A THESIS FOR THE DEGREE OF

MASTER OF SCIENCE

Underwater Image Analysis of the High Latitude Scleractinian Coral *Alveopora japonica* (Eguchi 1968) Occurring in Shallow Subtidal Hard Bottom in Jeju Island: Spatial Distribution Pattern and Association with Macrobenthic Algae

Kyeong-Tae Lee

Department of Marine Life Science

GRADUATE SCHOOL

JEJU NATIONAL UNIVERSITY

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Kyeong-Tae Lee

(Advised by Professor Kwang-Sik Choi)

A dissertation submitted in partial fulfillment of the requirement for the degree of

Master of Science

August 2021

This dissertation has been examined and approved.

Park Heungsik

Thesis director, Dr. Heung-Sik Park, Principal Research Scientist, Research Project Development Department, Korean Institute of Ocean Science & Technology

Kang Do-Hyung

Dr. Do-Hyung Kang, Principal Research Scientist, Jeju Marine Research Institute, Korean Institute of Ocean Science & Technology

Dr. Kwang-Sik Choi, Professor, Department of Marine Life Science, Jeju National University

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Date

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ABSTRACT

High latitude coral *Alveopora japonica* extends its geographic range from the warm southern area to the northern shallow subtidal in Jeju Island, possibly due to the surface seawater temperature increase and decline in macroalgae. This study investigated the abundance of the coral occurring on the shallow subtidal in the northern Jeju (Shinheung, SH, and Bukchon, BC, Seongsan, SS) and their association with other benthic organisms using underwater photography and subsequent image analysis. Images of macro-benthic organisms appearing on a 1 × 20 m line transect installed at depths of 5, 10, and 15 m were recorded using an underwater digital camera. Species identification and abundance as a percentage area in the transect were estimated using the image analyzing software photoQuad®. The underwater images revealed that of the three sites investigated in this study, *A. japonica* colonies were most abundant at BC, where the coral accounted for 45.9 % (10 m) and 72.8 % (15 m) of the total transect area. At SS, *A. japonica* occupied 15.3 % of the total area at 15 m, whereas *A. japonica* covered less than 1 % of the transect at depths of 5 and 10 m. At SH, *A. japonica* accounted for 10 % of the total area, whereas the percent cover area was limited to less than 1 % at depths of 10 and 15 m. Dead and bleached colonies of *A. japonica* could be identified from the images, which accounted for 5.6-11.5 % and 1.8-5.7 % of the coral populations at SH and BC. At SS, the underwater canopy-forming brown algae *Ecklonia cava* and *Sargassum* spp. accounted for 20.2 and 24.3 % of the total transect area, respectively at 5 m depth. In contrast, the percent cover of *E. cava* and *Sargassum* spp. at SH and BC ranged from 0.1 to 1.8 %, respectively. The underwater images also revealed that at SH, non-geniculate coralline algae dominated the subtidal substrate, ranging from 60.2 (15 m) to 69 % (10 m). Comparatively low percent cover of *A. japonica* at a depth of 5 m at SS coincided with a high percent cover of underwater canopy-forming brown algae. Such canopy-forming kelps were rare at all depths at SH and BC, where calcium-carbonate secreting coralline algae and the scleractinian coral dominated the bottom. Underwater photography and image analysis used in this study were non-destructive methods that provided qualitative and quantitative

information on the surface-dwelling benthic organisms and were considered to be a method of choice in hard-bottom ecosystem analysis.

Key words: percent cover, density, *Alveopora japonica*, kelp, coralline algae, benthic community, underwater photography, image analysis, Jeju Island

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1. Introduction

The consequences of climate change-related changes, potentially deleterious, needs to be monitored to understand, protect or minimize the impact on marine ecosystems. The structure and composition of the benthic community may be rearranged by climate change, which is escalated by natural and anthropogenic activities. These changes may cause an evident decline in the population of the benthic species that fail to adapt and/or acclimatize to changing climate, resulting in new interactions with the altered species, which may appear for the first time in ecosystems. In particular, the association might be altered between benthic organisms when the keystone species of that particular marine ecosystem disappear (Connell, 1983; Muko et al. 2001; Vergés et al. 2014). This idea has already been explored in several studies in the recent year under the premise of the "tropicalization" of high-latitude communities. In benthic ecosystems, space is a limiting factor for sessile benthic assemblages, affecting recruitment, growth rate, and distance from other populations (Baird et al. 2000; Herrero-Pérezrul 2008).

Several studies have been carried out on the benthic species composition in the waters of Jeju Island (Denis et al. 2015; Vieira et al. 2016; Hong et al. 2015; Park et al. 2020), mainly with respect to the dominant coral species *Alveopora japonica* (Fig. 1). This scleractinian coral occurs commonly in non-reefal temperate waters and is widely distributed from Taiwan to Japan, including Jeju Island, off the south coast of Korea (Harii et al. 2001; Park et al. 2020). In Jeju Island, this species dominates mainly in the northern part of the Island (between 5-20 m in depth) and associates and shares space with mollusks, algae, and soft corals (Denis et al. 2015; Noseworthy et al. 2016; Vieira et al. 2016). According to Vieira et al. (2016), *A. japonica* has a short life span (12–13 years) and fast turnover rates with a growth rate of 4.8mm year^{-1}. Such growth and turnover rates may result in the high density of *A. japonica* (ranging from 58 to 155 colonies m^{-2}) in the shallow subtidal, depending on the water depth (Noseworthy et al. 2016; Viera et al. 2016). Furthermore, it recruits and re-populates abundantly with an estimated recruitment rate of 7.8 colonies m^{2} yr^{-1} via sexual reproduction (Hong et al. 2015; Park et al. 2020). A detailed study on the assemblage of molluscans association with *A. japonica* collected from several locations in Jeju has been reported by Noseworthy et al. (2016). Nonetheless, few studies have paid attention to the dynamics of *A. japonica* and coralline algae and kelp in Jeju. While increased abundances could be a factor for kelp decline in Jeju, crustose coralline algae have considerable coverage in some locations and have replaced large macroalgae in density (Buenau et al. 2012; Vieira et al. 2016; Denis et al. 2015).

Anecdotal evidence has reported that until 1980, there was a mass population of macroalgae (*Sargassum* sp., *Laminaria* sp., and *Ecklonia* sp.) playing a vital role, ecologically and economically, in coastal Jeju Island (Kang et al. 2012; Vieira et al. 2016). The brown macroalgal beds were utilized as breeding grounds for finfish and shellfish and were an essential environment for juveniles (Kang et al. 2011; Ohno 1985; Vanderklift et al. 2020). However, through time, complex combinations of several causes such as rapid grazing by sea urchins, intense fishing or aquaculture activities, seawater pollutions, and global warming lead to a mass decline in the macroalgal population. In particular, growth rate metabolism, canopy forming, and other physiological activities collapsed due to increasing seawater temperature and led to a shift from the brown macroalgae (i.e., kelp) to deforested barrens then coral-algal dominant ecosystem (Denis et al. 2013; Vieira et al. 2016).

Benthic composition survey studies have utilized various techniques including, line intercept transect, point intercept transect, photoquadrats and video transect. A higher degree of precision has become possible with recent advances in photography and image classification tools in various quantitative methods (English et al. 1997). Underwater imaging has improved survey studies due to high-resolution imagery. Underwater photography has become one of a major evaluation tool for science, policy, and public understanding of coastal marine ecology (Durden et al. 2016). Urbina-Barreto et al. (2021) have shown that while traditional in-situ techniques (transects and recording) are less time consuming and effective for species-level taxonomic identification, imaging is better in terms of data outputs and representativeness of the ecosystem. Moreover, if the area survey is not very large, number of photos obtained are still manageable in terms of their analysis in a short period of time. Photogrammetry enables the quantitative monitoring of physical (e.g., structural complexity: slope, fractal dimension, surface complexity) and biological features (e.g., cover of benthic communities, colonies size and abundance) of ecosystems over time (Urbina-Barreto et al. 2021).

Although several studies have looked at various aspects of different benthos in Jeju Island, there are no studies analysing combined composition and diversity at a spatial scale (horizontally – at different locations and vertically- at different depths). The main purpose of the present study was to analyze benthic community structure and dynamics at three sites in Jeju Island by utilizing high-resolution photographs. We discuss about the diversity of benthos, the abundance and relationship of *A. japonica* with the benthos in Jeju and the possible role of different benthic organisms at three different sites and depths.

