Article

Changes in the Dynamics and Nutrient Budget of a Macroalgal Community Exposed to Land-Based Fish Farm Discharge Off Jeju Island, Korea

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Abstract: This study aimed to investigate the dynamics of the nutrient budget of a macroalgal community exposed to water discharged from aquaculture farms. This study was conducted in the coastal area exposed to water discharged from aquaculture farms located on Jeju Island, Korea, in May and October of 2017. Water-column-dissolved inorganic nutrient concentrations were higher in the intertidal zone than in the subtidal zone. High nutrient concentrations in the intertidal zone resulted in the bloom of *Ulva* spp., consequently leading to a low species number. This indicates the vulnerability of the intertidal macroalgal community to discharge from land-based aquaculture. *Ecklonia cava* contributed to 29–53% of the total incorporation of carbon (C), nitrogen (N), and phosphorus (P) in the subtidal zone. In the intertidal zone, the highest tissue N content was found in *Ulva* spp. due to the high and rapid nutrient uptake rate from the effluent with high nutrient concentrations, thereby indicating high total N incorporation. The estimated total C, N, and P incorporation rates by macroalgae were 181.5, 8.6, and 0.95 tons year^{−1}, respectively. These results suggest that the macroalgal community in this area absorbs or removes large amounts of nutrients from the water column and plays an important role in the budgets and cycling of nutrients in the surrounding coastal areas.

Keywords: ecological role; fish farm effluent; macroalgal community structure; nutrient incorporation; nutrient sink; *Ulva* spp.; *Ecklonia cava*

1. Introduction

Coastal areas are among the most valuable ecosystems in the world due to their high biodiversity and productivity [1]. However, coastal areas have been severely affected by natural and anthropogenic events such as climate change, coastal development, and excessive nutrient release from various human-related activities [2–4]. In particular, effluents from aquaculture and sewage treatments cause coastal eutrophication, which results in algal blooms, hypoxia, and changes in the macroalgal community [5–7]. Green macroalgal blooms in the Gulf of California are caused by fertilizer runoff through channels and

streams [8]. Since 1986, the number of land-based fish farms on Jeju Island, Korea, has increased rapidly, with more than 350 land-based fish farms along the coast of Jeju Island as of 2020 [9]. As a result of this increase, a large amount of fish farm effluent with high nutrient concentrations is discharged off the coast of the island [10,11]. Therefore, macroalgal dynamics in terms of changes in community structure and nutrient incorporation by macroalgae have received considerable attention in an attempt to understand the nutrient budgets and current status of the coastal ecosystems off Jeju Island.

Macroalgae have been used as bioindicators in the assessment of ecosystem health status in the world [12,13]. Due to the sensitivity of macroalgae to various stresses, macroalgal assemblages are widely considered as ecological indicators for monitoring and impact evaluation studies [14–16]. In contrast to mobile marine organisms, the macroalgal assemblage on a rocky shore reflects the present, as well as previous, environmental conditions [17,18]. Macroalgae exhibiting distinct zonation patterns in the intertidal and subtidal zones are exposed to highly variable environmental conditions, depending on the tidal level [19–21]. Given that effluents from fish farms flow into nearby coastal areas, intertidal macroalgal communities are more sensitive to effluent exposure, compared with other communities [22,23]. Thus, the structure of a given macroalgal community has been used as an effective tool for investigating the effects of nutrient enrichment in rocky shore coastal ecosystems [6,21]. In particular, the macroalgal community of Jeju Island is expected to have distinctive distributional characteristics due to exposure to effluents from land-based fish farms.

Macroalgae are the primary producers in rocky shore coastal ecosystems, providing material circulation, food sources, habitats, and spawning grounds for various marine organisms such as fish and shellfish [21,24,25]. Macroalgae are involved in rapid carbon cycling due to short-lived perennials or annual ephemerals [26]. Specifically, the bloom-forming macroalgae or kelp species take up and sequester large amounts of nutrients such as carbon (C), nitrogen (N), and phosphorus (P), thereby serving as an efficient nutrient sink [27,28]. Macroalgae play an important role in nutrient cycling in coastal and estuarine ecosystems [29]. Macroalgae can be used as bioremediation agents for heavy-metal-contaminated effluents [30]. Recent studies have focused on the potential role of kelp forests as carbon sinks in blue carbon assessments [29,31]. In addition, macroalgae act as efficient biofilters for reducing excessive nutrients from fish farm effluents in integrated multi-trophic aquacultural systems [32]. Thus, the macroalgal community plays an important role in maintaining the global ecosystem balance by absorbing nutrients and heavy metals [30,33–35].

The purpose of this study was to investigate the dynamics of a coastal macroalgal community exposed to water discharged from aquaculture farms. In addition, we examined the total C, N, and P budgets of the macroalgal community based on biomass and biochemical composition measurements. We hypothesized that changes in the macroalgal community structure due to fish farm effluent exposure would occur in the intertidal zone and that this rocky shore macroalgal community plays important ecological roles in carbon sequestration and as a nutrient sink. The distribution, coverage, biomass, and biochemical composition of macroalgae from the intertidal to subtidal zones were investigated to test these hypotheses, with the aim of providing important scientific information on the ecological roles of macroalgal communities in the coastal area off Jeju Island.

2. Materials and Methods

2.1. Study Area

The study site was located off Handong (33°32′42.8″ N, 126°50′03.2″ E) on the northeastern coast of Jeju Island, Korea (Figure 1). This area has a rocky shore that is composed of flat volcanic bedrock and sand. Here, the coast is exposed to high wave action and rapid water flow due to high winds. Land-based fish aquaculture farms operate in the vicinity of the coastal area and discharge large amounts of inorganic nutrients [36]. Additionally, a considerable amount of submarine groundwater discharge with high nutrient concen-

trations flows into the area [10]. The high inflow of concentrated nutrients has resulted in eutrophication [10,37]. Oh et al. [36] provided detailed information related to the pattern in coastal waters caused by land-based fish farms' wastewater-borne nutrients.

Figure 1. Study area off Handong on the northeastern coast of Jeju Island, Korea. Each color represents a rocky shore zone in the study area. Total area of Handong is approximately 2,150,000 m².

