JMLS
한국해양생명과학회지[Journal of Marine Life Science]
December 2021; 6(2): 117-123
https://dx.doi.org/10.23005/ksmls.2021.6.2.117
http://jmls.or.kr

[Article]

Post-disturbance Recovery Pattern in the Soft Corals-Macroalgae Mixed Habitat in Jeju Island, Korea

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Received : November 29, 2021
Revised : December 02, 2021
Accepted : December 03, 2021

Post-disturbance recovery pattern of subtidal soft corals-macroalgae mixed community and the role of water depth were investigated. The experiment was conducted in a subtidal rock wall of Munseom, Jeju Island, Korea for 2.5 years. Artificial disturbance was done at established treatment plots at depths of 10, 15 and 20 m and were then compared with undisturbed control plots. After disturbance, recovery of soft corals was very slow, whereas macroalgae quickly occupied the plots and reached a similar level as the control in 6 months, and this pattern was consistent at all water depths. This unbalanced speed of recovery caused higher macroalgae establishment than soft corals in treatment compared to control plots, indicating a possible phase shift in the community structure. This study provides an important implication for the necessity of monitoring the influence of disturbance at a larger scale, from a conservation perspective of soft corals in Jeju coast.

Keywords: Disturbance, *Ecklonia*, Recovery, Soft coral, Subtidal

Introduction

In marine benthic habitats, physical disturbance causes a rapid decrease in living biomass and leads to changes in community structure during recovery process (Sousa, 1984; Pickett and White, 1985). Disturbance creates a new space and causes succession which starts with the settlement of opportunistic species resulting in the later recolonization of various species. This can lead to a different community assemblage or a return to the pre-disturbed assemblage (Levin and Paine, 1974; Glitzenstein et al., 1986; Cifuentes et al., 2007; Yang and Kim, 2021). In this respect, understanding post-disturbance events is considered an important tool for characterizing various community parameters such as diversity, dominance, structure, and stability in marine benthic habitats (Emslie et al., 2008; Aquilino and Stachowicz, 2012; Kang et al., 2019).

In coral communities, many efforts have been done focusing on community resilience after disturbance events, but most research was carried out in hard coral communities (Hughes, 1994; Wakeford et al., 2008; De'ath et al., 2012), with a few research done in soft coral communities (Madeira et al., 2015; Lopes et al., 2018). Furthermore, unlike coral reefs in tropical regions, soft coral communities in temperate regions often have overlapped habitats with seaweeds, which may imply a more complex process in a post-disturbance event. Linares et al. (2012) reported the possibility that seaweeds might inhibit the recruitment and juvenile survival of soft corals where the two groups shared habitats. However, not much information is available about the ability of soft corals and seaweeds to occupy new space or their competition for space, and thus there is scarce experimental evidence.

Jeju Island, Korea, is one of the rarest habitats of soft corals in the world and its coastal area provides a unique habitat where seaweed and soft coral communities are mixed and commonly distributed along the vertical rock walls sharing the same depth zone (Kang et al., 2005). In this study, we investigated the patterns of post-disturbance recovery of the two groups as the function of water depth. We also discuss the stability and conservation perspectives of soft coral communities in Jeju Island where seasonal typhoons are common disturbance factors.

Materials and Methods

1. Study site

This study was conducted in the subtidal zone of Munseom in

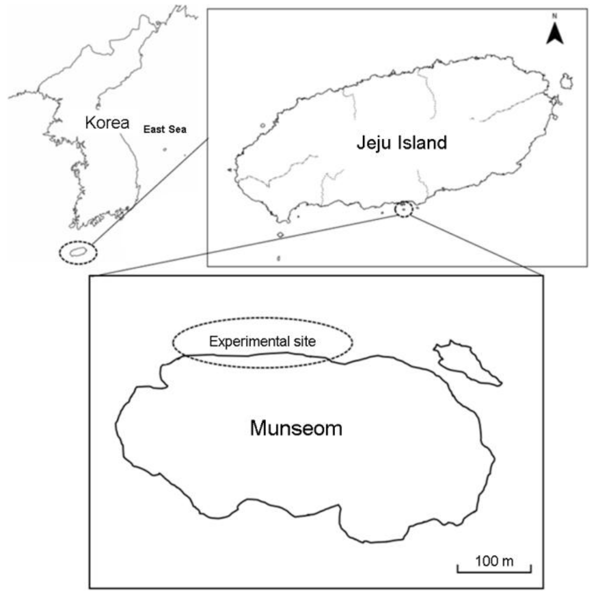

Fig. 1. The location of study site. Munseom, Jeju Island, Korea (33°13'N, 126°34'E).