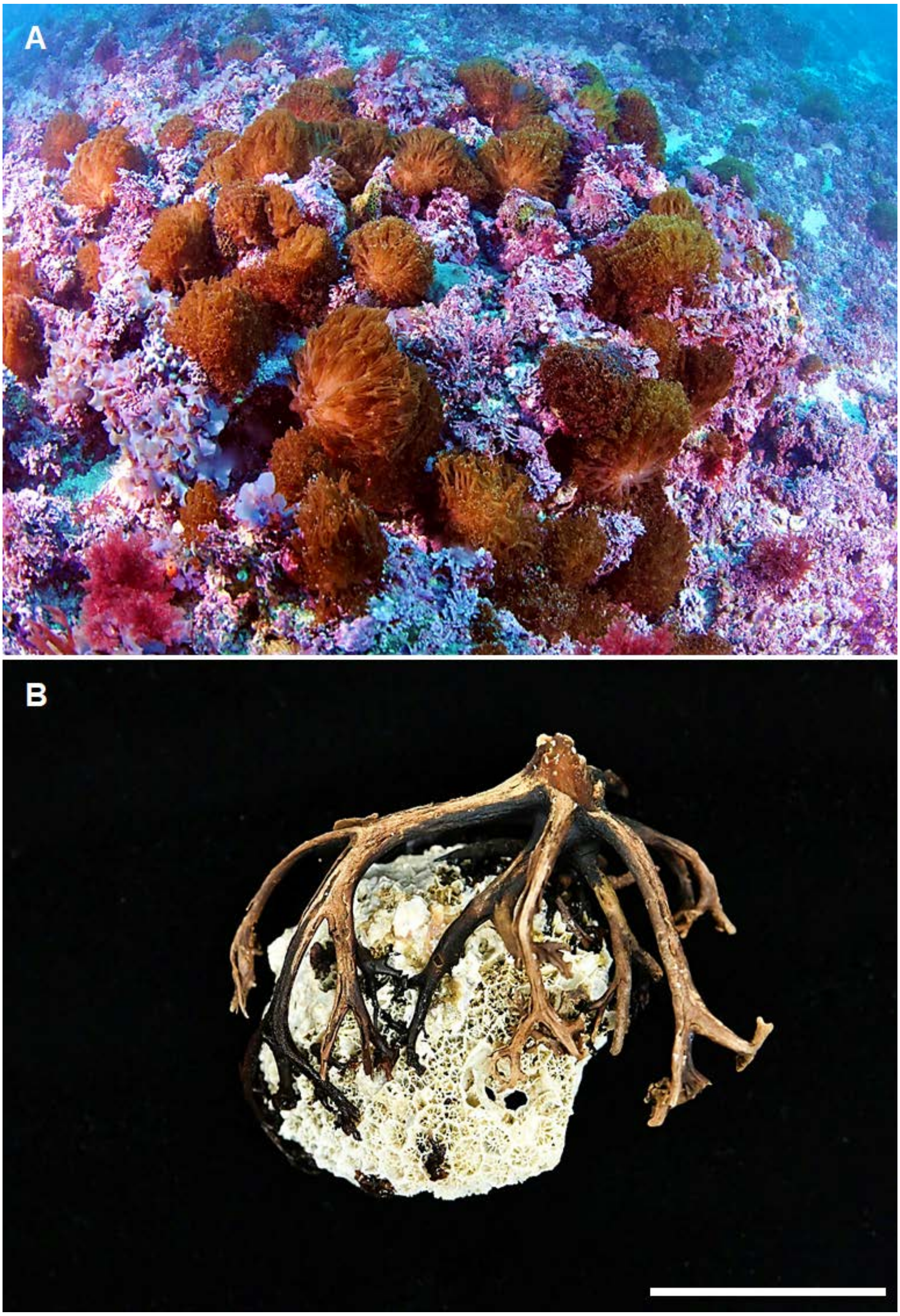

Fig. 1. (A) A close-up picture of *A. japonica* at Shinheung, a depth of 5 m. Live colonies with long polyps extended. (B) A close-up picture of *A. japonica* corallum with hemispherical growth form. Kelp (*Ecklonia* sp.) holdfast attached to *A. japonica* colony skeleton. Scale for picture is 3 cm.

2. Materials and Methods

2.1. Study site

The study was conducted at three sites, Shinheung (SH); Bukchon (BC); Seongsan (SS), along the northeast and east coast of Jeju Island, Korea (Fig. 2). The Jeju Island is located at off the southwestern tip of Korean peninsula, strongly influenced by the warm Tsushima Current (Kang et al. 2005; Vieira et al. 2016). Jeju Island characterized as warm humid temperature climate with distinct four seasons and average annual seawater temperature ranged from 13.7 ^{o}C to 25 ^{o}C (Park et al. 2020).

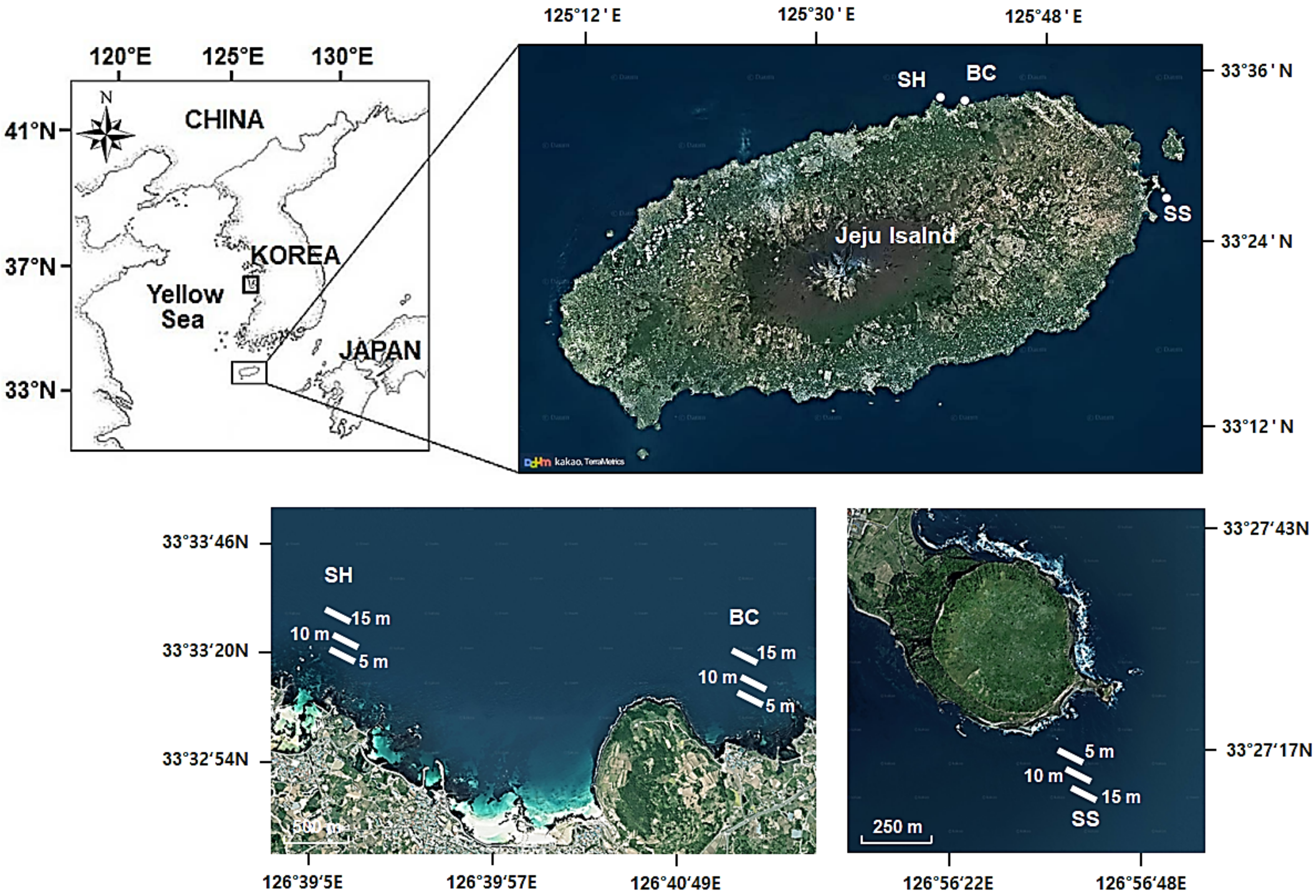

Fig. 2. Map showing the sampling locations of 20-m line transects installed at depths of 5 m, 10 m, 15 m of 3 survey sites (SH: Shinheung; BC: Bukchon; SS: Seongsan).

2.2. Underwater images collection

In January 2014, 20 high-resolution photographs were captured (1 m × 1 m) consecutively over a 20 × 1 m line transect installed at 1 m intervals during each 30-minutes dives using SCUBA with a digital underwater camera, at depths of 5, 10, 15 m, respectively (Fig. 3). The diver used Nikon D90 digital camera (a maximum resolution of 4288 × 2848 pixels; using Patima housing) at a vertical position away from the rocky subtidal substrate to take photographs. The camera housing was equipped with two strobes for provided additional light. The total area examined was 180 m^2 for this study.

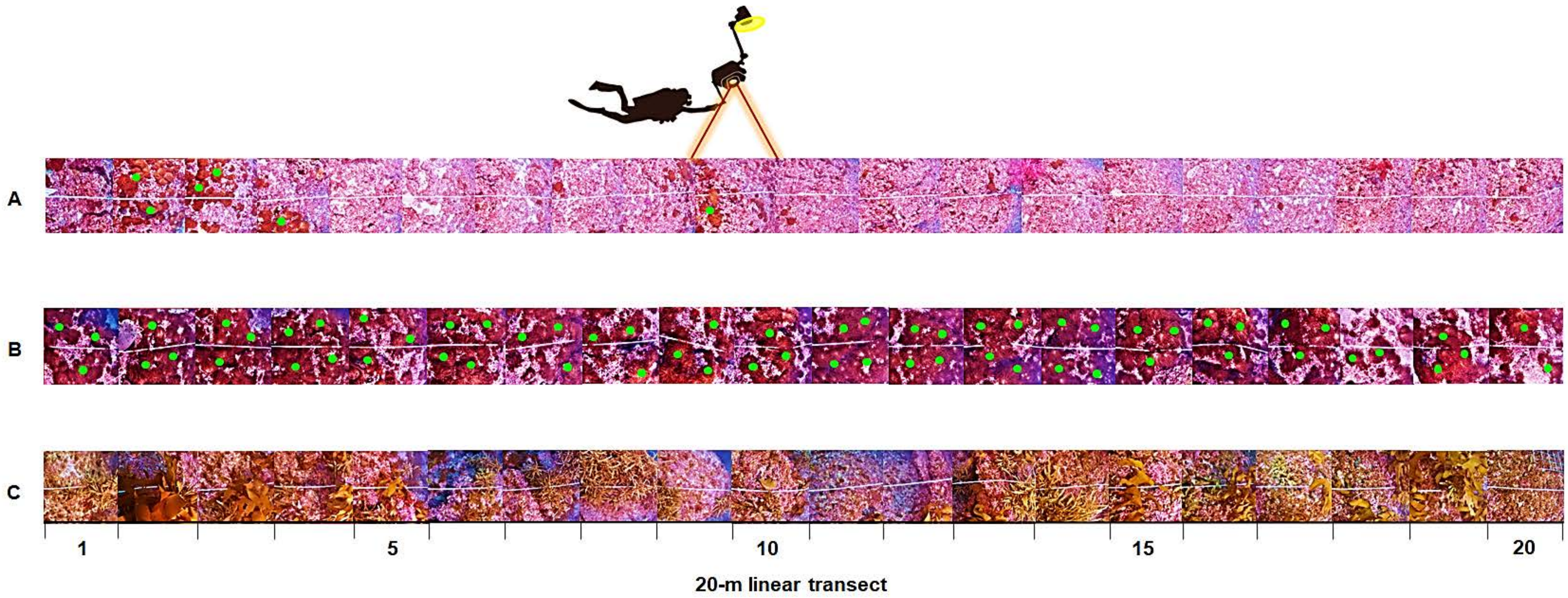

Fig. 3. 20-m line transects installed at (A) a depth 5 m of Shinheung; (B) a depth 15 m of Bukchon; (C) a depth 5 m of Seongsan in Jeju Island, Korea. Photographs were captured continuously at 1 m interval (20 photographs per transect) using underwater digital camera (a full resolution of 4288 × 2848) with 1 m stand off the substrate over the transect. Green points indicate *A. japonica* appeared at 20-m line transects.