The tidal regime in this area is semidiurnal and mesotidal, with a maximum tidal range of approximately 2.2 m during spring tides (Tide Tables for the Coast of Korea, Korea Hydrographic and Oceanographic Administration; <http://www.khoa.go.kr>, accessed on 20 October 2021). *Ulva* spp., *Corallina pilulifera*, *Chondracanthus tenellus*, and crustose coralline algae are the most common algae in the intertidal zone. *Undaria pinnatifida*, *Dictyota coriacea*, *Gelidium amansii*, and crustose coralline algae dominate at a water depth range of 0–7 m, whereas the predominant species at 7–22 m are the red alga *Peyssonnelia caulifera* and the large brown alga *Ecklonia cava*.

2.2. Environmental Factors

Water temperature (°C) at 0–0.5 m below mean sea level was measured in Seongsan on the east coast of Jeju Island, approximately 13 km from the study area; measurements were taken every 10 min from January to December of 2017 using HOBO temperature data loggers (Onset Computer Corp., Bourne, MA, USA). Measured water temperatures were averaged daily. Four replicate surface water samples were collected in the study area in May and October of 2017 to determine the inorganic nutrient concentrations (NH₄⁺, NO₃[−] + NO₂[−], and PO₄^{3−}) in the water column. All samples were filtered through GF/F filters (Whatman, pore size: 0.7 µm). The samples were stored in 50 mL conical tube and frozen until analysis. The NO₃[−] + NO₂[−] concentration in each sample was determined after running the sample through a column containing copper-coated cadmium, which reduces NO₃[−] to NO₂[−]. Water column nutrient concentrations were analyzed using standard colorimetric techniques, following the procedures of Parsons et al. [38].

2.3. Experimental Design and Data Collection

Field surveys were conducted along the rocky shore (approximately 1.42 km² from the supratidal zone to the subtidal zone) in May and October of 2017. This study area was divided into six zones according to physical and biological factors establishing precise limits of distribution—two intertidal zones (upper intertidal zone (UI) and lower intertidal zone (LI)) and four subtidal zones (0–4 m (S1), 4–7 m (S2), 7–17 m (S3), and 17–22 m (S4) below mean sea level)—based on the macroalgal community structure. However, there were no macroalgae in the supratidal zone and in the 22–25-m zone of the subtidal zone.

The area of rocky substrate was estimated for each zone based on actual measurement data acquired from scuba diving and satellite imagery via Google Earth. Six quadrats (0.25 m^2) were randomly placed on rocky substrate in each zone to determine the coverage and biomass of macroalgae. The percentage cover of each species was measured in the field using a 0.25 m^2 stainless-steel frame with 100 subplots. Only macroalgal thalli with holdfasts in the quadrat were included when recording data on cover. The recorded macroalgal percentage cover sometimes exceeded 100% because data on both canopy and understory cover were recorded. The percentage cover of each species was estimated using an efficient and accurate visual estimation method [39]. All quadrats were photographed for reconfirmation, and then all macroalgae, except for crustose coralline algae, inside the quadrat were collected for species identification and biomass measurement. Macroalgae were identified to the lowest possible taxonomic level, except coralline algae. For species identification, the scientific names were checked to see if they were currently accepted on “AlgaeBase” (<http://www.algaebase.org>, accessed on 20 October 2021). Additionally, species identification was determined using the following literature: Bae et al. [40], Boo et al. [41], Kang [42], Kim [43], Kim and Boo [44], Kim et al. [45], Kim and Hwang [46], Lee [47], Nam [48], Nam and Kang [49,50], and Yoshida [51]. The collected samples were thoroughly cleaned of epiphytes and sediment with tap water and dried at 60°C to a constant weight. Dried samples were weighed, and the biomass of each species was converted into a dry weight per unit area estimate (g DW m^{-2}).

2.4. Elemental Analysis and Nutrient Incorporation

Macroalgal samples ($n = 3$ per each species) were collected in May 2017 to determine tissue C, N, and P contents. The whole blade or thallus of samples was dried at 60°C . The dried samples were then ground using a tissue grinder (TissueLyser II, QIAGEN, Hilden, Germany). Approximately 1.5–2.5 mg of ground tissue was placed in a tin capsule for the determination of tissue C and N contents using a CHN elemental analyzer (Flash EA 1112; Thermo Finnigan, Milan, Italy). Tissue P content was analyzed using the molybdovanadophosphate method after nitric acid/perchloric acid digestion [52]. Approximately 10–15 mg of ground macroalgal tissue was combusted at 550°C for 5 h. The ash was dissolved with 2N hydrochloric acid, and distilled water was then added. Ammonium-vanadomolybdate reagent was added to the extracts, and colorimetric measurements were taken at 410 nm. Nutrient contents were calculated on a dry weight basis, and elemental ratios were calculated on a mole:mole basis.

The amounts of C, N, and P incorporated into tissues were estimated from the biomass and nutrient contents of each species. Most macroalgae recruit during the fall and winter, achieve their highest biomass during the spring, and then disappear during the summer. Thus, we used the biomass of each species measured between May and October of 2017 to estimate annual production. Nutrient incorporation, defined as the amount of C, N, or P allocated to macroalgal tissues, was calculated using the following equation:

$$\begin{aligned} & \text{Nutrient (C, N or P) incorporation (g C, N or P dry weight m}^{-2}\text{)} \\ &= \text{macroalgal biomass (g dry weight m}^{-2}\text{)} \times \text{tissue nutrient (C, N, or P) content}/100. \end{aligned} \quad (1)$$

The total C, N, and P amounts incorporated by the macroalgae in each zone were estimated by multiplying macroalgal C, N, and P incorporation by the macroalgal distributional area (area of rocky substrate $\times$ macroalgal percent cover) in each zone.

2.5. Data Analysis

The data are shown as the mean $\pm$ standard error. All data were tested for normality and homogeneity of variance to meet the assumptions of parametric statistical analysis. The significance of differences in dissolved inorganic nutrient (NH_4^+ , $\text{NO}_3^- + \text{NO}_2^-$, PO_4^{3-}) concentrations in the water column and the coverage and biomass of macroalgae among sampling times and zones was determined using two-way analysis of variance (ANOVA). Differences in tissue nutrient (C, N, and P) contents among macroalgal species

were assessed using one-way ANOVA. When significant differences were observed among treatments, a Student–Newman–Keuls (SNK) post hoc test was performed. We used an alpha level of 0.05 for all statistical tests. All statistical analyses were performed using SPSS Statistics 20.0 (IBM Corporation, Armonk, NY, USA).