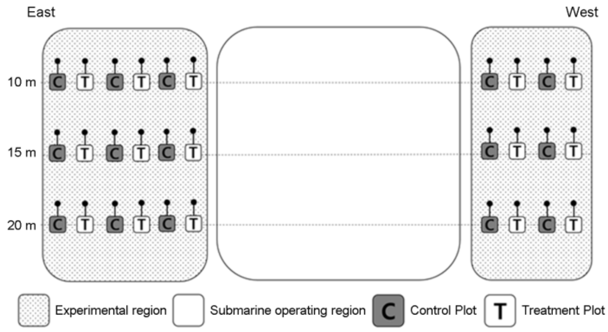

Fig. 2. Layout of experimental plots (50 × 50 cm), located on the north-face wall of Munseom, Jeju Island.

Seogwipo City, Jeju Island, Korea (33°13'N, 126°34'E) (Fig. 1). Due to the influence of the warm Tsushima Current, the seawater temperature around Munseom ranges from 16 to 25℃ year-round. Typically, Jeju coast exhibits significantly high marine biodiversity compared to other East Asian regions because it is remote from the populated Korean Peninsular and located under the mixed environment of temperate and subtropical climate (Noseworthy et al., 2007). In Munseom, subtidal algae at the shallow zone (1~5 m) are composed of *Sargassum sagamianum* Yendo, *Ulva prolifera* O.F.Müller, and *Plocamium telfairiae* (W.J.-Hooker & Harvey) Harvey ex Kützing. Deeper zone (5~20 m) is represented by *Ecklonia cava* Kjellman, *Sargassum* spp., and *Undaria pinnatifida* (Harvey) Suringer, which are dominant species in the region (Kang et al., 1993; Ko et al., 2008). Munseom has been known as the core habitat of soft corals in the coastal Jeju region featuring more than 70% of Korea's 120 coral species (Ko et al., 2008; Park et al., 2018). In addition, the southern coast of Jeju Island, including Munseom, was designated as a protected area under the category of natural monument (Natural Monument No.421) in 2000 for the preservation of soft coral habitat. The soft coral community of Munseom is largely dominated by *Scleronephthya gracillimum* Kükenthal, *Dendronephthya gigantea* Verrill, and *Dendronephthya castanea* Utinomi (Choi and Kim, 2008), showing a mixed distribution with seaweed beds (mostly *E. cava*) along the vertical rock wall depending on depth. *Scleronephthya gracillimum* and *D. castanea* appear dominantly in the shallow zone (5~10 m) and *S. gracillimum* predominate in the deeper zone (>15 m) with occasional appearance of *D. gigantia*. Additionally, the north-facing vertical rock wall of Munseom, where the present study was conducted, is also a place of active underwater eco-tourism by submarine tour and SCUBA diving. Therefore, this area is also a place of continuous issue in terms of conservation versus utilization.

2. Experimental design and data collection

Experimental setting was done on the vertical rock in the subtidal zone of the Munseom north wall, where soft coral and macroalgal communities were well mixed. The site was divided into two areas, leaving the area of submarine operation in between to avoid possible interference. We fixed stainless steel anchor bolts to the upper point of each zone and attached the vertical line using a hanging weight, marked at every 5 m. At depths of 10, 15, and 20 m on the vertical line, we placed another transect line horizontally, marked every meter to set the permanent plots. For each depth, 10 permanent plots (50 × 50 cm) were set up and small buoys with rope were additionally attached at two corners of each plot to locate the exact position of plot during the monitoring period. Ten plots for each depth were then divided into the treatment plot (5 plots) and the control plot (5 plots), consisting of 3 depths (10 m, 15 m, 20 m) × 2 conditions (treatment, control) × 5 replicate plots = 30 plots in total (Fig. 2). Treatment and control were alternately arranged, and in October 2016, all living organisms on the rock surface of treatment plots were eliminated using metal brush and scrapers to imitate physical disturbance. We cleared an area of 60 × 60 cm and used a 50 × 50 cm quadrat for monitoring to prevent the organisms living on the plot marginal area from being included in the data.

Monitoring and data collection were done for 2.5 years, from November 2016 to May 2019. We photographed all quadrats using digital cameras as non-destructive sampling by SCUBA diving to measure quantitative data every 6 months (spring and fall season), and percent coverage of benthic living organisms appearing inside the plot was calculated using Image J program (Schneider et al., 2012). In the case of canopy forming algae, data were considered only when the holdfast was included in the quadrats.