2.3. Image analysis

The image analysis was performed using photoQuad® software that operates in a layer-based environment following multiple analyses to be performed on the same source photograph (Trygonis et al. 2012). Digital images were outlined in the form of a 1 m^2 virtual photoquadrats and were converted to real distance from the pixel size using software tools. The abundance of *A. japonica* occurring in the transects was estimated using freehand regions and random point counts method.

Freehand regions method was used to count the number of *A. japonica* colonies in the transects (Fig. 4). Bleached and dead colonies of *A. japonica* could be identified from the photoquadrats. Attempt was made to divide the coral colonies into (1) live colonies with long polyps extended, (2) bleached colonies with white coral tissue and (3) dead colonies with only skeleton remaining, following Meesters and Bak (1993), Bak and Meesters (1998). The minimum size that can be identified as individual colonies of *A. japonica* on PC monitor screen that was typically more than 1 cm. Even if part of a colony was visible on the transect, it was included in analysis, so the numbers maybe a slight overestimation of the real abundance.

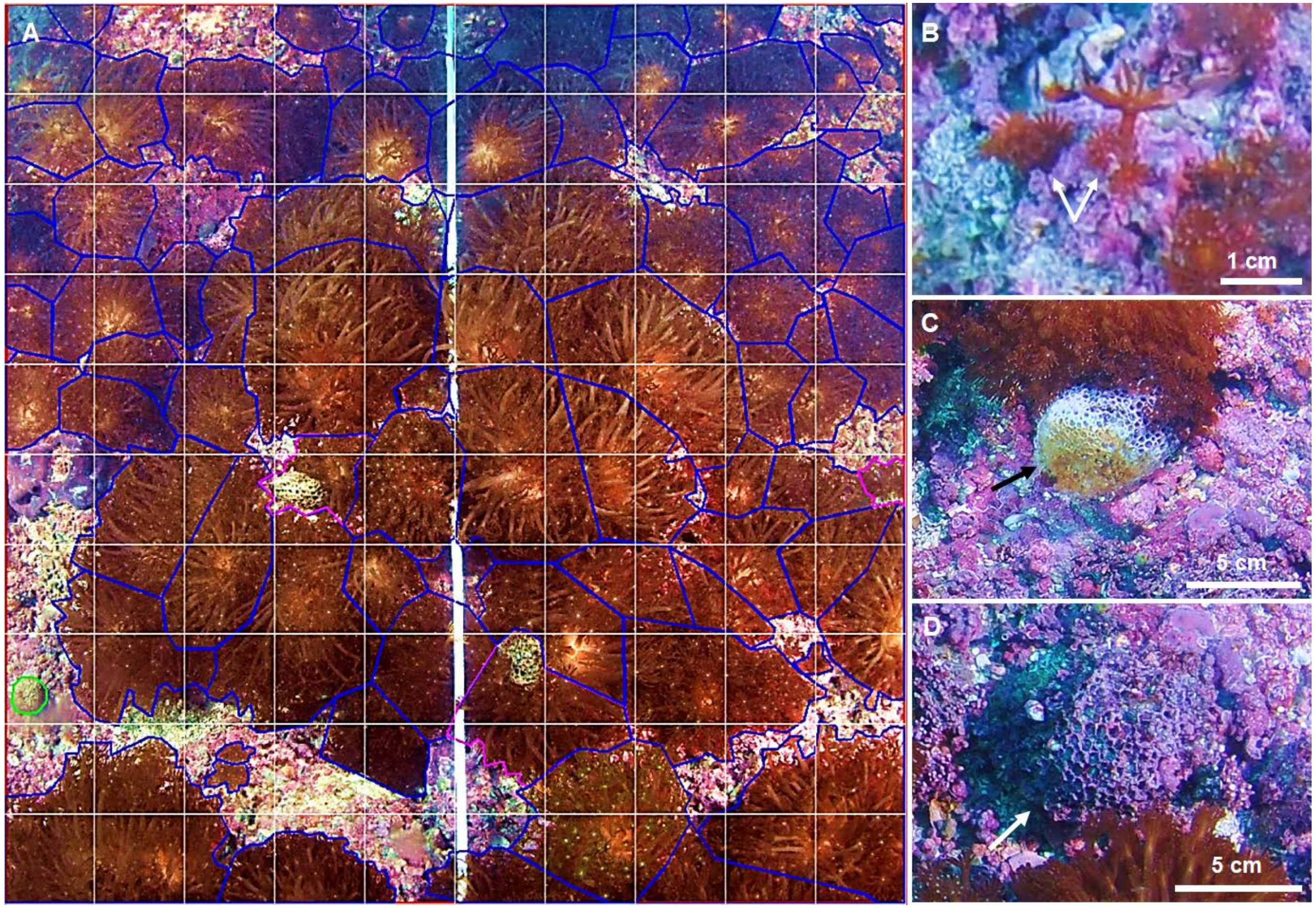

Fig. 4. The density estimation of *A. japonica* colonies. (A) 1 m^2 photoquadrat taken from a depth 15 m of Bukchon using underwater camera and the method of freehand regions for extraction of *A. japonica* colonies density using photoQuad® software. (B) A close-up picture of small colonies (arrow) of *A. japonica* identified from underwater image. (C) Bleached colony (arrow) with coral tissue lost it color and whiting colonies. (D) Dead colony (arrow) with all coral tissue disappeared.

Random point counts method was used to estimate the percent cover of benthic organisms including *A. japonica* in the transects (Fig. 5). Fifty randomly assigned points were used for each 1 m^2 virtual photoquadrat outlined and the underlying benthic organisms were identified according to visual information such as color, texture, shape, size. The percent cover of benthic organisms was estimated from 1,000 random points per transect. The points were excluded from analysing if allocated point was unclear (i.e., shadow or blurry) or was located in sand, rock, fish, and transect hardware. Coralline algae assemblages were identified conspicuous morphological characteristics based on their growth forms into non-geniculate growth form and geniculate growth form as described in McCoy et al. (2015). The benthic organisms were classified into six major categories: hard coral (only *A. japonica*), other invertebrates (such as soft corals, sponges, mollusks, bryozoans, echinoderms, ascidians, anemones, and annelids), kelps, corresponding to canopy-forming brown algae (i.e., *E. cava* and *Sargassum* spp.), geniculate corallines, such as geniculate growth form; non-geniculate corallines, including both crustose and rhodolith forms; other macroalgae, such as chlorophyte, phaeophyte, and rhodophyte excluding kelps and coralline algae.

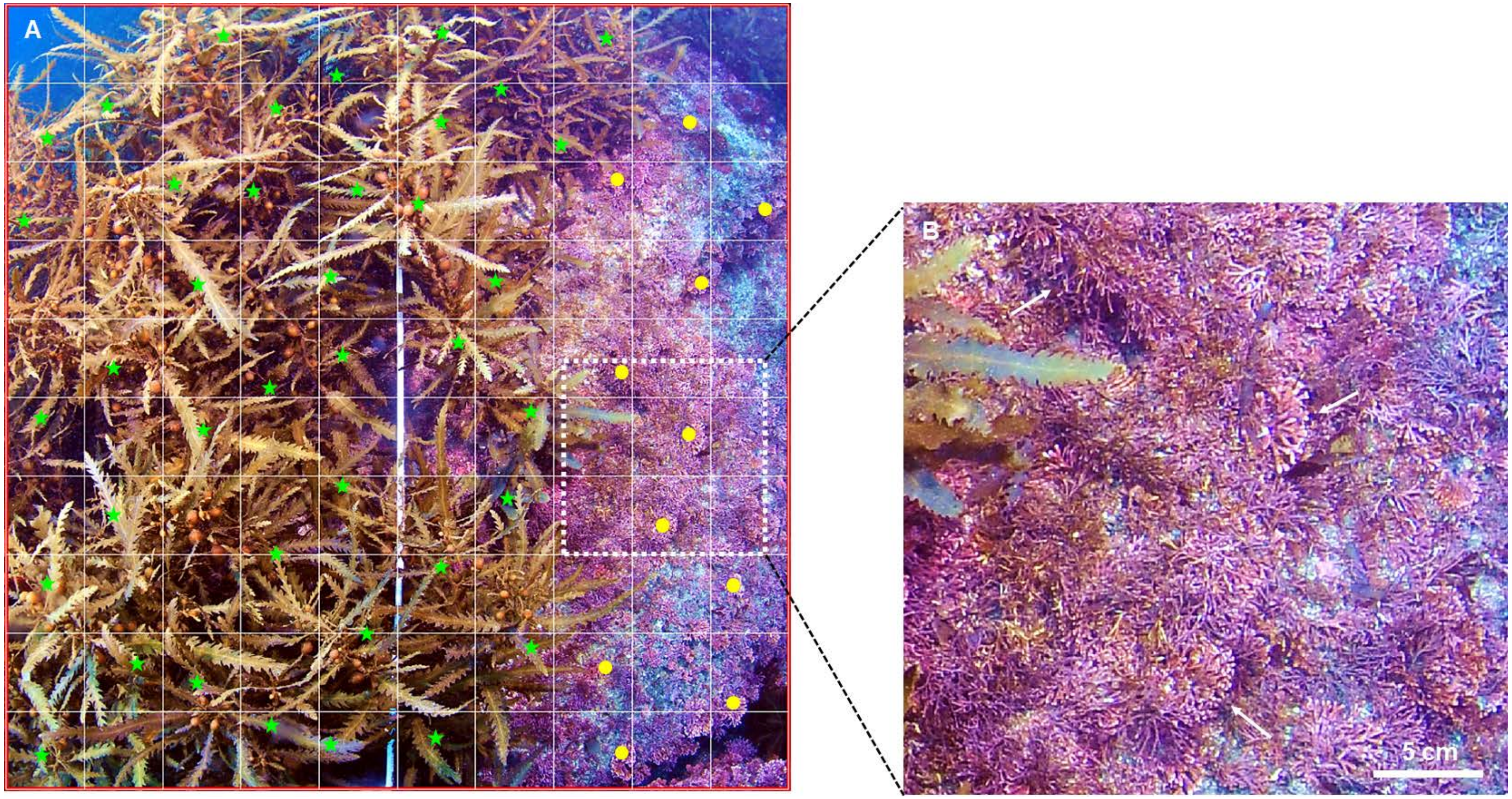

Fig. 5. The percent cover estimation of benthic community. (A) 1 m^2 photoquadrat taken from a depth 5 m of Seongsan using underwater camera and the method of random point counts for extraction of percent cover with 50 randomly allocated points using photoQuad® software. Red points indicate blown macroalgae (*Sargassum* sp.) and yellow points indicate geniculate corallines. (B) A close-up picture of geniculate corallines (*Amphiroa* sp.) appeared on 1 m^2 photoquadrat.