3. Results

3.1. Environmental Factors

Daily water temperature exhibited a clear seasonal trend, being highest (28.5 °C) in August and lowest (13.7 °C) in March (Figure 2). The mean annual water temperature in 2017 was 19.1 °C. Water-column-dissolved inorganic nutrient (NH_4^+ , $\text{NO}_3^- + \text{NO}_2^-$, PO_4^{3-}) concentrations at 0 m from the coastline were significantly ($P < 0.001$ in all) higher than those at 300 m from the coastline in both May and October (Figure 3). The water column NH_4^+ concentration at 0 m ranged from 2.4 ± 0.1 to 3.4 ± 0.1 μM , whereas the average NH_4^+ concentration at 300 m was less than 1 μM . In particular, the water column $\text{NO}_3^- + \text{NO}_2^-$ concentration was highest at 0 m (51.8 and 73.7 μM in May and October, respectively). At 300 m, the $\text{NO}_3^- + \text{NO}_2^-$ concentration in the water column was 1.5 μM in May and 3.4 μM in October. The average water column PO_4^{3-} concentrations at 0 and 300 m were 2.2 and 0.3 μM , respectively.

Figure 2. Water temperature in the study area off Jeju Island from January to December 2017.

Figure 3. Surface water NH_4^+ , $\text{NO}_3^- + \text{NO}_2^-$, and PO_4^{3-} concentrations in the study area off Jeju Island, Korea. Water-column nutrient concentrations are represented as the mean $\pm$ standard error (n = 4).

3.2. Distributional Area, Cover, and Biomass of Macroalgae

The total area of the study site was about 1,420,862 m² (Figure 1; Table 1). Of this, the total areas of rocky and sand substrates were 1,058,600 (74.5%) and 362,262 m² (25.5%), respectively. The rocky area in the intertidal zone was 123,312 m² (8.7%), consisting of the UI zone (55,701 m²) and the LI zone (67,611 m²). The rocky area in the subtidal zone was 864,824 m² (60.9%); notably, macroalgae were not found in the 22–25-m zone (84,483 m², 5.9%). The S3 and S2 areas in the subtidal zone accounted for 24.6% and 15.3% of the total area, respectively.

Table 1. Areas and distance from the coastline of rocky and sandy substrates and tidal zones and their percentages relative to the total study area.

Location	Distance from the Coastline (m)	Area (m ²)	% of Total Area
Sandy substrate, total		362,262	25.5
Rocky substrate, total		1,058,600	74.5
Supratidal zone		70,664	5.0
Intertidal zone, total		123,312	8.7
Upper intertidal zone (UI)	73–174	55,701	3.9
Lower intertidal zone (LI)	119–227	67,611	4.8
Subtidal zone, total		864,824	60.9
0–4-m zone (S1)	251–459	127,689	9.0
4–7-m zone (S2)	493–872	217,960	15.3
7–17-m zone (S3)	940–1277	349,053	24.6
17–22-m zone (S4)	1044–1316	85,639	6.0
22–25-m zone (S5)	1228–1338	84,483	5.9
Total		1,420,862	100.0

Thirty-eight macroalgal species (2 Chlorophyta, 6 Phaeophyceae, and 30 Rhodophyta) were identified in the study area during the experimental period (Tables 2 and 3). The total species numbers in the intertidal zone and subtidal zone were 19 and 23, respectively, with the highest numbers recorded in May and the lowest in October. The total species number was higher in the LI zone than in the UI zone throughout the experimental period (Table 2). Total algal cover in the two intertidal zones was highest (average 94.2%) in May and lowest (average 61.2%) in October. *Ulva* spp. were the dominant species in the intertidal zone in May (Table 2). The cover (and relative cover) of *Ulva* spp. in the UI and LI zones was 61.8% (70.3%) and 46.3% (46.9%), respectively. By contrast, the algal community in the two intertidal zones was dominated by crustose coralline algae in October, with the relative percentage cover of crustose coralline algae exceeding 50%. In the subtidal zone, the total species number was lowest in the S3 zone (Table 3). The total percentage cover in zones S1, S2, and S3 exceeded 100% due to the presence of a macroalgal canopy in those areas, whereas the macroalgal cover in zone S4 was less than 70% during May. The total algal percentage cover ranged from $50.5 \pm 1.0\%$ in zone S4 to $108.3 \pm 5.8\%$ in zone S3 in October. The dominant species were crustose coralline algae and *Gelidium amansii* in zone S1 and *Ecklonia cava* and erect coralline algae in zone S2. In particular, *E. cava* was the dominant species in terms of percentage cover ($82.3 \pm 3.9\%$ in May and $56.6 \pm 3.3\%$ in October) in zone S3, with a relative percentage cover of more than 50%. Additionally, the percentage cover of *Peyssonnelia caulifera* and *Grateloupia angusta*, crustose and erect coralline algae, exceeded 10%. In zone S4, the percentage cover (and relative cover) of *P. caulifera* was $46.3 \pm 4.5\%$ ($66.9 \pm 3.8\%$) in May and $36.5 \pm 1.0\%$ ($72.3 \pm 2.1\%$) in October.

Table 2. Macroalgal species number, percentage cover, relative percentage cover, and biomass in the intertidal zone in May and October of 2017. Values are presented as the mean $\pm$ standard error (n = 6).

