaching has been taking place for decades and is predicted to become more frequent [3, 12]. Coral bleaching leaves dead coral skeletons that provide a substrate for algae to colonize [6, 13]. Colonizing algae might inhibit coral settlement, coral growth, and coral physiology and delay the regeneration of coral tissue [14–16]. At that point, the reef has shifted from coral- to algal-dominated communities [3, 12, 17]. However, algal successional patterns and population dynamics in tropical subtidal bleached coral reef communities are not well understood. Additionally, the ability and potential of reef communities to recover from the disturbance are still unclear. Many studies have suggested that bleached corals have different recovery abilities depending on the severity of the disturbance to the reef ecosystem [6, 18].

Loss of herbivory has been put forward as one of the factors that drives phase shifts from coral- to algal-dominated communities on tropical reefs [13]. Herbivores play an important role in coral reef communities. By grazing their preferred algal species, they decrease the abundance, standing stock and diversity of algae and alter algal succession [19, 20]. However, overfishing has severely reduced populations of herbivorous fishes all over the world. Consequently, grazing on coral reefs has declined, and then reefs are overgrown by macroalgae [21]. Macroalgae degrade reefs by suppressing coral cover, growth, and reproduction, inhibiting coral recruitment and settlement, and triggering coral diseases [6, 14, 22].

The differences in rates of herbivory might have direct and indirect impacts on coral-algal community dynamics and coral recovery. To predict and manage coral reefs, it is necessary to understand coral-algal community dynamics after coral disturbances, to unravel the impacts of herbivory and to assess the potential of reefs to recover from disturbances. Thus, the aim of this study was to determine the influences of herbivory on coral-algal abundance and dynamics in a tropical subtidal reef community.

## MATERIALS AND METHODS

### Study sites

The study was carried out at the subtidal reef crest at Ko Tan, Mu Ko Thale Tai National Park, (9°19′20″ N, 99°46′80″ E), Gulf of Thailand, Southern Thailand (Fig. 1). There are 2 seasons in this location: a rainy season dominated by the northeast monsoon from October–January and a dry season dominated by the southwest monsoon from February–September. The tides are semi-diurnal with a range of about 0.8–3.0 m [23]. In this area, approximately 60 species of benthic algae have been reported, including 23 species of Chlorophyta, 19 species of Phaeophyceae, 16 species of Rhodophyta, and 2 species of Cyanobacteria [23, 24]. Four common genera were represented: red turf algae, *Padina*, *Sargassum*, and *Turbinaria*. Among the corals on the reef, the massive coral of the genus *Porites lutea* was dominant. Moreover, other coral species had been found in this study site including *Montipora digitata*, *Pavona frondifera*, *Pocillopora damicornis*, and *Fungia fungites*. *Abudefduf vaigiensis*, *Abudefduf bengalensis*, *Abudefduf sexfacsiatus*, and *Neoglyphidodon nigroris* were the dominant herbivorous fish species at this study site. *Diadema setosum* was observed on reef slope. Light intensity and temperature of this study area were 4,176.97 ± 556.97 µmol photon/m/s and 33.67 ± 0.45 °C, respectively.

### Sampling design and method

The effect of herbivore exclusion on coral-algal community dynamics was experimentally investigated in 3 different coral conditions, after the mass coral bleaching event in the Gulf of Thailand in 2016, resulting in 18% of coral mortality [25]. From our preliminary survey, we found many bleached corals in this study site, and there was around 10% cover of live *P. lutea* in the bleaching coral areas. Then, 3 different reef conditions in this study were categorized: 1) healthy (initially having 100% cover of live *P. lutea*), 2) bleached (10% cover of *P. lutea*), and 3) severely bleached patches (100% cover of dead *P. lutea* with no algal colonization). A total of 48 coral patches ($20 \times 20$ cm$^2$) were delineated and permanently marked using thread and concrete nails. Sixteen patches were permanently marked using labeled thread at each bleaching category (contained the same coral species). Each patch was around 5 m apart.