2.4. Data analysis

Cluster analysis based on Bray-Curtis coefficient was performed to evaluate similarity by the percent cover of each benthic organism in the transects. A similarity profile (SIMPROF) was conducted to test the hierarchical groups by group average cluster analysis. Similarities between groups were tested using analysis of similarities (ANOSIM) in which global R = 1 indicates complete separation of groups and global R = 0 indicates no separation (Clarke et al. 2001). A similarity percentages analysis (SIMPER) was performed to examine the contribution to the similarity of individual species or functional groups (i.e., non-geniculate corallines, geniculate corallines) within each group. All statistical analyses were performed using PRIMER ver. 6 software (PRIMER-E Ltd).

3. Results

3.1. Analysis of benthic composition

A total of 9 transects from three depths at three sites were investigated for analysis the benthic composition. The benthic organisms of various sizes were recorded, from relatively small-sized species (i.e., *Herdmania* sp., *Colpomenia* sp.) to large-sized species (i.e., *Dendronephthya* sp., *E. cava*). The benthic organisms identified and their percent cover in the transects was shown in Table 1, Figures 6, 7, 8 and 9. Only *A. japonica*, *E. cava*, *Sargassum* spp., geniculate corallines, non-geniculate corallines, rhodophyte including *Plocamium* sp., *Peyssonnelia* sp., and chlorophyte including *Cladophora* sp. reported more than 5 % average percentage cover in at least any of the sampling sites (Table 1). *A. japonica* colonies were present in all three sites and were most abundant at BC (Fig. 10). At SS, macroalgae were the most abundant and diverse and especially, the canopy-forming brown algae *E. cava* and *Sargassum* spp. occurred at 5 m depth. In contrast, non-geniculate corallines covered the rocky substrate widely at BC and SH.

Fig. 6. Hard coral, soft coral, sponge. Underwater images of benthic organisms identified from 20-m line transects installed at depths of 5 m, 10 m, 15 m of 3 survey sites (SH: Shinheung; BC: Bukchon; SS: Seongsan). (A) hard coral (*A. japonica*) SS, 5 m; (B) soft coral (*Dendronephthya* sp.) SH, 15 m. The benthic substrate covered with sponges including massive or encrusting sponges and branching sponges (C) *Spirastrella* sp. SH, 15 m; (D) *Halichondria* sp. SS, 15 m; (E) *Haliclona* sp. SH, 15 m; (F) *Hymeniacidon* sp. BC, 5 m; (G) *Callyspongia* sp. SS, 10 m; (H) *Petrosia* sp. SH, 10 m.

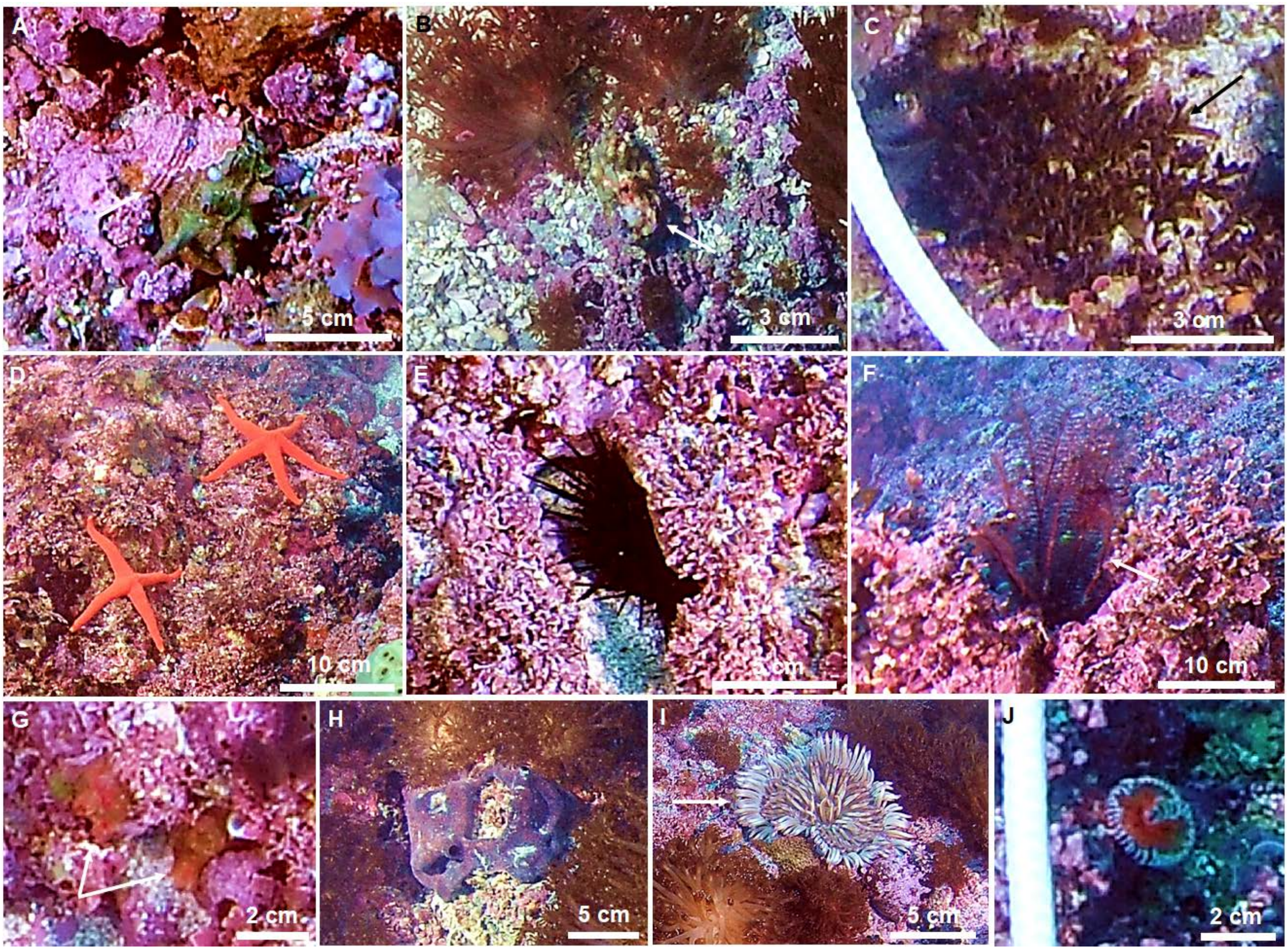

Fig. 7. Mollusk, bryozoan, echinoderm, ascidian, anemone, annelid. Underwater images of benthic organisms identified from 20-m line transects installed at depths of 5 m, 10 m, 15 m of 3 survey sites (SH: Shinheung; BC: Bukchon; SS: Seongsan). (A) gastropod (*Turbo* sp.) partially encrusted with non-geniculate corallines SH, 5 m; (B) bivalve (*Cardita* sp.) BC, 15 m. (C) bryozoan (*Adeonella* sp.) SH, 15 m; (D) asteroid (*Certonardoa* sp.) SH, 15 m; (E) echinoid (*Heliocidaris* sp.) SH, 5 m; (F) crinoid (*Comatula* sp.) SH, 10 m; (G) individual ascidian (*Herdmania* sp.) SH, 5 m; (H) colonial ascidian (*Lissoclinum* sp.) BC, 15 m; (I) anemone (*Heteractis* sp.) BC, 10 m; (J) Unidentified annelid SH, 10 m.