Species Name	Species Number		Percentage Cover		Relative Percentage Cover		Biomass	
	May	October	May	October	May	October	May	October
Upper intertidal zone (UI)								
Chlorophyta	1	1	61.8 $\pm$ 6.9	24.5 $\pm$ 3.2	70.3 $\pm$ 8.3	41.2 $\pm$ 4.8	202.7 $\pm$ 26.5	7.1 $\pm$ 1.3
<i>Ulva</i> spp.	✓	✓	61.8 $\pm$ 6.9	24.5 $\pm$ 3.2	70.3 $\pm$ 8.3	41.2 $\pm$ 4.8	202.7 $\pm$ 26.5	7.1 $\pm$ 1.3
Phaeophyceae	0	0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0
Rhodophyta	7	4	27.5 $\pm$ 8.2	34.8 $\pm$ 2.8	29.7 $\pm$ 8.3	58.8 $\pm$ 4.8	182.3 $\pm$ 82.4	3.9 $\pm$ 2.2
<i>Ahnfeltiopsis flabelliformis</i>	✓		1.7 $\pm$ 0.3		1.9 $\pm$ 0.4		8.2 $\pm$ 2.4	
<i>Chondracanthus intermedius</i>		✓		1.3 $\pm$ 0.8		2.3 $\pm$ 1.4		+
<i>Chondracanthus tenellus</i>	✓		+		+		+	
<i>Chondrus ocellatus</i>	✓		+		+		2.9 $\pm$ 1.2	
<i>Corallina pilulifera</i>	✓	✓	17.5 $\pm$ 8.0	3.0 $\pm$ 1.8	18.4 $\pm$ 8.3	4.7 $\pm$ 2.7	158.8 $\pm$ 80.0	3.6 $\pm$ 2.4
Crustose coralline algae	✓	✓	4.8 $\pm$ 0.3	29.5 $\pm$ 2.3	5.5 $\pm$ 0.6	50.0 $\pm$ 4.5	*	*
<i>Gelidium amansii</i>	✓		+		+		+	
<i>Gelidium divaricatum</i>		✓		+		1.8 $\pm$ 1.1		+
<i>Polyopes prolifer</i>	✓		2.3 $\pm$ 0.3		2.6 $\pm$ 0.3		11.3 $\pm$ 1.9	
Total	8	5	89.3 $\pm$ 4.9	59.3 $\pm$ 2.9	100.0 $\pm$ 0.0	100.0 $\pm$ 0.0	385.0 $\pm$ 69.3	11.0 $\pm$ 2.9
Lower intertidal zone (LI)								
Chlorophyta	1	1	46.3 $\pm$ 6.2	2.3 $\pm$ 0.3	46.9 $\pm$ 6.4	3.7 $\pm$ 0.7	159.3 $\pm$ 30.8	2.9 $\pm$ 1.2
<i>Ulva</i> spp.	✓	✓	46.3 $\pm$ 6.2	2.3 $\pm$ 0.3	46.9 $\pm$ 6.4	3.7 $\pm$ 0.7	159.3 $\pm$ 30.8	2.9 $\pm$ 1.2
Phaeophyceae	2	0	+	0.0 $\pm$ 0.0	+	0.0 $\pm$ 0.0	1.1 $\pm$ 1.0	0.0 $\pm$ 0.0
<i>Colpomenia sinuosa</i>	✓		+		+		+	
<i>Sargassum fulvellum</i>	✓		+		+		+	
Rhodophyta	10	7	52.2 $\pm$ 6.2	60.8 $\pm$ 5.5	52.6 $\pm$ 6.2	96.3 $\pm$ 0.7	394 $\pm$ 51.4	65.5 $\pm$ 7.9
<i>Ahnfeltiopsis flabelliformis</i>	✓	✓	2.0 $\pm$ 2.0	+	2.0 $\pm$ 2.0	+	10.4 $\pm$ 10.4	+
<i>Chondracanthus tenellus</i>	✓	✓	14.3 $\pm$ 2.6	8.3 $\pm$ 0.9	14.4 $\pm$ 2.6	13.1 $\pm$ 0.8	109.4 $\pm$ 38.6	18.7 $\pm$ 2.9
<i>Chondrus ocellatus</i>		✓		+		1.4 $\pm$ 0.9		1.8 $\pm$ 1.1
Crustose coralline algae	✓	✓	3.3 $\pm$ 0.6	37.5 $\pm$ 4.1	3.4 $\pm$ 0.6	59.2 $\pm$ 1.8	*	*
<i>Eucheuma</i> sp.	✓		+		+		8.8 $\pm$ 8.8	
<i>Fushitsunagia catenata</i>	✓		4.3 $\pm$ 1.7		4.4 $\pm$ 1.7		21.8 $\pm$ 8.6	
<i>Gelidium amansii</i>	✓	✓	18.0 $\pm$ 2.7	3.8 $\pm$ 1.7	18.2 $\pm$ 2.7	5.5 $\pm$ 2.2	186.6 $\pm$ 25.5	6.2 $\pm$ 3.8
<i>Gracilaria incurvata</i>	✓		+		+		5.6 $\pm$ 3.9	
<i>Grateloupia elata</i>	✓	✓	7.3 $\pm$ 1.4	9.5 $\pm$ 1.9	7.4 $\pm$ 1.5	15.7 $\pm$ 3.4	43.5 $\pm$ 13.7	37.9 $\pm$ 10.5
<i>Grateloupia elliptica</i>	✓		+		+		2.2 $\pm$ 0.9	
<i>Palisada intermedia</i>	✓		+		+		5.7 $\pm$ 5.7	
<i>Pterocladia capillacea</i>		✓		+		+		+
Total	13	8	99.0 $\pm$ 0.4	63.0 $\pm$ 5.4	100.0 $\pm$ 0.0	100.0 $\pm$ 0.0	554.3 $\pm$ 40.9	68.4 $\pm$ 7.0

✓ Presence of algal species; + Percentage cover or biomass of less than 1% or 1.0 g dry weight m⁻², respectively. * Represents the biomass of crustose coralline algae, which could not be measured due to the crustose characteristic of these species.

Table 3. Macroalgal species number, percentage cover, relative percentage cover, and biomass in the subtidal zone in May and October of 2017. Values are presented as the mean $\pm$ standard error (n = 6).