To investigate the effect of herbivory, patches were fully caged and uncaged (cage size was $25 \times 25 \times 25$ cm$^3$). Eight of each bleaching category were caged, and another 8 patches were left uncaged. Cages made of a stainless-steel frame covered with wire mesh (size of $2 \times 2$ cm$^2$) were used to exclude herbivores. In order to test cage artifacts, light intensity and wave motion inside and outside cages were measured using a HOBO data logger (Pendant® Temperature and light data logger Model: UA-002-64, Onset Computer Corporation, USA) and a gypsum ball [24]. Cages decreased light intensity and water motion by around 3.78 ± 18.85% and 0.79 ± 0.53%, respectively, compared with uncaged patches. The light intensity and water motion between caged and uncaged patches were not significantly different ($t$-test, $p = 0.510$ and $p = 0.950$, respectively). Then, partial cages were not used in this study, and these slightly lower light intensity and slower water motion might not affect algae inside cages [26, 27].

Cages were fixed to the top of massive coral patches with concrete nails and plastic cable ties. Cages were cleaned of algae, sediment, and settling organisms every month using a wire brush. In all patches, percent covers of algae and coral were monitored every month from May 2017 to May 2018 using quadrats of the same size as the experimental plots ($2 \times 2$ cm$^2$ subplots). All patches were photographed using an underwater digital camera (Olympus TG-5, Japan). Unknown algal specimens were collected and taken to the laboratory for identification using algal taxonomical identification guides from Coppejans et al [23].

### Data analysis

T-tests and Mann-Whitney U-test were used to test the effect of herbivory on the percent covers of coral and 3 algal dominant species and coral-algal species diversity of all different bleaching treatments. Normal distribution and data homogenization were tested with Shapiro-Wilk and Levene's test. Species diversity was calculated using the Shannon-Weiner index. Light intensity and water velocity outside and inside cages were tested by $t$-test. All data were analyzed using SPSS version 16.0 for Windows. The difference in coral-algal species composition between caged and uncaged in all different bleaching was visualized using Principal component analysis (PCA) and tested with permutational multivariate analysis of variance (PERMANOVA) with Past version 4.03.

## RESULTS

A total of 26 algal species were found in this study, including 11 Rhodophyta, 6 Chlorophyta, 6 Phaeophyceae, and 2 Cyanobacteria (Table 1). There were differences in algal composition and abundance between the different coral bleaching categories. Species diversity was around 0.07–1.19, and the highest algal species diversity was found in the bleached treatment (10% cover of live coral tissue) ($H' = 2.16$). Meanwhile, species diversity was lowest on the healthy coral

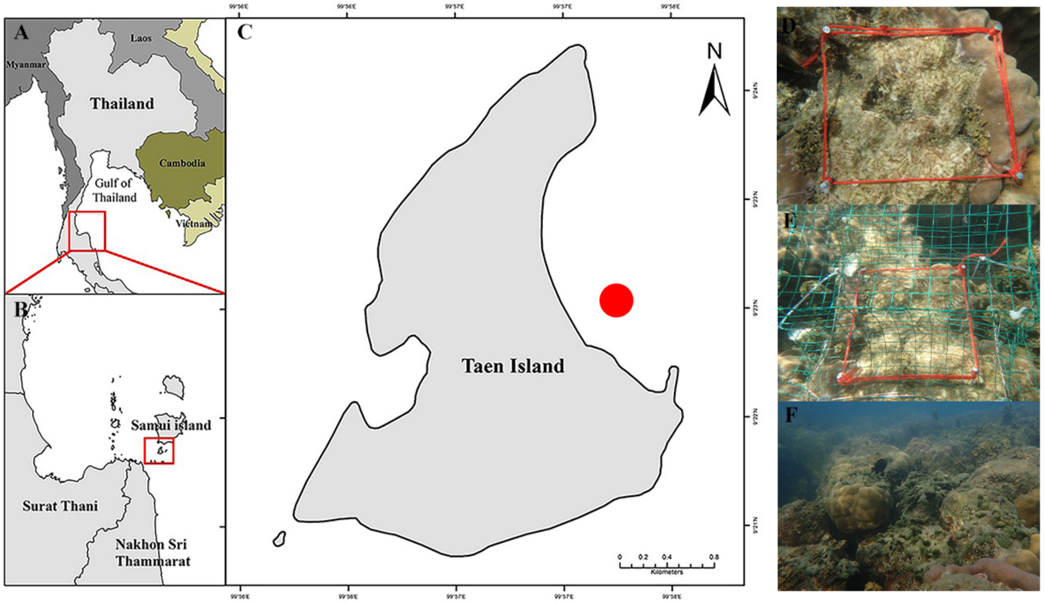

**Fig. 1** Maps of Thailand (A), Samui Island (B), and Taen Island (C). The study area was located at 9°19′20″ N, 99°46′80″ E. The photographs showing uncaged patch (D), caged patch (E), and the benthic community structure in study site (F).