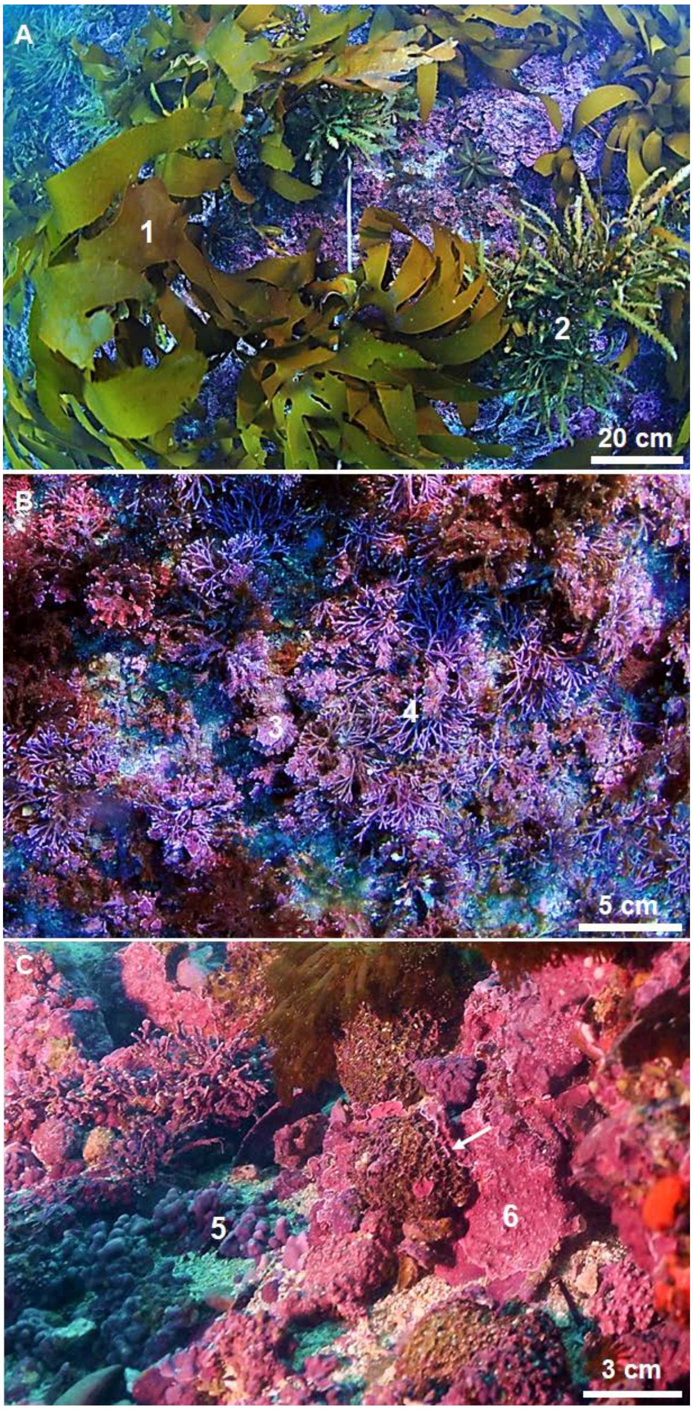

Fig. 8. Kelps, geniculate corallines, non-geniculate corallines. Underwater images of benthic organisms identified at depths of 5 m, 10 m, 15 m of 3 survey sites (SH: Shinheung; BC: Bukchon; SS: Seongsan). (A) Prolific growth of large canopy-forming kelps 1) *Ecklonia* sp., 2) *Sargassum* sp. SS, 5 m. (B) Geniculate growth form 3) *Corallina* sp., 4) *Amphiroa* sp. SS, 5 m. (C) Non-geniculate growth forms 5) rhodolith, 6) crustose (arrow) overgrowing the dead colony (*A. japonica*) SH, 5 m.

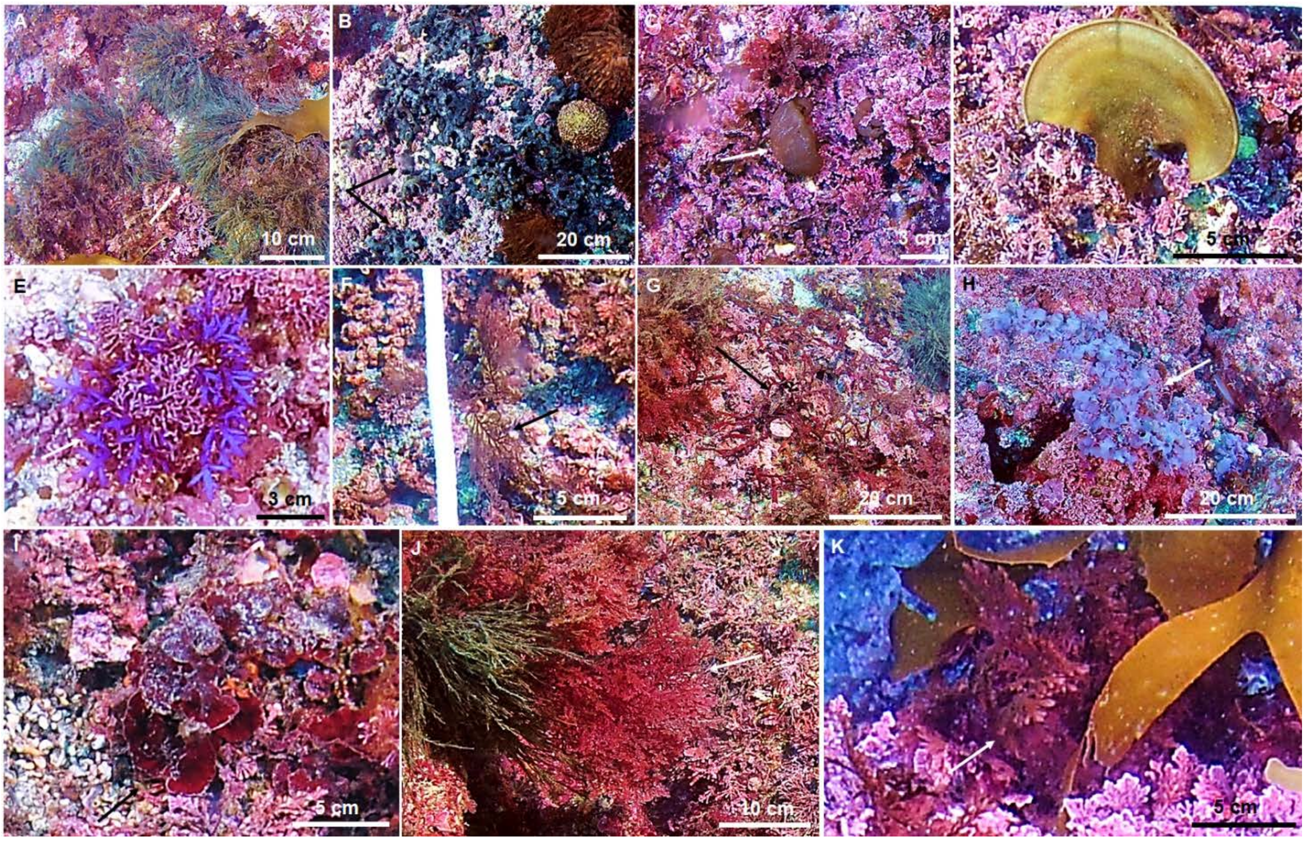

Fig. 9. Chlorophyte, phaeophyte, rhodophyte. Underwater images of benthic organisms identified from 20-m line transects installed at depths of 5 m, 10 m, 15 m of 3 survey sites (SH: Shinheung; BC: Bukchon; SS: Seongsan). (A) *Cladophora* sp. SS, 10 m; (B) *Codium* sp. BC, 10 m; (C) *Colpomenia* sp. SS, 5 m; (D) *Padina* sp. SS, 5 m; (E) *Champia* sp. SH, 5 m; (F) *Gelidium* sp. SS, 10 m; (G) *Grateloupia* sp. SS, 10 m; (H) *Martensia* sp. SH, 10 m; (I) *Peyssonnelia* sp. SS, 15 m; (J) *Plocamium* sp. SS, 10 m; (K) *Pterocladiella* sp. SS, 5 m.

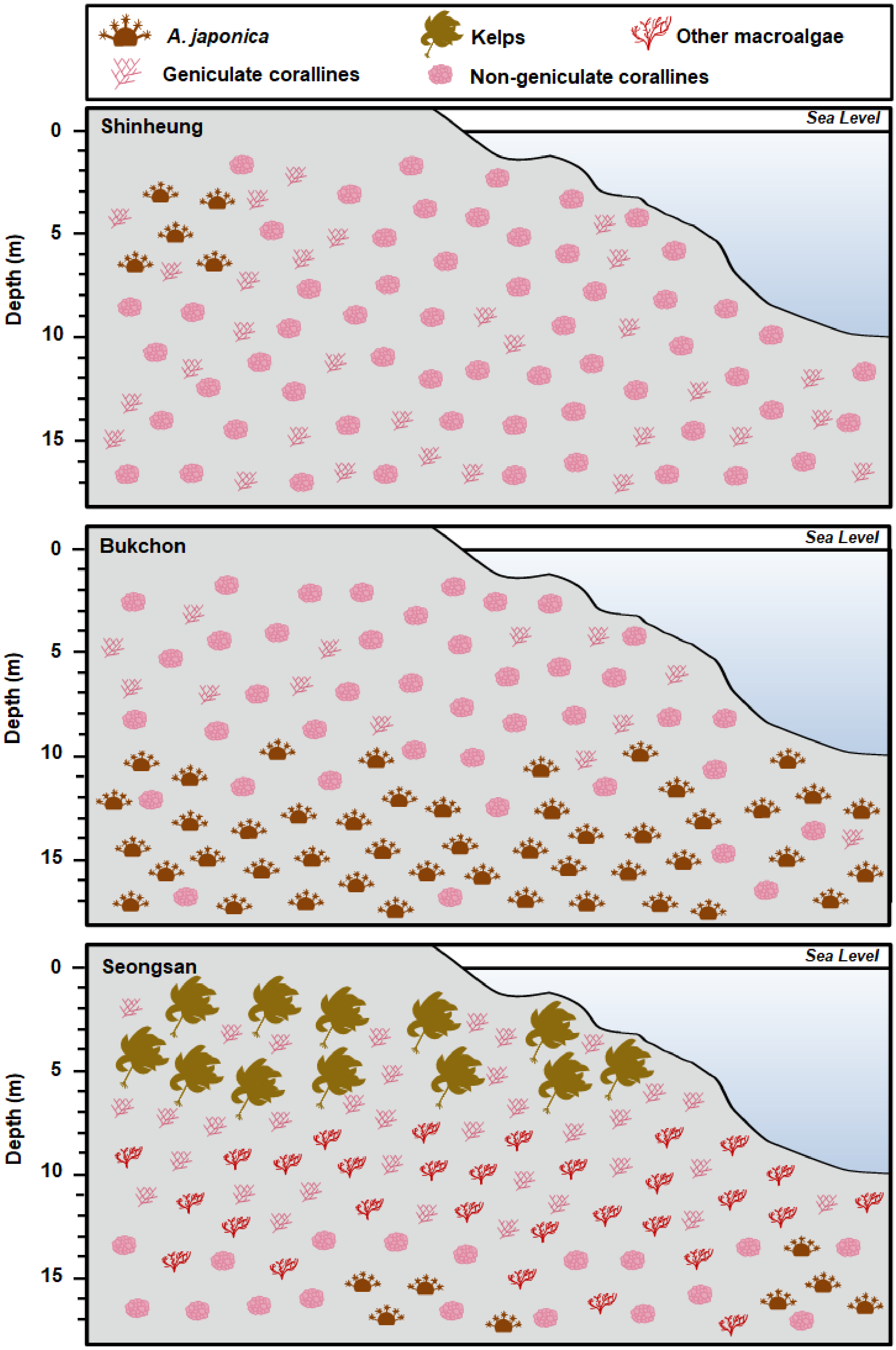

Fig. 10. Illustration of major benthic community occurring at different depths in 3 survey sites in Jeju Island, Korea.