Species Name	Species Number		Percentage Cover		Relative Percentage Cover		Biomass	
	May	October	May	October	May	October	May	October
0–4 m depth zone (S1)								
Chlorophyta	1	0	5.4 $\pm$ 5.4	0.0 $\pm$ 0.0	4.3 $\pm$ 4.3	0.0 $\pm$ 0.0	+	0.0 $\pm$ 0.0
<i>Codium contractum</i>	✓		5.4 $\pm$ 5.4		4.3 $\pm$ 4.3		+	
Phaeophyceae	3	0	35.6 $\pm$ 11.1	0.0 $\pm$ 0.0	31.5 $\pm$ 9.7	0.0 $\pm$ 0.0	30.6 $\pm$ 9.1	0.0 $\pm$ 0.0
<i>Dictyota coriacea</i>	✓		33.4 $\pm$ 10.4		29.6 $\pm$ 9.2		29.5 $\pm$ 8.7	
<i>Ecklonia cava</i>	✓		+		+		+	
<i>Rugulopteryx okamurae</i>	✓		2.0 $\pm$ 0.6		1.7 $\pm$ 0.5		+	
Rhodophyta	7	4	70.8 $\pm$ 14.0	93.5 $\pm$ 1.3	64.2 $\pm$ 12.5	100.0 $\pm$ 0.0	150.5 $\pm$ 86.6	119.7 $\pm$ 20.0
Crustose coralline algae	✓	✓	35.8 $\pm$ 5.7	44.5 $\pm$ 4.1	32.7 $\pm$ 6.2	47.8 $\pm$ 5.0	*	*
Erect coralline algae	✓		6.6 $\pm$ 3.1		5.5 $\pm$ 2.3		27.1 $\pm$ 15.1	
<i>Gelidium amansii</i>	✓	✓	18.6 $\pm$ 15.5	47.3 $\pm$ 5.4	18.1 $\pm$ 15.5	50.3 $\pm$ 5.1	106.1 $\pm$ 90.6	116.6 $\pm$ 19.7
<i>Gelidium yoshidae</i>	✓		6.4 $\pm$ 6.4		4.9 $\pm$ 4.9		6.4 $\pm$ 6.4	
<i>Gracilaria textorii</i>	✓		+		+		1.6 $\pm$ 1.6	
<i>Pachymeniopsis lanceolata</i>	✓	✓	1.2 $\pm$ 1.2	+	+	+	1.9 $\pm$ 1.9	2.8 $\pm$ 2.0
<i>Plocamium leptophyllum</i>	✓	✓		1.3 $\pm$ 0.3		1.3 $\pm$ 0.3		+
<i>Pterocladia capillacea</i>	✓		1.2 $\pm$ 0.6		1.2 $\pm$ 0.6		7.2 $\pm$ 4.2	
Total	11	4	111.9 $\pm$ 7.3	93.5 $\pm$ 1.3	100.0 $\pm$ 0.0	100.0 $\pm$ 0.0	181.4 $\pm$ 77.8	119.7 $\pm$ 20.0
4–7 m depth zone (S2)								
Chlorophyta	0	1	0.0 $\pm$ 0.0	+	0.0 $\pm$ 0.0	+	0.0 $\pm$ 0.0	+
<i>Codium contractum</i>		✓		+		+		+
Phaeophyceae	4	1	56.3 $\pm$ 7.7	29.8 $\pm$ 1.3	41.7 $\pm$ 4.7	33.9 $\pm$ 2.8	194.8 $\pm$ 28.1	214.9 $\pm$ 41.6
<i>Colpomenia sinuosa</i>	✓		+		+		+	
<i>Ecklonia cava</i>	✓	✓	39.7 $\pm$ 13.0	29.8 $\pm$ 1.3	29.9 $\pm$ 9.8	33.9 $\pm$ 2.8	119.4 $\pm$ 51.1	214.9 $\pm$ 41.6
<i>Rugulopteryx okamurae</i>	✓		+		+		+	
<i>Undaria pinnatifida</i>	✓		16.0 $\pm$ 11.4		11.3 $\pm$ 8.0		75.0 $\pm$ 67.3	
Rhodophyta	5	5	78.3 $\pm$ 6.1	58.8 $\pm$ 4.7	58.3 $\pm$ 4.7	65.9 $\pm$ 2.7	405.8 $\pm$ 46.4	157.4 $\pm$ 26.2
Crustose coralline algae	✓	✓	6.0 $\pm$ 2.1	26.8 $\pm$ 7.1	4.6 $\pm$ 1.8	29.3 $\pm$ 6.9	*	*
<i>Dichotomaria apiculata</i>	✓		8.7 $\pm$ 2.6		6.6 $\pm$ 2.2		34.9 $\pm$ 20.2	
<i>Dichotomaria falcata</i>	✓		+		+		1.4 $\pm$ 1.4	
Erect coralline algae	✓	✓	62.3 $\pm$ 7.4	28.0 $\pm$ 4.7	46.1 $\pm$ 4.1	32.1 $\pm$ 6.0	359.8 $\pm$ 62.0	150.6 $\pm$ 29.8
<i>Gelidium amansii</i>		✓		1.3 $\pm$ 1.3		1.3 $\pm$ 1.3		1.9 $\pm$ 1.9
<i>Gelidium yoshidae</i>		✓		2.3 $\pm$ 0.6		2.5 $\pm$ 0.7		4.6 $\pm$ 1.9
<i>Grateloupia angusta</i>	✓	✓	+	+	+	+	9.8 $\pm$ 9.8	+
Total	9	7	134.7 $\pm$ 5.9	88.8 $\pm$ 3.9	100.0 $\pm$ 0.0	100.0 $\pm$ 0.0	600.6 $\pm$ 66.9	372.3 $\pm$ 67.3

Table 3. Macroalgal species number, percentage cover, relative percentage cover, and biomass in the subtidal zone in May and October of 2017. Values are presented as the mean $\pm$ standard error (n = 6).