**Table 1** Algal species list and the occurrence on each shore and site.

| Taxa | Uncaged | | | Caged | | |
|---|---|---|---|---|---|---|
| | Healthy | Bleached | Severely Bleached | Healthy | Bleached | Severely Bleached |
| **Phylum Chlorophyta** | | | | | | |
| *Caulerpa verticillata* | – | – | – | – | * | * |
| *Dictyosphaeria* sp. | – | * | * | – | * | * |
| *Parvocaulis* sp. | – | * | * | * | * | * |
| *Rhipidosiphon javensis* | – | * | * | – | * | * |
| *Ulva compressa* | * | *** | *** | * | ** | ** |
| **Phylum Rhodophyta** | | | | | | |
| *Amphiroa* sp. | – | – | – | – | * | – |
| *Acanthrophora* sp. | – | – | – | - | * | – |
| *Ceratodictyon spongiosum* | – | * | * | – | * | * |
| *Champia* sp. | – | * | – | – | – | * |
| *Gelidiella* sp. | – | – | – | – | – | * |
| *Gelidium pusillum* | – | * | * | – | * | * |
| *Gracilaria* sp. | – | – | – | – | – | * |
| *Hypnea* sp. | – | * | – | * | * | * |
| *Hypnea pannosa* | – | * | – | – | * | * |
| *Hypnea spinella* | – | – | – | – | * | * |
| Crustose coralline algae | – | * | * | – | * | * |
| Red turf algae | * | ******** | ******* | * | ******** | ***** |
| **Class Phaeophycaea** | | | | | | |
| *Dictyota* sp. | – | * | – | – | * | – |
| *Lobophora variegata* | – | ** | ** | * | * | ** |
| *Padina* sp. | * | ** | *** | * | **** | ******** |
| *Sagrassum* sp. | – | * | * | – | * | * |
| *Sphacelaria* sp. | – | ** | ** | * | * | * |
| *Turbinaria decurrens* | – | * | * | – | * | * |
| *Turbinaria ornata* | – | ** | * | – | * | * |
| **Cyanobacteria** | | | | | | |
| Cyanobacteria sp. 1 | – | * | * | – | – | – |
| Cyanobacteria sp. 2 | – | * | – | – | * | * |

********: 36–40%; *******: 31–35%; ******: 26–30%; *****: 21–25%; ****: 16–20%; ***: 11–15%; **: 6–10%; *: 1–5%; and –: no occurrence.

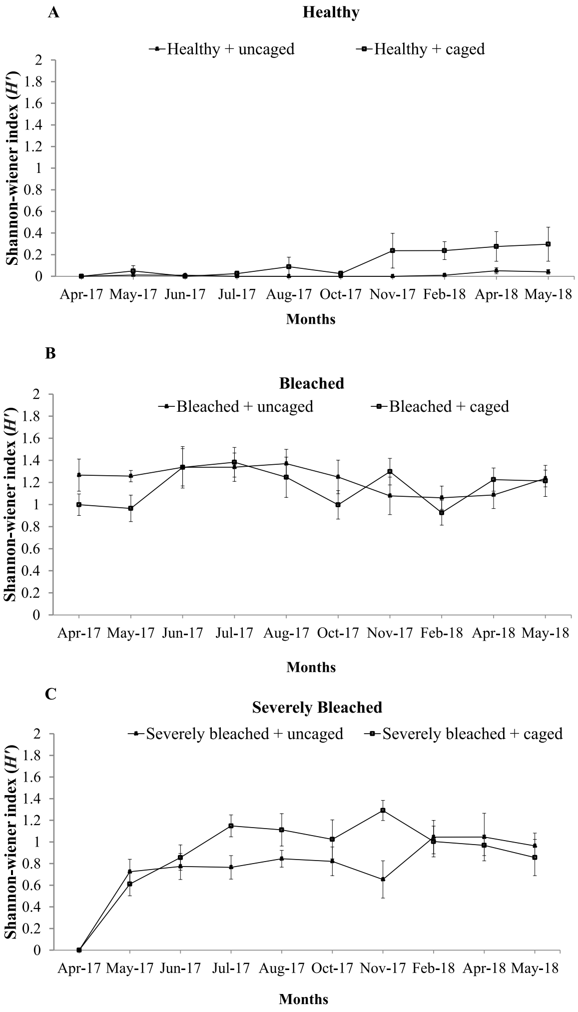

**Fig. 2** Species diversity (measured by the Shannon Wiener index) of coral-algal community in caged and uncaged patches of different coral bleaching treatments from April 2017 to May 2018. Healthy (A), bleached (B), and severely bleached patches (C).

patches (Fig. 2).