Table 1. Average percent cover of benthic organisms estimated on 20-m line transects installed at depths of 5 m, 10 m, 15 m of 3 survey sites (SH: Shinheung; BC: Bukchon; SS: Seongsan).

Phylum	Species	Average percent cover (%)								
		SH			BC			SS		
		5 m	10 m	15 m	5 m	10 m	15 m	5 m	10 m	15 m
Porifera	*Callyspongia* sp.						0.1	0.1	0.1	0.1
	Halichondria sp.			0.1			0.2			0.1
	Haliclona sp.		0.1	0.4			0.1			
	Hymeniacidon sp.	0.1	1.1	0.7	0.5	0.2	0.4			
	Petrosia sp.		0.2							
	Spirastrella sp.	0.1	0.3	2.2			0.6		0.2	
Cnidaria	*Dendronephthya* sp.	1.0	0.2	4.2						
	Heteractis sp.	0.1	0.1			0.2				
	A. japonica	10.0	0.8	0.2	0.4	45.9	72.8	0.1		15.3
Mollusca	*Cardita* sp.						0.1			
	Turbo sp.	0.1	0.2		0.1			0.1		
Annelida	Unidentified annelid		0.1							
Bryozoa	*Adeonella* sp.			0.1						
Echinodermata	*Comatula* sp.		0.1							
	Certonardoa sp.	0.1		0.2		0.1			0.1	
	Heliocidaris sp.	0.2	0.1		0.3			0.1		
Chordata	*Herdmania* sp.		0.1	0.1						
	Lissoclinum sp.			0.1			0.1			
Chlorophyta	*Cladophora* sp.	0.1	0.5	0.1	0.1	0.2			6.5	0.7
	Codium sp.	0.1		0.8	0.1	4.5				0.1
Phaeophyta	*Colpomenia* sp.							0.1		
	E. cava	0.1	0.1	0.3	0.4			20.2	3.2	3.1
	Padina sp.							0.2		
	Sargassum spp.				1.4			24.3	0.3	1.0
Rhodophyta	*Champia* sp.	0.9	0.3	0.1	0.1			0.5		
	Gelidium sp.	0.1	0.3						0.8	
	Grateloupia sp.			0.1				0.5	4.4	4.2
	Martensia sp.	0.6	0.4		4.1	0.1				
	Peyssonnelia sp.						0.1	0.2	1.9	8.0
	Plocamium sp.	0.7	0.1		0.1	0.1		3.1	32.0	16.5
	Pterocladiella sp.							0.3	1.6	
	Geniculate corallines	16.9	21.5	24.3	20.8	4.8	0.4	36.9	25.3	4.9
	Non-geniculate corallines	63.3	69.0	60.2	68.6	42.3	22.3	11.6	19.7	39.4

At BC, *A. japonica* accounted for 45.9 % (10 m), and 72.8 % (15 m) of the cover on the transects. At SS 15 m depth, *A. japonica* occupied 15.3 % on the transect, and less than 1 % at depths of 5 and 10 m (Fig. 11). At SH, *A. japonica* accounted for 10.0 % of the total area at 5 m depth, whereas the coverage was limited to less than 1 % at depths of 10 and 15 m. However, at 5 m depth of SS, the coverage of the canopy-forming kelps was 44.5 % on the transect, and geniculate corallines occupied 36.9 % on the transect. At SS 10 m depth, major categories that contributing to the coverage were other macroalgae (47.2 %) and geniculate corallines (25.3 %). In contrast, kelps ranged from 0 to 1.8 % and other macroalgae ranged from 0.1 to 4.9 %, respectively at SH and BC. Non-geniculate corallines dominated the rocky substrate, ranging from 60.2 to 69.0 % of the total area at all depths of SH and BC 5 m. At SH, other sessile invertebrates ranged from 1.7 to 8.1 %, and their abundance was higher than BC and SS.

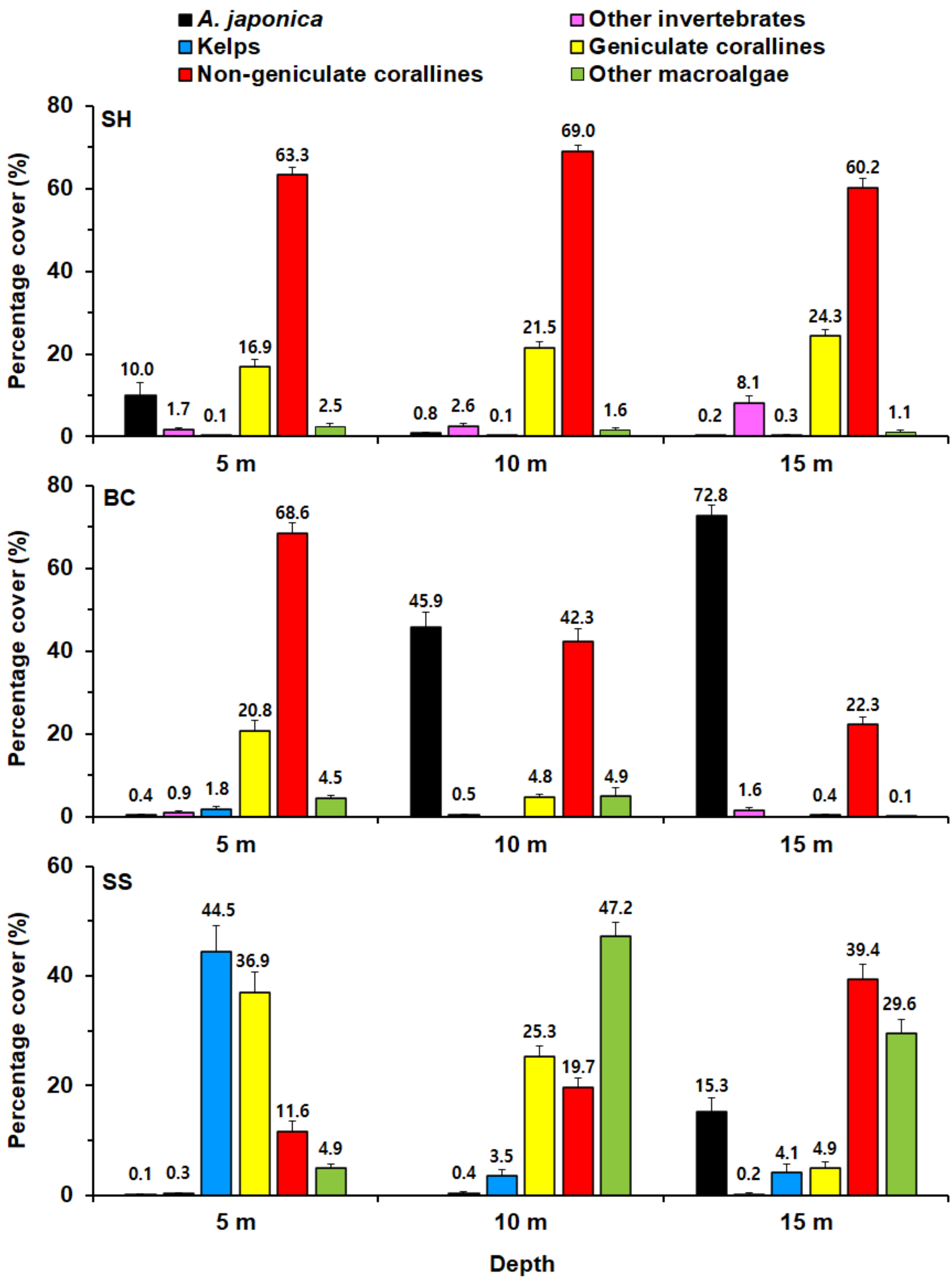

Fig. 11. Average percent cover of benthic community estimated on 20-m line transects installed at depths of 3 survey sites (SH: Shinheung; BC: Bukchon; SS: Seongsan). The percent cover is followed by standard error**.**

3.2. *A. japonica* population dynamics

The underwater photography revealed considerable differences in the percent coverage and density of *A. japonica* within and between sites (Table 2). The density of *A. japonica* in BC was 58.4 and 65.7 colonies m^{-2} at 10 m and 15 m depths respectively. Contrary to BC, the coral density was 29.0 and 40.4 colonies m^{-2} at 5 m and 15 m depths at SH and SS respectively. In the other transects, *A. japonica* was not observed, or less than 1 colony m^{-2} was accounted. The range of bleached and dead colonies of *A. japonica* were between1.8-5.7 % and 1.2-11.5 % respectively in the study sites, whereas the highest percentage (96.3 %) of live colonies was recorded as at 15 m depth at SS (Fig. 12). Even though the highest coral coverage and density were seen at BC, surprisingly the highest percentage of dead colonies (11.5 %) and bleached colonies (5.7 %) were reported at 10 m depth of BC as well.

Table 2. Summary of the percentage cover and density of *A. japonica* reported from Jeju Island, Korea.

Survey area (m^2)	**Depth (m)**	**Percent cover (%)**	**Density (colonies/m^2)**	**Location**	**Reference**
20	5	10.0 ± 3.1	29.0*	33°33′22″N, 126°39′14″E	Present study
	10	0.8 ± 0.4	0.8*		
	15	0.2 ± 0.1	0.1*		
20	5	0.4 ± 0.3	0.2*	33°33′12″N, 126°41′11″E	Present study
	10	45.9 ± 3.6	58.4*		
	15	72.8 ± 2.4	65.7*		
20	5	0.1 ± 0.1	0.1*	33°27′14″N, 126°56′39″E	Present study
	10	0	0*		
	15	15.3 ± 2.4	40.4*		
15.75	15	67.0 ± 4	Na	33°24′36″N, 126°13′12″E	Denis et al. 2015
10	10	75	87.8	33°26′56″N, 126°17′33″E	Vieira et al. 2016
10	10	75	154.7	33°17′44″N, 126°46′13″E	Vieira et al. 2016
10	10	na	57.9	33°23′42″N, 126°13′08″E	Noseworthy et al. 2016
1	15	na	7590	33°24′36″N, 126°13′12″E	Denis et al. 2015

Na, not available

*, whole colonies (live colony + bleached colony + dead colony).