Species Name	Species Number		Percentage Cover		Relative Percentage Cover		Biomass	
	May	October	May	October	May	October	May	October
7–17 m depth zone (S3)								
Chlorophyta	0	0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0
Phaeophyceae	1	1	82.3 $\pm$ 3.9	56.5 $\pm$ 3.3	58.6 $\pm$ 1.5	52.5 $\pm$ 3.8	346 $\pm$ 25.5	280.3 $\pm$ 31.1
<i>Ecklonia cava</i>	✓	✓	82.3 $\pm$ 3.9	56.5 $\pm$ 3.3	58.6 $\pm$ 1.5	52.5 $\pm$ 3.8	346.0 $\pm$ 25.5	280.3 $\pm$ 31.1
Rhodophyta	6	5	58.4 $\pm$ 4.6	51.8 $\pm$ 5.9	41.4 $\pm$ 1.5	47.5 $\pm$ 3.8	145.5 $\pm$ 20.2	85.0 $\pm$ 26.2
Crustose coralline algae	✓	✓	8.3 $\pm$ 1.7	21.3 $\pm$ 4.6	5.9 $\pm$ 1.0	19.3 $\pm$ 3.5	*	*
<i>Dichotomaria apiculata</i>	✓		4.0 $\pm$ 0.0		2.9 $\pm$ 0.2		4.9 $\pm$ 1.3	
Erect coralline algae	✓	✓	16.7 $\pm$ 3.9	11.8 $\pm$ 1.3	11.7 $\pm$ 2.4	10.9 $\pm$ 1.2	14.1 $\pm$ 2.6	16.0 $\pm$ 1.4
<i>Grateloupia angusta</i>	✓	✓	9.7 $\pm$ 2.4	9.8 $\pm$ 2.2	6.8 $\pm$ 1.6	9.1 $\pm$ 2.1	16.5 $\pm$ 3.1	31.6 $\pm$ 12.3
<i>Peyssonnelia caulifera</i>	✓	✓	19.3 $\pm$ 1.2	8.5 $\pm$ 1.6	13.9 $\pm$ 1.6	7.8 $\pm$ 1.1	110.0 $\pm$ 18.2	37.3 $\pm$ 15.4
<i>Plocamium telfairiae</i>	✓	✓	+	+	+	+	+	+
Total	7	6	140.7 $\pm$ 7.8	108.3 $\pm$ 5.8	100.0 $\pm$ 0.0	100.0 $\pm$ 0.0	491.5 $\pm$ 45.7	365.3 $\pm$ 14.5
17–22 m depth zone (S4)								
Chlorophyta	0	0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0
Phaeophyceae	1	1	3.3 $\pm$ 1.8	3.8 $\pm$ 1.1	4.6 $\pm$ 2.4	7.5 $\pm$ 2.3	6.7 $\pm$ 4.2	1.5 $\pm$ 0.3
<i>Ecklonia cava</i>	✓	✓	3.3 $\pm$ 1.8	3.8 $\pm$ 1.1	4.6 $\pm$ 2.4	7.5 $\pm$ 2.3	6.7 $\pm$ 4.2	1.5 $\pm$ 0.3
Rhodophyta	10	4	65.7 $\pm$ 2.2	46.8 $\pm$ 1.8	95.4 $\pm$ 2.4	92.5 $\pm$ 2.3	105.0 $\pm$ 9.2	97.4 $\pm$ 8.4
<i>Acrosorium polyneurum</i>	✓		1.3 $\pm$ 0.3		1.9 $\pm$ 0.4		+	
<i>Ardissonula regularis</i>	✓		2.0 $\pm$ 2.0		3.1 $\pm$ 3.1		1.2 $\pm$ 1.2	
Crustose coralline algae	✓	✓	5.7 $\pm$ 0.7	4.5 $\pm$ 0.5	8.2 $\pm$ 0.5	8.9 $\pm$ 0.9	*	*
<i>Dichotomaria falcata</i>	✓		2.7 $\pm$ 1.8		4.1 $\pm$ 2.8		1.8 $\pm$ 1.5	
<i>Gracilaria cuneifolia</i>	✓		1.7 $\pm$ 0.3		2.4 $\pm$ 0.4		+	
<i>Grateloupia angusta</i>	✓	✓	+	4.3 $\pm$ 1.3	+	8.3 $\pm$ 2.4	+	9.3 $\pm$ 3.5
<i>Osmundaria fimbriata</i>	✓		+		+		+	
<i>Peyssonnelia caulifera</i>	✓	✓	46.3 $\pm$ 4.5	36.5 $\pm$ 1.0	66.9 $\pm$ 3.8	72.3 $\pm$ 2.1	98.0 $\pm$ 11.0	88.0 $\pm$ 6.7
<i>Plocamium leptophyllum</i>	✓		+		+		+	
<i>Plocamium telfairiae</i>	✓	✓	4.7 $\pm$ 2.7	1.5 $\pm$ 0.6	6.8 $\pm$ 4.1	3.0 $\pm$ 1.3	2.6 $\pm$ 1.3	+
Total	11	5	69.0 $\pm$ 3.6	50.5 $\pm$ 1.0	100.0 $\pm$ 0.0	100.0 $\pm$ 0.0	111.7 $\pm$ 13.4	98.9 $\pm$ 8.4

✓ Presence of algal species; + Percentage cover or biomass of less than 1% or 1.0 g dry weight m⁻², respectively. * Represents the biomass of crustose coralline algae, which could not be measured due to the crustose characteristic of these species.

The macroalgal biomass was higher in May than in October (Tables 2 and 3). The total biomass of macroalgae in zone S2 was significantly higher ($P < 0.001$) than those in the other zones. Additionally, the biomass of macroalgae in the subtidal zone was higher than that in the intertidal zone. In May, *Ulva* spp. and *Corallina pilulifera* had the highest biomasses (202.7 ± 26.5 and 158.8 ± 80.0 g DW m⁻², respectively) in the UI zone, and the biomasses of three species (*Ulva* spp., *Chondracanthus tenellus*, and *G. amansii*) were more than 100 g DW m⁻² in the LI zone (Table 2). In the subtidal zone, only one species (*G. amansii*) in zone S1 was observed to have a biomass greater than 100 g DW m⁻² (Table 3). *Ecklonia cava* had the highest biomass in both S2 and S3. In zone S2, the biomass of erect coralline algae in May and October was 359.8 ± 62.0 and 150.6 ± 29.8 g DW m⁻², respectively. *Peyssonnelia caulifera* had high biomass in zones S3 and S4, ranging from 110.0 ± 18.2 to 37.3 ± 15.4 g DW m⁻².

3.3. Elemental Analysis and Nutrient Incorporation

The C, N, and P contents in macroalgal tissues varied according to the species (Table 4). *Dictyota coriacea* and *G. amansii* had the highest tissue C contents. The tissue C content across macroalgal species ranged from $15.7 \pm 0.2\%$ to $38.57 \pm 0.15\%$. The tissue N content was highest (average 4.25%) in *Ulva* spp., *Polyopes prolifer*, and *Grateloupia elata* and lowest (0.20%) in erect coralline algae. The macroalgal tissue P content ranged from $0.061 \pm 0.003\%$ in erect coralline algae to $0.368 \pm 0.013\%$ in *P. prolifer*, with an average of 0.167%. The atomic C:N ratio of macroalgal tissues was highest in erect coralline algae and lowest in *Ulva* spp., *P. prolifer*, and *G. elata* (Table 4). The N:P ratio of macroalgal tissues ranged from 7.78 ± 1.83 in erect coralline algae to 56.32 ± 2.07 in *Grateloupia textorii*.