3. Data analysis

We compared total percentage covers of coral and macroalgal groups for two experimental conditions using independent *t*-tests. Separate tests were done by depth zone and sampling time to specify the post-disturbance recovery patterns. Statistical analysis was conducted using SPSS 21.0 for Windows, and all data were tested for normality (Shapiro test) and homogeneity of variance (Levene's test) prior to *t*-tests, and if assumptions were not met, we used Wilcoxon rank sum test (equivalent to Mann-Whitney test; Fay and Proschan, 2010). Additionally, for the analysis of ecological characteristics of community during recovery, species diversity (Shannon and Wiener species diversity index, H') was used as a supplementary tool to evaluate the community at a qualitative scale.

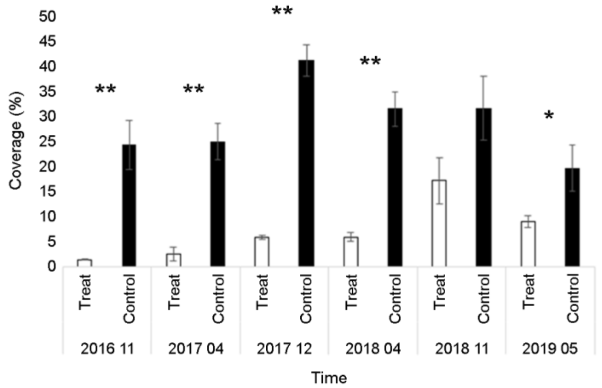

Fig. 3. Changes in mean (± SE) percent coverage of soft coral species. This data represents the average of all depths. Statistical significance was marked as * and ** symbols (*: $p<0.05$, **: $p<0.01$).

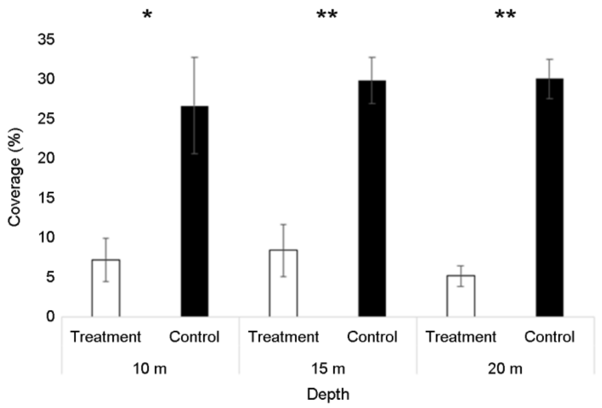

Fig. 4. Soft coral mean (± SE) coverage by depth. This data represents the average of all study periods. Statistical significance was marked as * and ** symbols (*: $p<0.05$, **: $p<0.01$).

Results

1. Recovery patterns of soft coral community

After disturbance, coverage of soft corals in the treatment plots was considerably lower than the control plots throughout the period (the average percent covers in treatment: 6.90%, in control: 28.78%, $p<0.01$, Wilcoxon rank sum test). Species diversity in the treatment plots was also lower than the control plots (treatment: 0.78, control: 1.06). Soft coral coverage in the treatment plots increased slightly over time until November 2018, which was when no statistical difference between treatment and control first occurred (Fig. 3). Patterns of lower recovery, both coverage and diversity, in soft corals were consistent at all depths (Fig. 4). The top five dominant species in the control were *S. gracillimum*, *Dendronephthya pütteri* Kükenthal, *Dendronephthya suensoni* Holm, *D. gigantea*, and *D. castanea*, and the treatment plots had *S. gracillimum*, *D. suensoni*, *D. pütteri*, *D. gigantea*, and *D. castanea*, indicating same component but a slight change in order. *Scleronephthya gracillimum* was solely the most dominant species in both experimental conditions for most periods, except for the early stage (i.e., November 2016 and April 2017), which was when *S. gracillimum*, *D. gigantea*, and *D. pütteri* formed a mixed dominant group.

2. Recovery patterns of macroalgal community

Unlike soft corals, macroalgae in the treatment plots showed a rapid recovery rate and reached the coverage level of the control in 6 months (Fig. 5). In April 2017, 6 months after disturbance, macroalgal coverage of the treatment plots recovered to the similar level as the control plots (control: 29%, treatment: 21.98%,

$p>0.05$, independent t-test). Fourteen months after disturbance (December 2017), the treatment showed higher macroalgal coverage than the control, and this pattern remained until the end of monitoring period (Fig. 5). Unlike the soft coral case, there was no difference in total macroalgal coverage between the treatment and control (control: 25.45%, treatment: 30.64%, $p>0.05$, independent t-test). In addition, species diversity in the treatment showed a similar level as the control (control: 2.20, treatment: 2.09). There was no conspicuous pattern of macroalgal coverage between the treatment and control according to water depth (Fig. 6). *Ecklonia cava* was solely the most dominant species in both experimental conditions throughout the study. The coverage of *E. cava* was highest at the depth of 10 m, and decreased with increasing depths, as shown in Fig. 6.