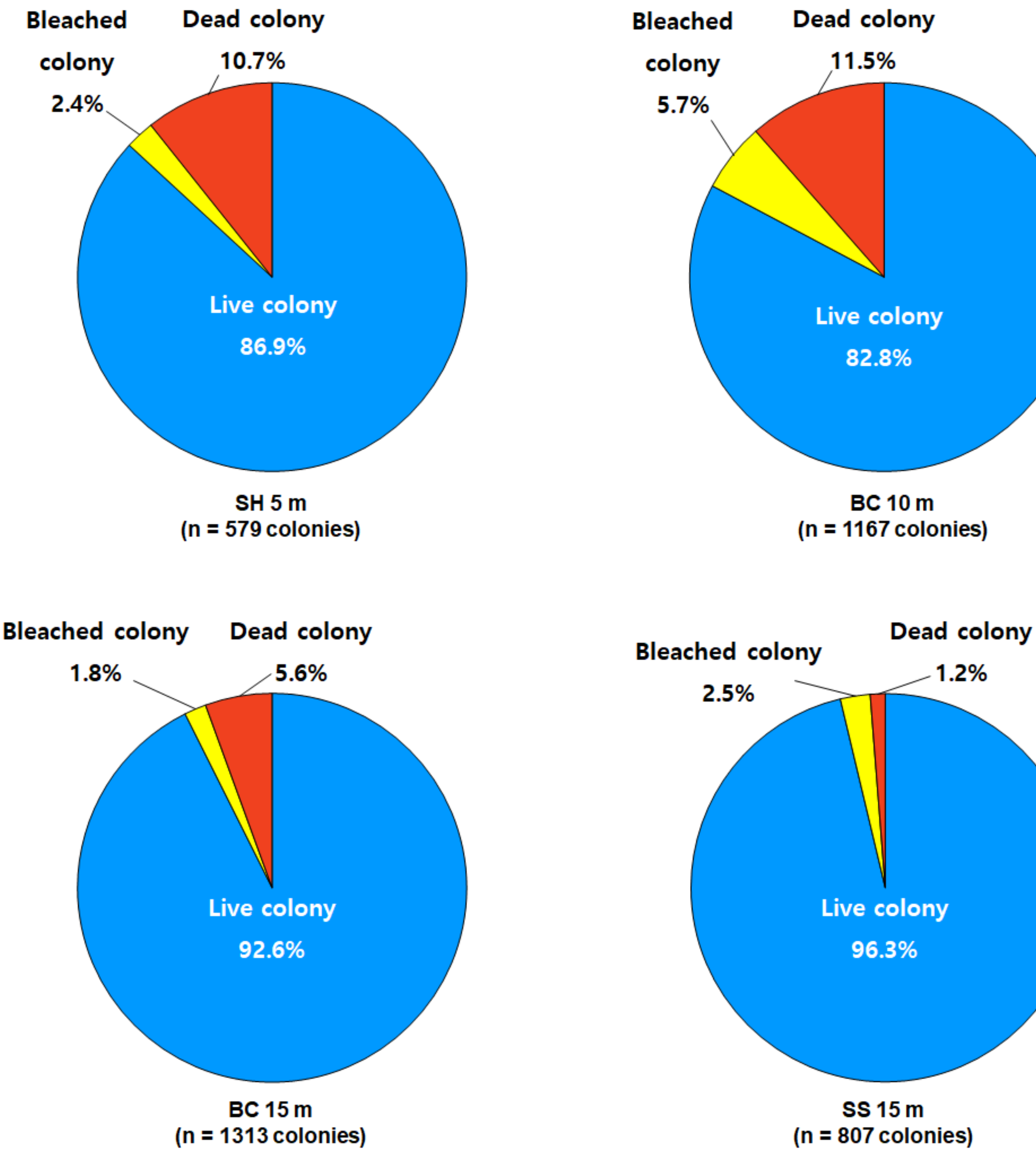

Fig. 12. The prevalence (%) of different conditions (live colony, bleached colony and dead colony) of *A. japonica* colonies observed on 20-m line transects installed at depths of 3 survey sites (SH: Shinheung; BC: Bukchon; SS: Seongsan). The total colonies (live colony + bleached colony + dead colony) are shown as “n”.

3.3. Cluster analysis

Cluster analysis based on percent cover of benthic organisms estimated from the transects showed two distinct groups corresponding to the northeast coast and east coast of Jeju Island (Fig. 13). The cluster analysis also suggested that the northeast coast could be subdivided into two subgroups. ANOSIM indicated significant differences between the groups (group 1-3; $p<0.005$; Fig. 13A). The three groups were characterized as follows: group 1 includes depths of 10 and 15 m at BC, group 2 contains all depths at SH and 5m depth at BC, and group 3 includes all depths at SS. SIMPER revealed *A. japonica* was a major benthic organism that contributed to the benthic community of group 1 and non-geniculate corallines were a common component at group 1 and 2. In contrast, group 3 consisted of various species such as geniculate corallines, *Plocamium* sp., *E. cava*, *Grateloupia* sp., *Peyssonnelia* sp., *Sargassum* spp. including non-geniculate corallines (Fig. 13B).

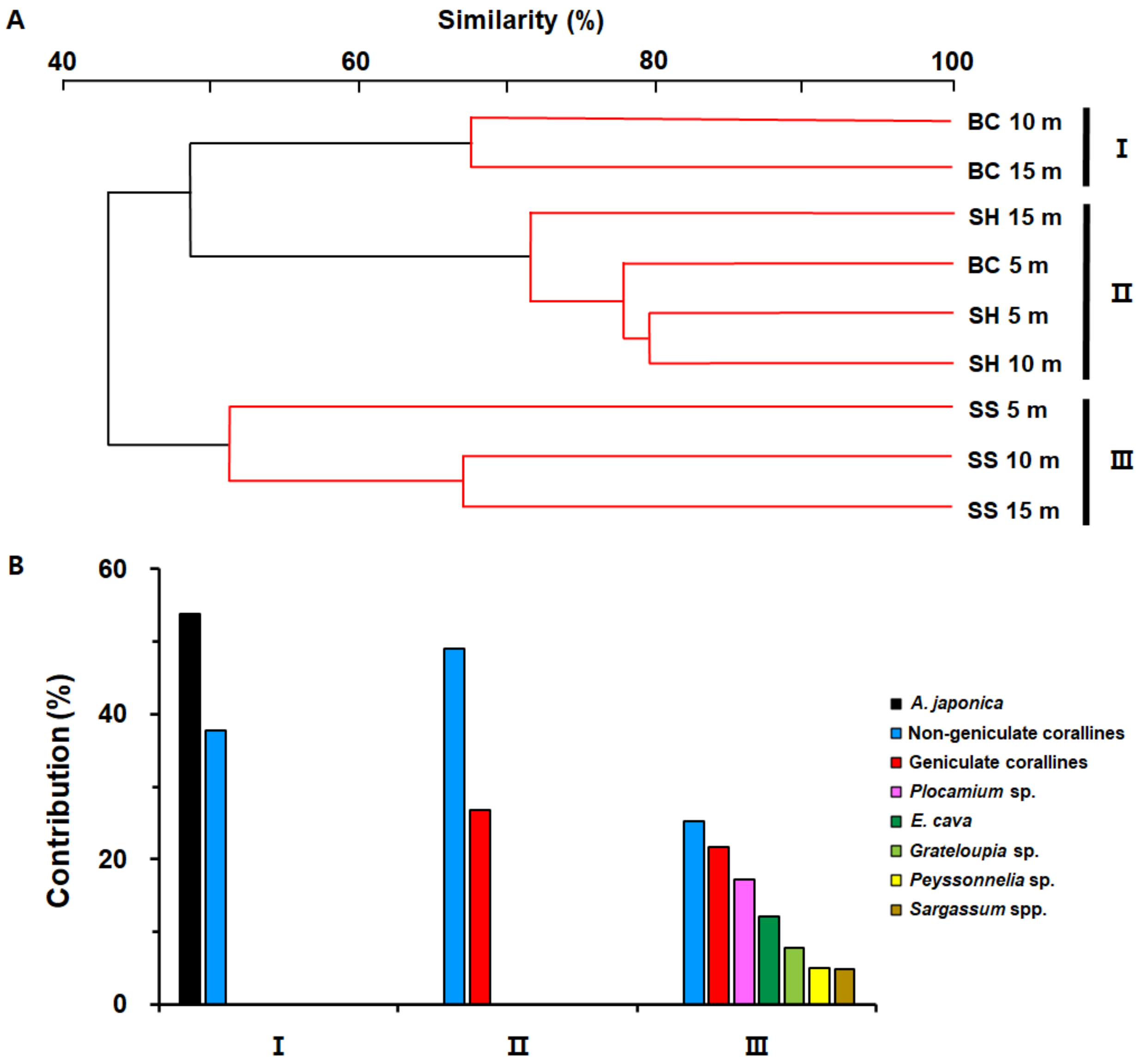

Fig. 13. (A) Dendrogram of cluster analysis (using Bray and Curtis similarity) based on the percent cover of benthic organisms at depths of 5 m, 10 m, 15 m of 3 survey sites (SH: Shinheung; BC: Bukchon; SS: Seongsan). Red lines are indicated groups by SIMPROF test. Three groups were detected (I: group 1; II: group 2; III: group 3; p<0.005). (B) The contribution of main benthic organisms (4 % <) among groups by SIMPER analysis.