Areal C, N, and P incorporation into macroalgal tissues varied with the season, with the largest amounts incorporated in May and the lowest in October (Figure 4A–C). In May, areal C, N, and P incorporation was higher in the LI zone than in any other zones, whereas the highest areal C, N, and P incorporation in October was recorded for zone S3. Areal C, N, and P incorporation was higher in the intertidal zone than in the subtidal zone in May, whereas very large amounts were incorporated in the subtidal zone compared with the intertidal zone in October. The amounts of C, N, and P incorporated per unit area at the study site were 122.0, 6.2, and 0.7 g m⁻² in May (79.0, 3.4, and 0.4 g m⁻² in October), respectively. The total amounts of C, N, and P incorporated were higher in May than in October, with the highest values recorded for zone S3 (Figure 4D–F). In addition, the total amounts of C, N, and P incorporated in the subtidal zone were 5.0–39.0-, 2.2–16.4-, and 3.7–31.4-fold those in the intertidal zone, respectively. Total C incorporation into macroalgal tissues was estimated to be approximately 181.5 tons C year⁻¹. The calculated N and P amounts incorporated annually into macroalgal tissues were about 8.6 and 1.0 tons, respectively. In this study, the total amounts of C, N, and P incorporated by perennial algae were higher than those by annual algae (Figure 5). *Ecklonia cava*, a perennial brown alga, incorporated the largest amounts of C, N, and P annually (96.9, 3.3, and 0.4 tons, respectively). Annual C incorporation by erect coralline algae, *P. caulifera* and *G. amansii*, was more than 10 tons. Only two annual species, *Ulva* spp. and *Undaria pinnatifida*, incorporated large total amounts of C, N, and P. In particular, *Ulva* spp. incorporated 0.9 tons of N in May, whereas the total P amounts incorporated by *P. caulifera* in May and October were 93.1 and 40.9 kg, respectively (Figure 5B,C).

Table 4. The tissue carbon (C), nitrogen (N), and phosphorus (P) content (%), C:N ratio, and N:P ratio of macroalgae in the study area off Jeju Island, Korea. Values are presented as the mean $\pm$ standard error (n = 3 per each species). UI: upper intertidal zone, LI: lower intertidal zone, S1: 0–4 m depth zone, S2: 4–7 m depth zone, S3: 7–17 m depth zone, S4: 17–22 m depth zone.

Species Name		Sampling Location	Tissue C Content	Tissue N Content	Tissue P Content	C:N Ratio	N:P Ratio
Chlorophyta	<i>Ulva</i> spp.	UI	35.21 $\pm$ 0.78	4.27 $\pm$ 0.10	0.242 $\pm$ 0.009	9.62 $\pm$ 0.17	40.52 $\pm$ 2.04
Pheophyceae	<i>Dictyota coriacea</i>	S1	38.26 $\pm$ 0.29	1.40 $\pm$ 0.09	0.095 $\pm$ 0.003	32.22 $\pm$ 2.25	33.56 $\pm$ 1.18
	<i>Ecklonia cava</i>	S3	32.96 $\pm$ 0.81	1.10 $\pm$ 0.06	0.150 $\pm$ 0.010	34.97 $\pm$ 1.46	16.87 $\pm$ 0.68
	<i>Undaria pinnatifida</i>	S2	30.12 $\pm$ 0.71	1.17 $\pm$ 0.06	0.197 $\pm$ 0.005	30.07 $\pm$ 0.87	13.58 $\pm$ 0.56
	<i>Ahnfeltiopsis flabelliformis</i>	LI	28.59 $\pm$ 0.56	2.72 $\pm$ 0.19	0.162 $\pm$ 0.007	12.41 $\pm$ 1.11	38.37 $\pm$ 1.12
Rhodophyta	<i>Chondracanthus tenellus</i>	LI	27.87 $\pm$ 0.19	1.40 $\pm$ 0.05	0.209 $\pm$ 0.003	23.34 $\pm$ 0.73	15.27 $\pm$ 0.36
	<i>Chondrus ocellatus</i>	UI	29.54 $\pm$ 0.92	2.71 $\pm$ 0.40	0.244 $\pm$ 0.011	13.32 $\pm$ 2.12	25.20 $\pm$ 2.88
	<i>Corallina pilulifera</i>	UI	15.74 $\pm$ 0.17	1.54 $\pm$ 0.02	0.167 $\pm$ 0.004	11.90 $\pm$ 0.04	21.07 $\pm$ 0.22
	<i>Dichotomaria apiculata</i>	S2	27.61 $\pm$ 0.69	2.13 $\pm$ 0.30	0.121 $\pm$ 0.005	15.81 $\pm$ 2.42	39.78 $\pm$ 4.21
	<i>Dichotomaria falcata</i>	S4	25.02 $\pm$ 0.53	1.75 $\pm$ 0.07	0.099 $\pm$ 0.003	16.70 $\pm$ 0.75	40.74 $\pm$ 2.05
	Erect coralline algae	S2	16.03 $\pm$ 0.18	0.20 $\pm$ 0.04	0.061 $\pm$ 0.003	100.22 $\pm$ 20.90	7.78 $\pm$ 1.83
	<i>Eucheuma</i> sp.	LI	17.33 $\pm$ 0.26	1.04 $\pm$ 0.01	0.116 $\pm$ 0.003	19.41 $\pm$ 0.37	20.64 $\pm$ 0.47
	<i>Fushitsunagia catenata</i>	LI	24.79 $\pm$ 0.23	2.53 $\pm$ 0.07	0.227 $\pm$ 0.007	11.46 $\pm$ 0.23	25.40 $\pm$ 0.37
	<i>Gelidium amansii</i>	LI	38.57 $\pm$ 0.15	2.57 $\pm$ 0.13	0.205 $\pm$ 0.009	17.58 $\pm$ 0.79	28.64 $\pm$ 0.97
	<i>Gracilaria incurvata</i>	LI	26.39 $\pm$ 0.14	2.14 $\pm$ 0.03	0.137 $\pm$ 0.005	14.42 $\pm$ 0.25	35.78 $\pm$ 0.81
	<i>Gracilaria textorii</i>	S1	31.84 $\pm$ 0.05	2.52 $\pm$ 0.04	0.102 $\pm$ 0.002	14.73 $\pm$ 0.23	56.52 $\pm$ 2.07
	<i>Grateloupia angusta</i>	S3	36.38 $\pm$ 0.35	2.65 $\pm$ 0.11	0.241 $\pm$ 0.009	16.04 $\pm$ 0.66	25.18 $\pm$ 0.85
	<i>Grateloupia elata</i>	LI	35.83 $\pm$ 0.23	4.29 $\pm$ 0.09	0.201 $\pm$ 0.013	9.74 $\pm$ 0.15	49.22 $\pm$ 2.74
	<i>Grateloupia elliptica</i>	LI	33.16 $\pm$ 0.08	2.89 $\pm$ 0.09	0.241 $\pm$ 0.016	13.42 $\pm$ 0.38	27.53 $\pm$ 1.09
	<i>Pachymeniopsis lanceolata</i>	S1	31.87 $\pm$ 0.29	1.15 $\pm$ 0.04	0.087 $\pm$ 0.002	32.27 $\pm$ 0.86	30.28 $\pm$ 0.27
	<i>Palisada intermedia</i>	LI	26.50 $\pm$ 1.09	1.82 $\pm$ 0.04	0.105 $\pm$ 0.003	17.02 $\pm$ 0.72	39.69 $\pm$ 1.13
	<i>Peyssonnelia caulifera</i>	S3	24.22 $\pm$ 0.42	2.10 $\pm$ 0.16	0.199 $\pm$ 0.008	13.59 $\pm$ 0.92	24.08 $\pm$ 0.92
	<i>Plocamium telfairiae</i>	S4	32.74 $\pm$ 0.56	2.98 $\pm$ 0.04	0.168 $\pm$ 0.004	12.85 $\pm$ 0.41	40.42 $\pm$ 0.64
	<i>Polyopes prolifer</i>	UI	35.49 $\pm$ 0.38	4.20 $\pm$ 0.08	0.368 $\pm$ 0.013	9.86 $\pm$ 0.28	26.19 $\pm$ 1.31
	<i>Pterocladia capillacea</i>	S1	36.25 $\pm$ 1.00	1.97 $\pm$ 0.06	0.119 $\pm$ 0.001	21.56 $\pm$ 1.16	37.76 $\pm$ 1.52