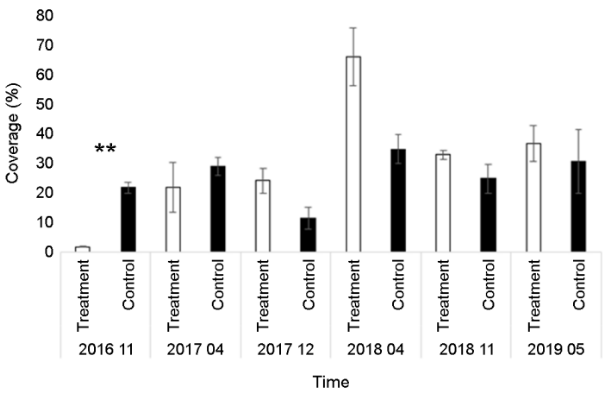

Fig. 5. Changes in mean (± SE) percent coverage of macroalgal species. This data represents the average of all depths. Statistical significance was marked as * and ** symbols (*: $p<0.05$, **: $p<0.01$).

3. Relative comparison between soft coral and macroalgal coverage

There was no difference in average percent cover between soft corals and macroalgae in the control plots (soft corals: 28.79%, macroalgae: 25.46%, $p>0.05$, Wilcoxon rank sum test). Furthermore, there was a seasonal trend in the control plots with higher soft coral coverage in autumn and higher macroalgal coverage in spring, which was consistent for three years at all depths (Fig. 7). However, in the treatment plots, the coverage of macroalgae were significantly higher than that of soft corals throughout the study (soft coral: 6.90%, macroalgae: 25.48%, $p<0.05$, Wilcoxon rank sum

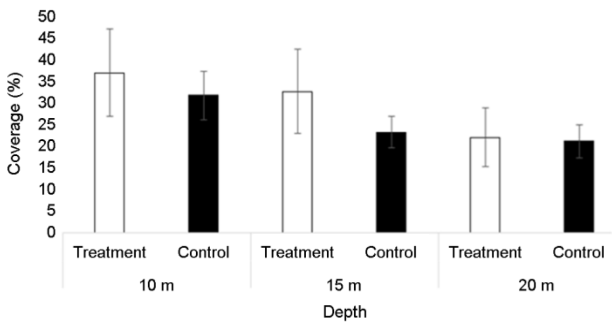

Fig. 6. Macroalgal mean (± SE) coverage by depth. This data represents the average of all study periods.

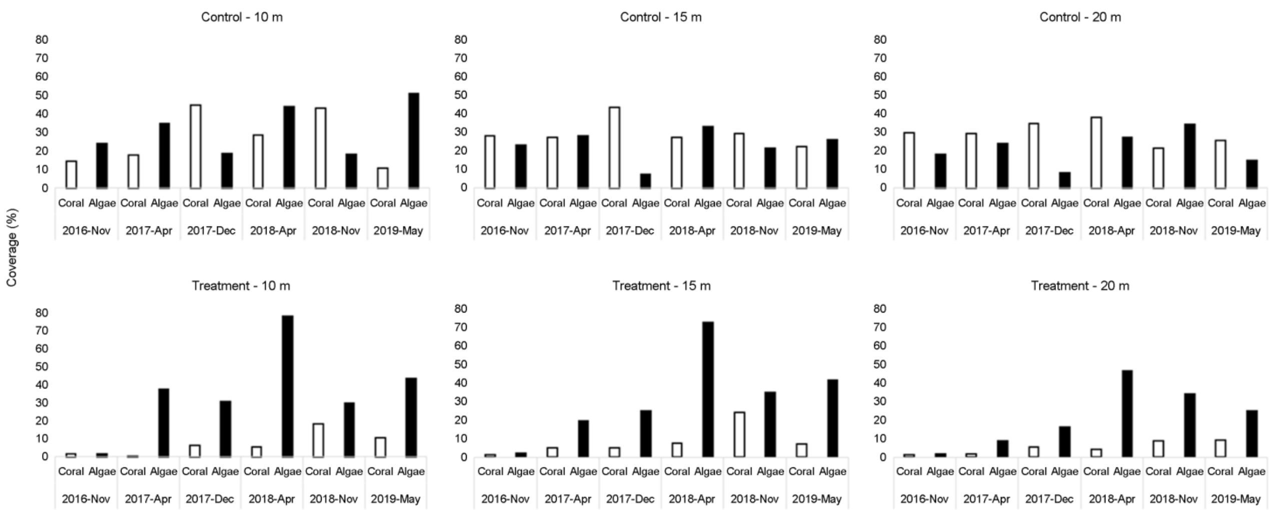

Fig. 7. Comparison between macroalgae and soft coral coverage in each plot.

test), also consistent at all depths until the end of monitoring.