For the herbivory effect on coral-algal community dynamics at different degrees of bleaching, there was a significantly higher coral-algal species diversity in caged compared with uncaged patches of the healthy coral ($p = 0.006$) (Fig. 2A). For the massive coral on healthy patches, *Porites* was common and presented the highest cover in uncaged patches, consistently maintaining coverage of around 100% over the year (Fig. 3A). The cover of *Porites* in caged patches slightly decreased after one month of study and remained at nearly 90% throughout the year (Fig. 3B). In addition, there was a significantly higher coral cover in uncaged compared with caged patches ($p = 0.001$). On the healthy coral patches, red turf algae and *Padina* in the *Vaughaniella* stage occupied the patches with cages during 5 months of study (Fig. 3B). However, there were no significant differences in the composition of macroalgae and coral between caged and uncaged treatments ($p = 0.068$) (Fig. 4A).

In the bleached patches, there was no significant difference in algal species diversity between caged and uncaged patches ($p = 0.252$). Species diversity in the uncaged patches increased continuously from April 2017 to August 2017 and showed the highest diversity ($H'$) of around 1.37 and decreased afterward (Fig. 2B). In the caged patches, species diversity increased steadily from the first month and reached 1.30 in November 2017. Red turf algae, *Padina* sp., and *Lobophora variegata* (J.V. Lamouroux) Womersley ex E.C. Oliveira were the first group of colonizers, and they persisted until the end of this study (Fig. 3C,D). Red turf algae predominated in uncaged and caged patches with average percent covers of around 37.91 ± 2.82% and 37.28 ± 3.12%, respectively (Fig. 3C,D). It was similar in the cover of red turf algae between caged and uncaged treatments ($p = 0.778$). Herbivory had a significant effect on the percent cover of *Padina* ($p = 0.041$). A significant effect of herbivory on the percent cover of *Padina* was suggested by higher coverage in the caged patches than in the uncaged patches over the year (Fig. 3C,D). For *L. variegata*, the cover was significantly higher in uncaged compared with caged patches ($p = 0.003$). The percent cover of *Porites* showed a significant difference between caged and uncaged patches ($p = 0.0001$). The cover of *Porites* in the uncaged patches remained at nearly 10% throughout the year but decreased significantly in the caged patches to 4.50 ± 1.20% by May 2018 (Fig. 3C,D). For coral-algal species composition, there were no significant differences between caged and uncaged patches ($p = 0.0109$) (Fig. 4B).

In the severely bleached patches, there was no significant difference in algal species diversity between caged and uncaged patches ($p = 0.069$). Species diversity increased rapidly after one month of study and fluctuated throughout the year. The highest species diversity was found in the caged patches ($H' = 1.76$) (Fig. 2C). In these severely bleached patches, the first 3 dominant algal species recruited in the plots were the red turf algae, *Padina* in the *Vaughaniella* stage, and *L. variegata*. In the uncaged patches, the red turf algae were the first colonizer, became the dominant species, and persisted in these patches throughout the year, covering around 32.08 ± 3.61%. The cover of red turf algae reached 63.00 ± 13.00% in November 2017 (Fig. 3E). There was a significantly higher abundance of red turf algae in uncaged patches than in caged patches ($p = 0.025$). The average cover of red turf algae in uncaged and caged was 32.08 ± 3.61% and 22.19 ± 2.98%, respectively. In the caged patches, meanwhile, *Padina* sp. was the dominant algal group,