4. Discussion

This study used high-resolution underwater photographs to identify and characterize benthic organisms living in the subtidal rocky substrate and extracted quantitative data (i.e., percent cover, density) on the benthic organisms including *A. japonica*. Our analysis revealed and as observed in previous studies, the percent cover of *A. japonica* estimated at BC (15 m depth) was similar to those reported in the previous study (Denis et al. 2015). However, the density of *A. japonica* reported was different from those in the previous study (Denis et al. 2015; Vieira et al. 2016; Noseworthy et al. 2016). These differences were probably due to several factors such as survey method, date, area and depth. Denis et al. (2015) reported juvenile coral density by counting the single polyps observed at 15 m depth, representing a mean number of 7590 recruits m^{-2}. In this study, the minimum size of *A. japonica* colonies that could be observed and analyzed was more than 1 cm and it seems likely that the resolution of camera used *in-situ* was insufficient to count small colonies. Diversity and distribution studies comes with a caveat. We acknowledge here that, on some occasions, camera image resolution cannot perform as expected due to uncontrollable underwater conditions. Also, it is difficult, form the images, to distinguish between geniculate and non-geniculate corallines composed of several species or have similar morphological features. Thus, these organisms were classified as one functional group. Long-term studies in future on spatial and temporal distribution patterns of benthos including *A. japonica* populations are necessary to understand the trends in changes related to the effects of climate change.

Association with Symbiodiniaceae species confer competitive advantages to their host (Cooper et al. 2011). In case of *A. japonica*, depending on the location they are known to associated with *Cladocopium* and *Fugacium* species respectively (Lien et al. 2012; LaJeunesse et al. 2018; Kang et al. 2020) and in some cases both *Cladocopium* sp. and *Fugacium* sp. simultaneously (Lien et al. 2012). The interaction between corals and their symbionts is known to exhibit specific activities depending on environmental conditions (Lien et al. 2012; Hughes et al. 2017). In this study, bleached and dead colonies of *A. japonica* at shallow depths (i.e., depths of 5 and 10 m) in a high light environment were found to be higher than that at a deeper depth, hence the abundance and preference of *A. japonica* to thrive at depths of 15 m. Innis et al. (2018) have shown that the coral *Montipora capitata* occurs as orange and brown color morphs due to the strong influence of depth and symbiont associations, and that light is the most crucial factor driving the distribution. Hence future studies to understand the distribution of *A. japonica* among depths can provide more information on their dominance and increasing population in Jeju Island.

Space competition is the main important interaction between scleractinian corals and algae in benthic communities (Underwood 2000; McCook et al. 2001). *A. japonica* has benefited from parallel occurrences of macroalgae decreasing in Jeju Island (Denis et al. 2015; Vieira et al. 2016; Kang et al. 2020). In this study, *A. japonica* colonies were most abundant at BC, whereas canopy-forming kelps were rare at all depths. In contrast, the lowest of abundance of *A. japonica* at depths of 5 to 10 m at SS coincided with a high percent cover of the macroalgal communities including kelps, geniculate corallines, and other macroalgae. A comparison of the benthic communities between BC and SS indicated that the space competition was observed for *A. japonica*, which interacted with kelps and rarely won, whereas competed successfully against other macroalgae, resulting in a higher relative abundance of *A. japonica* at BC. *A. japonica* growth forms are sub-massive, massive, or hemispherical (Sugihara et al. 2014). According to Swierts et al. (2016), coral growth forms associated with slow growth (i.e., massive, encrusting growth form) are successful in competing with benthic algae. The massive and encrusting forms survive stressful conditions better than other coral forms from the community-structural shift in Japan (Loya et al. 2001). Thus, *A. japonica* may dominate in Jeju Island more aggressively on their morphological characteristics.

Serisawa et al. (2004) reported the decline in *E. cava* population in Tosa Bay (Kochi-Japan), associated with the rising seawater temperature, resulting in bare grounds. This phenomenon is similar to 'getnoguem' in Korea (Kim et al. 2011; Vieira et al. 2016). Kelp forests were abundant around the coast until the end of 1980s in Jeju Island (Chung et al. 1998; Vieira et al. 2016). However, kelp forests have decreased its population size and non-geniculate corallines are rapidly occupying the empty space in Jeju Island (Chung et al. 1998; Denis et al. 2015; Vieira et al. 2016). Denis et al. (2015) mentioned that crustose coralline algae (i.e., non-geniculate corallines) represent dominant taxa in areas not colonized by *A. japonica* in Jeju Island. In this study, non-geniculate corallines were the dominant taxa in the barren grounds, where macroalgae rarely appeared at BC and SH. At the rocky substrate covered, predominantly by non-geniculate corallines were observed that various benthic fauna such as sponges and colonial ascidians including *A. japonica*.

In this survey, rhodolith and crustose growth forms of non-geniculate corallines with two morphological features were observed (Fig. 8C). Both rhodolith and crustose growth forms have been reported to provide important ecological functions towards the constitution of the benthic ecosystem (McCoy et al. 2015). Rhodolith forms provide an important rigid substrate for the attachment of benthic macroalgae (Fredericq et al. 2019), and the growth of rhodolith is promoted by the shaded from the canopy-forming kelp (Irving et al. 2004). Kamenos et al. (2008) reported that the high latitude rhodolith has slow-growth 200-300 μm year^{-1}. Temperate rhodolith are generally low light-adapted (Burdett et al. 2012; McCoy et al. 2015), and exposure to high light results in the reduction of photosynthetic activity and subsequent bleaching response (Irving et al. 2004; McCoy et al. 2015). In contrast, crustose forms are essential components of tropical reef systems (Burdett et al. 2014), providing suitable substrates or sufficient structures for coral larval settlement (Adey 1978; Burdett et al. 2014; McCoy et al. 2015). Crustose coralline algae (CCA) occupy a high proportion of the benthic bottom as a relatively flat form and thin thickness that makes them easy to overgrow (Dethier et al. 2001; McCoy et al. 2015). Tropical CCA are known fast-growing under high light through the ability of their dynamic photoinhibition strategies (Steneck et al. 1976; Adey 1978, 1998; Burdett et al. 2014; McCoy et al. 2015). Kim et al. (2011) documented that the cover of CCA, which were partly distributed in Jeju Island increased 10.9 % from 1998 to 2003 due to its persistence and continued northward range expansion. These changes could have a major irreversible impact on the benthic ecosystem in Jeju Island. Therefore, it is crucial to understand the changes in the benthic community compositions, and monitoring will be helpful to predict the changes by documenting the expansion or contraction of benthic organisms.

A. japonica and CCA opportunistically occupy the benthic substrates left vacant due to the decrease in the kelp forests in Jeju Island (Denis et al. 2015; Vieira et al. 2016). Such dominance of new benthic groups might create an altered biogenic habitat potentially available for other benthic organisms by providing suitable substrates or sufficient structures (McCoy et al. 2015; Vieira et al. 2016; Noseworthy et al. 2016). Noseworthy et al. (2016) reported that *A. japonica* provides a habitat for twenty-seven bivalves and gastropods attached to the surface or incorporated inside the skeleton. This indicates that the benthic interactions are crucial to the diversity of the community and may be subject to change as the benthic community changes occur through time.

5. Conclusion

In conclusion, this study utilized a non-destructive method to provide qualitative and quantitative information on the dynamics of benthic organisms at three sites in Jeju Island. The present study reveals that *A. japonica* dominates in the widest distribution with high density at depths of 10 and 15 m of BC where regionally endemic kelp forests almost disappeared and non-geniculate corallines covered to the benthic substrate. These results support the scenario of a recent *A. japonica* population increasing around Jeju Island from a small previously existing population (Vieira et al. 2016; Kang et al. 2020). *A. japonica* dominated the benthic communities of Jeju Island in the past two decades, which arouses environmental concern for its monitoring due to its kelp forests decline potential. The information obtained in this study contributes to our understanding of the major benthic community compositions in Jeju Island and provides a valuable baseline for exploring the interactions of benthic communities to future environmental changes.

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Acknowledgement

많은 분들의 도움이 없었다면 이 논문은 결코 완성될 수 없음을 고백합니다. 논문을 작성하는 동안 올바른 방향으로 나아갈 수 있도록 지도해주신 최광식 교수님께 깊은 감사를 드립니다. 교수님의 진심 어린 조언으로 한 발짝 더 성장할 수 있었으며, 그 가르침을 따라 연구자로서 의미 있는 삶을 살기 위해 최선을 다하겠습니다.

바쁘신 와중에 귀중한 시간을 내주시고 논문심사를 해주신 강도형 박사님과 박흥식 박사님께 진심으로 감사드립니다. 박상률 교수님과 연안생태학 연구실의 도움으로 논문의 실험을 진행할 수 있었습니다. 특히, 논문이 좋은 결과로 이어지기까지 먼저 손 내밀어 도움을 준 송병수께 감사의 마음을 전합니다. 또한 논문의 결과 해석 및 많은 조언을 해주신 Shashank keshavmurthy 박사님께 감사드립니다.

지난 2 년여 간의 논문을 작성하는 석사과정은 저에게 새로운 도전이었고, 그 과정에서 포착되는 것들이나, 그 안에 수놓으려는 것들, 채우려는 것들에 대해 믿음, 자신감, 떳떳함을 갖기 위한 수많은 힘겨운 순간들이 있었습니다. 그 때마다 아낌없는 응원과 조언을 해주신 홍현기 박사님, 김현중 박사님, 이혜미 박사님께 깊은 감사를 드립니다. 학위과정 동안 함께 한 영관이형, 칸트, 상현, 종섭, 진수, 정화, 마이, 윤화 덕분에 석사과정을 잘 마무리할 수 있었고, 감사한 마음을 전합니다.

언제나 한결같은 마음으로 응원해주는 우리 가족, 사랑하는 아버지와 어머니, 지원, 지선 진심으로 감사드립니다. 많이 부족한 남편이지만 자신보다 더 소중하게 여겨주는 우리 아내 김지은, 사랑스러운 우리 아들 이시완, 진심으로 감사하고 사랑합니다. 또한 저를 믿고 힘이 되어주시는 장인어른, 장모님, 처남 그리고 이외에도 저의 곁에서 용기와 격려를 건네주신 모든 분들께 진심으로 감사드립니다.

이경태 올림

But he knows the way that I take; when he has tested me, I will come forth as gold.

(Job 23:10)