Discussion

1. Possible phase shift due to disturbance in soft corals and macroalgae mixed communities

Soft corals showed patterns of slow and suppressed recovery after disturbance compared to macroalgae, which exhibited a rapid and dramatic recovery rate. As a result, benthic community in Munseom would possibly change to a more *E. cava* dominated state due to disturbance. In general, community shift to a macroalgae-dominated state in coral-algal interplaying communities has often been reported (Done, 1992; Hughes, 1994; McManus and Polsenberg, 2004). Many studies described the ability of space preemption of foliose algae within weeks after disturbance (Olsen et al., 2015; Leong et al., 2018). In addition, the phase shift to a macroalgae-dominated community might occur because the settlement and survival of coral planulae and asexual propagules were interrupted by macroalgal thalli establishment (Holbrook et al., 2016; Lamy et al., 2016). However, most reports have been studied in coral reefs in tropical regions, thus this study provides valuable experimental evidence on the possibility of phase shift in soft coral and macroalgae mixed communities.

Regarding other causes of macroalgal predominance over corals, herbivorous fish decrease and nutrient increase have been reported (McManus et al., 2000; Szmant, 2002); however, no such a change was observed in our study. One possible explanation for macroalgal success could be the reproductive characteristic of temperate soft corals such as the genus *Dendronephthya*, which has a low possibility of fertilization due to low spawning synchrony compared to hard corals in tropical regions (Hwang and Song, 2009). With this perspective, the shift to macroalgal phase in our study could be driven by both low reproductive capacity of temperate corals and fast preemption of space led by plentiful macroalgal spore supply.

The low recovery rate of soft corals could be another notable factor on top of their quantitatively low coverage during the study period. During the 2.5 years of monitoring, soft corals gradually increased in the treatment plots, but the rate was very slow. This phenomenon could be found in some previous studies dealing with recovery of coral communities after natural disturbance (Connell, 1997; Adjeroud et al., 2018; Gouezo et al., 2019). Adjeroud et al. (2018) claimed that it took 4 years after disturbance to find some degree of recovery in a hard coral community and 2 more years to reach the pre-disturbance state. Furthermore, Gouezo et al. (2019) reported that community-level resilience took 9 to 12 years in coral reefs. Although differences in disturbance scale and coral types exist between our study and previous research, results of this study showing a low recovery rate may reflect a common coral characteristic, particularly in comparison with macroalgae under the competitive situation for space occupation.

2. Function of water depth in the post-disturbance recovery

Macroalgae showed a linear coverage pattern according to water depth in our site, but soft corals did not. Algal communities in coastal Jeju Island, including Munseom, are the representative habitat for *E. cava* in Korea. *Ecklonia cava* in the Jeju coast is commonly distributed at 5~15 m, but the distribution area expands to around 25 m depending on the clarity of water (Kang et al., 2001). According to previous research done around Munseom, *E. cava* was the predominant species among the macroalgal flora and showed the highest biomass at the depth of 5~10 m (Ko et al., 2008; Kwak et al., 2014). Likewise, results of this study showed that the coverage of *E. cava* was highest at 10 m and getting lower as going deeper. Since recruitment can be considered the most important event on the recovery of macroalgal populations after disturbance, it is regarded that recovery process could be most active at the 10 m depth region, where the highest biomass exists and plentiful spore supply is possible. Our data of explosive increase in *E. cava* coverage at 10 m in the treatment plots in April 2017 may support this speculation. Therefore, at this depth zone, corals' recovery could be inhibited in part by spatial competition with *E. cava*.

Finally, we emphasize that the 15 m depth zone could be the most dynamical spot for post-disturbance event between the two groups in Munseom habitat because this depth is the critical overlapping zone for the two groups with respect to the maintenance of soft coral beds, considering the vertical range of *E. cava*. This study also suggests the necessity of monitoring for the influence of a larger scale disturbance, such as typhoons, to better understand the dynamics of community regulation in this soft coral-macroalgae mixed habitat.

Acknowledgment

This study was supported in part by Cultural Heritage Administration of Korea and Seogwipo Submarine Tour. Authors specially thank to the SCUBA diving team of SST for their assistance in the field. Much appreciation goes to two anonymous reviewers for their valuable comments.

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