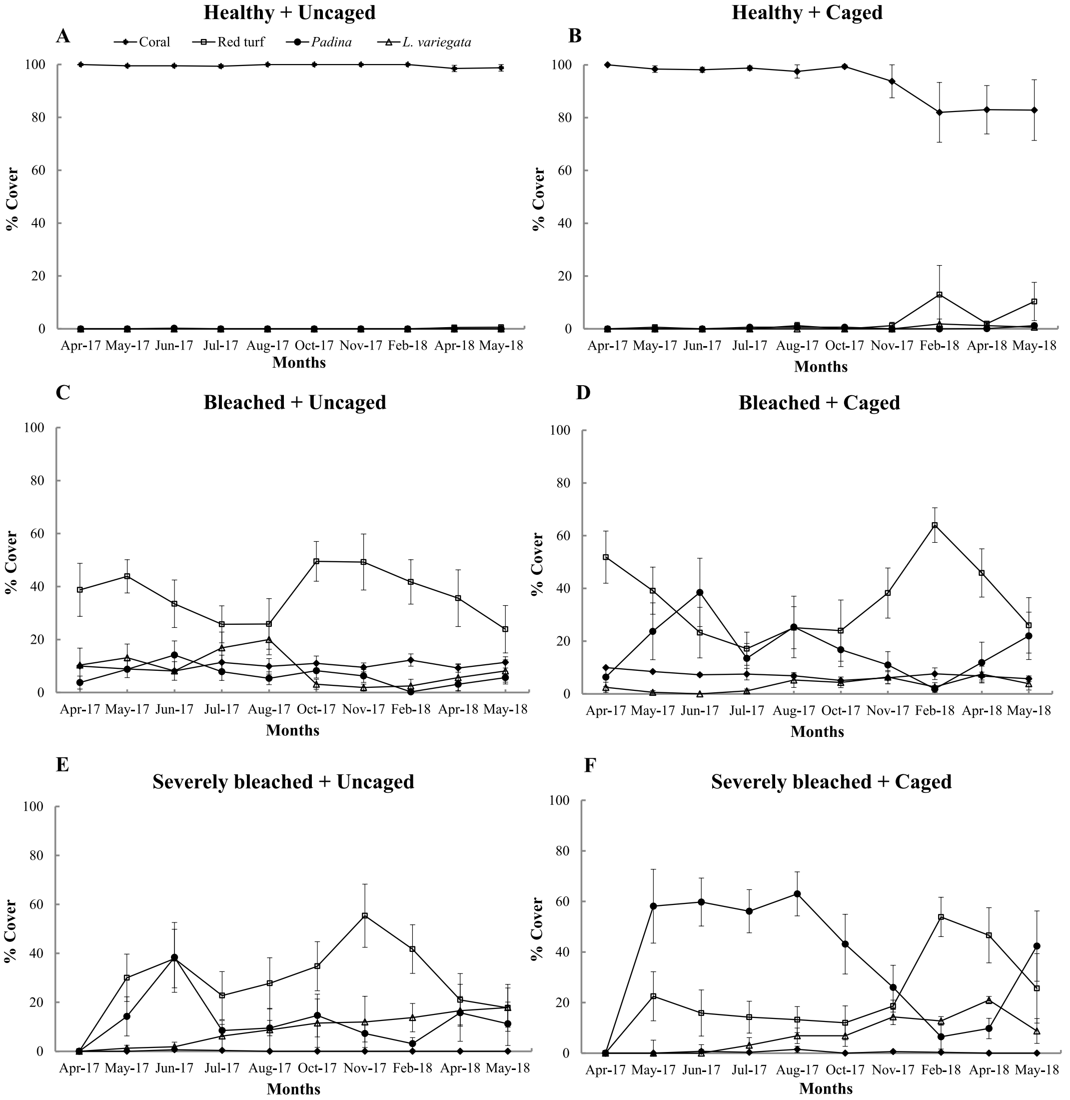

**Fig. 3** The charts showing percent covers of coral and 3 dominant benthic algae on bare substrate and coral in healthy, bleached, and severely bleached patches from April 2017 to May 2018 (mean ± S.E., $n = 8$). (◆ = Coral, □ = Red turf, ● = *Padina* sp., and △ = *L. variegata*).

occupying 58.12 ± 14.60% after the first month of study and increased to the highest abundance (63.00 ± 8.68%) in August 2017 (Fig. 3F). The percent cover of *Padina* was significantly higher in the caged patches than in the uncaged patches ($p = 0.0001$). The foliose form of *Padina* was found in the caged patches while the filamentous or turf form, *Vaughaniella* stage was found in the uncaged patches. The percent cover of *L. variegata* increased over a year but was never more than 20%. The coverage of this species did not significantly differ between herbivory treatments ($p = 0.807$). The settlement of coral juveniles was found in both caged and uncaged patches with coverage of less than 1% and disappeared after 2 months (Fig. 3E,F). For coral-algal species composition, there were significant differences between caged and uncaged patches ($p = 0.0007$) (Fig. 4C).

## DISCUSSION

In this study, the bleached corals were colonized and overgrown by turf and fleshy algae and then followed by *Padina* in the *Vaughaniella* stage and *L. variegata*. Algal colonization in this study showed a simple pattern [6, 28]. The first colonizer, red turf algae, achieved a high relative abundance and persisted over the year because they are competitive and have a fast growth rate and a high total reproductive capacity, producing large numbers of propagules throughout the year [6, 29, 30]. In addition, the rapid colonization by this species might reduce the growth

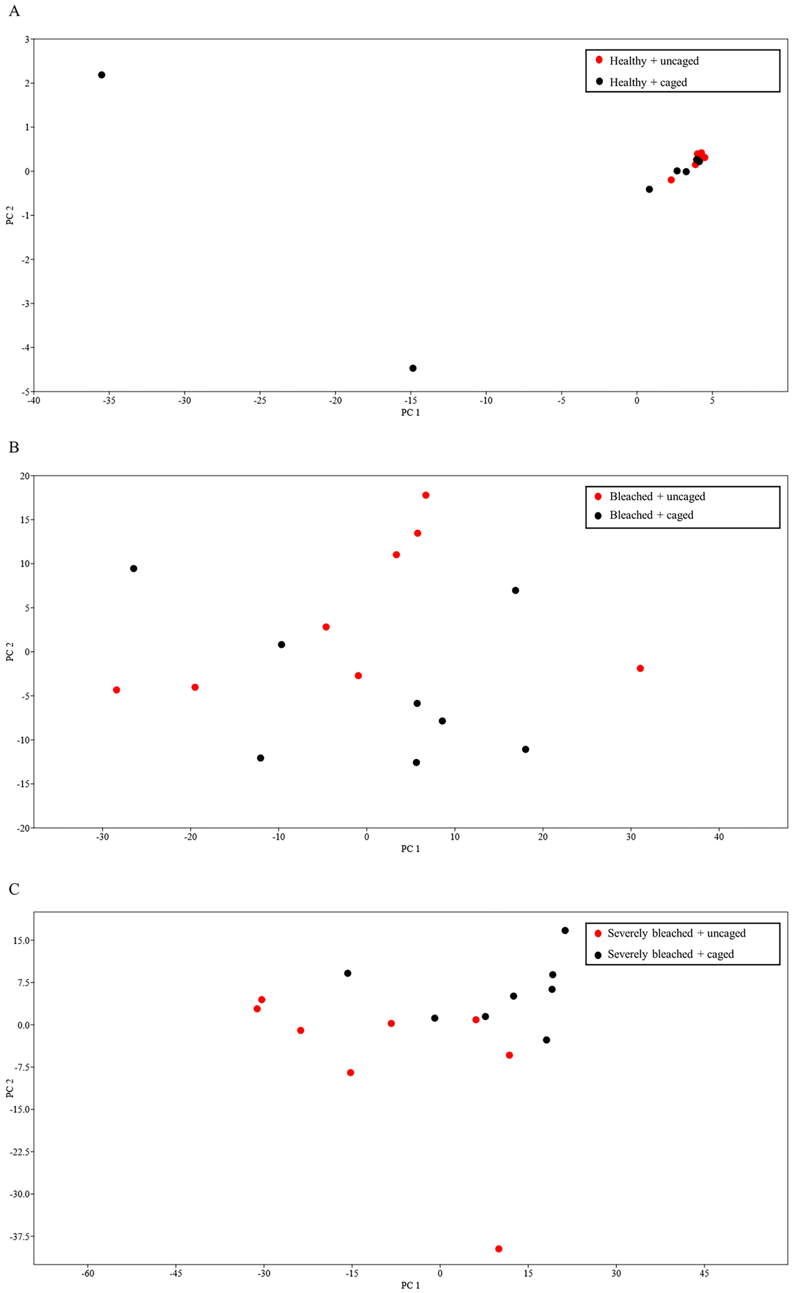

**Fig. 4** Principal component analysis (PCA) of coral-algal species composition in caged and uncaged patches of 3 different coral bleaching treatments. Healthy (A), bleached (B), and severely bleached patches (C).

rate and inhibit settlement and colonization of later species [14, 31, 32]. The later colonists, *Padina* in the *Vaughaniella* stage and *L. variegata*, might be slower colonizers and have slower growth rates compared with red turf algae [28].

Algae were less common in healthy coral patches with the highest cover, around 5%. It might be because corals can produce a mucus layer that serves as a defensive mechanism against algal colonization [33]. So, the live corals in the healthy patches were not easily overgrown by algae unlike the dead corals in the heavily bleached patches. A study by Diaz-Pulido and McCook [6] showed that algal cover in healthy coral patches was never more than 5%. However, turf algae and filamentous algae rapidly colonized bleached and severely bleached plots and persisted for a long period. Persistent colonization can result in shifts from coral-dominated to algae-dominated communities. Previous studies found that increasing macroalgal abundance could inhibit coral settlement and decrease coral growth rate, reproduction, and survivorship [14, 22, 34], but variations occurred in algal composition and abundance between different bleaching treatments, depending on the severity of bleaching, availability of algal propagules, and herbivory [6, 28, 30].

For the effect of herbivory on coral-algal community, the results from this study showed that herbivory had significant effects on the cover of *Padina* and *L. variegata* and might contribute to differences in algal composition and abundance. Among brown macroalgae, the percent cover of *Padina* and *L. variegata* was higher in the caged patches than the uncaged patches. In addition, the foliose form of *Padina* was found in the caged patches while the filamentous or turf form, *Vaughaniella* stage was found in the uncaged patches, where grazing could directly affect algal abundance and form [13, 19, 28, 30]. This result showed that herbivory regulated the morphological plasticity of *Padina*. Many studies reported that this morphological plasticity is a phenotypic response to different levels of grazing pressure and *Padina* can change from a turf to a foliose form when grazing pressure is low [28, 35]. The abundance of red turf algae was significantly higher in uncaged, severely bleached patches. This might be because there were benthic-feeding herbivorous damselfishes of the genus *Neoglyphidodon nigroris* in this area. The dominance of this damselfish might influence the abundance of red turf algae in uncaged patches since these fishes exhibit aggressive territorial behavior that can drive away other herbivorous species [28, 36]. In addition, damselfishes can maintain their favorite red filamentous algae in their territories by eliminating other algal groups from their algal farms [36, 37]. Studies by Ceccarelli et al [38] and Mayakun et al [28] also found that turf and filamentous algae dominated inside the territory of damselfishes as they did outside. Damselfishes maintained the red turf algae in their territories because the red turf algae have the necessary rich nutrition and aid digestion [39]. However, the composition of algal species differed among damselfish territories depending on the feeding habits of the species [36].

Grazing can influence algal recruitment, abundance, and succession [20, 28]. Rates of herbivory on coral at different stages of bleaching might have direct and indirect impacts on coral-algal community dynamics and coral recovery. Reduced herbivory due to overfishing could increase algal abundance and result in the overgrowth of algae, which inhibited coral settlement and recruitment [14, 34]. These conditions also can trigger coral disease, leading to coral degradation and eventual mortality [40]. From that point, coral-to-algal phase shifts might take place.

## CONCLUSION

This work studied the effect of herbivory on coral-algal community dynamics in different coral bleaching conditions on a tropical subtidal reef community. The significant effect of herbivory on the abundance of *Padina* in the *Vaughaniella* stage was revealed along with the possible contribution of herbivory to differences in algal composition and abundance. Herbivory likely plays important roles in coral-algal abundance; however, this impact of herbivory varies according to degrees of coral bleaching that might also directly or indirectly influence coral-algal community dynamics. However, the effect of herbivory on coral-algal community dynamics in different coral bleaching conditions requires more replication in other sites with the same experimental design in Thai waters and long-term monitoring. Future work should investigate the impact of herbivory on the patterns of coral-algal succession.

*Acknowledgements*: This research was funded by Science Achievement Scholarship of Thailand (SAST) and the Graduated school, Prince of Songkla University. Scuba diving equipment and sample collection was supported by Seaweed and Seagrass Research Unit, and Division of Biological Science, Prince of Songkla University. The authors thank Mr. Thomas Duncan Coyne for assistance with the English text.

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