Figure 4. Areal and total estimates of carbon (A,D), nitrogen (B,E), and phosphorus (C,F) incorporation by the macroalgal community off Handong, Jeju Island, Korea, in May and October. UI, upper intertidal zone; LI, lower intertidal zone; S1, 0–4 m below the mean sea level; S2, 4–7 m zone; S3, 7–17 m zone; S4, 17–22 m zone; I, intertidal zone; S, subtidal zone.

Figure 5. Total estimates of carbon (A), nitrogen (B), and phosphorus (C) incorporated by the main macroalgae off Handong, Jeju Island, Korea in May and October; Ec, *Ecklonia cava*; Er, erect coralline algae; Pe, *Peyssonnelia caulifera*; Ge, *Gelidium amansii*; UI, *Ulva* spp.; Un, *Undaria pinnatifida*; Ch, *Chondracanthus tenellus*; Di, *Dictyota coriacea*; Co, *Corallina pilulifera*.

4. Discussion

4.1. Macroalgal Community Dynamics

In the present study, changes in macroalgal community structure across the rocky shore may be affected by variations in water-column concentrations between the intertidal and subtidal zones. The macroalgal community in the intertidal zone clearly responded, in terms of changes in structure, to effluent from fish farms with high nutrient concentrations, especially in May. Higher N concentrations in the water allowed for an increase in the tissue N content of *Ulva* spp. (4.27 ± 0.10). This result is similar to that of Kim et al. [6], who reported the tissue N content of *U. australis* (4.34 ± 0.30) at the study site, which was close to a sewage treatment plant. Thus, this facilitated the growth and development of *Ulva* spp. Overall, *Ulva* spp. dominated in the intertidal zone where higher N concentrations in the water were observed. Additionally, only four species had a cover of more than 1% in the intertidal zone. *Ulva* spp. are characterized by high growth at high nutrient concentrations and a rapid uptake rate of nutrients, resulting in algal blooms [32,53]. Several studies have reported a decline in species diversity and an increase in opportunistic species, such as *Ulva* spp., upon exposure to sewage discharge [54–56]. Blooms of *Ulva* spp. resulted in a decline in species richness and diversity in a macroalgal community near a sewage outfall [57].

Erect and crustose coralline algae commonly observed in both intertidal and subtidal areas play an important role in ecological marine systems and are often found with over 50% coverage on rocky reefs in temperate climates [58,59]. Essentially, erect and crustose coralline algae showed high coverage along the coast of Jeju Island [60–62]. In this study, erect and crustose coralline algae exhibited high coverage from the intertidal to subtidal zones. In particular, the biomasses of erect coralline algae in the UI and S2 zones accounted for approximately 50% of the total biomass in May. Currently, their biomass and coverage are expanding from the intertidal to subtidal zones due to climate change and herbivory [63]. This may be due to the responses of coralline algae to rising seawater temperatures. The sea surface temperature in the coastal waters of Jeju Island has increased by 1.94 °C for the last 86 years (1924–2009) [64]. Although global ocean acidification results in low pH levels, which have negative impacts on the growth of coralline algae [65], elevated water temperature offsets the negative effects of ocean acidification [66]. This suggests that the decline of erect and crustose coralline algae may not be observed on the coast of Jeju Island.

In 2003, brown algae such as *Sargassum thumbergii* and *S. fusiforme* (reported as *Hizikia fusiformis*) were dominant in the intertidal zone along the northeastern coast of Jeju Island [62]. However, the brown alga, *S. fulvellum*, was recorded at less than 1% in this study. Large brown algae have been observed to decline in a macroalgal benthic community exposed to high N conditions [55,67]. Exposure to sewage effluent resulted in a decline in zygote germination, a delay in embryo growth, and increases in embryo mortality and the photosynthetic efficiency of brown algae [68,69]. Additionally, large brown or perennial algae were replaced by opportunistic or turf-forming species due to differences in their nutrient uptake rates [67,70]. Thus, these results indicate that large brown algae in the intertidal zone may be seriously affected by fish farm effluent with high nutrient concentrations.

In this study, the macroalgal community in the subtidal zone exhibited a distinct zonation pattern. Specifically, *E. cava* was the dominant species in terms of coverage and biomass (approximately >50%) in zones S2 and S3 in May and October. Kelp forests are called “ecosystem engineers” as they provide complex habitats for many organisms and affect the abiotic and biotic environments around them [12,71]. *Ecklonia cava* is a representative perennial alga that forms kelp forests in the subtidal zone off rocky coasts of Korea and Japan [72,73]. Overall, the number, cover, and biomass of macroalgal species in zones S2 and S3 were higher than those in intertidal areas, similar to the results of previous studies of other Jeju Island sites [60,62]. This indicates that the macroalgal community structure in the subtidal zone was not strongly affected by the effluent. Thus, our results strongly support our first hypothesis—that the response of the macroalgal

community, in terms of changes in structure, to fish farm effluent would primarily occur in the intertidal zone.

4.2. Ecological Role as a Nutrient Sink

Discussion of the ability of vegetated coastal ecosystems to store and sequester large amounts of organic carbon (called “blue carbon”) is largely restricted to tidal marshes, mangrove forests, and seagrass beds [74]. Seaweed habitats including kelp forests have not been included in the blue carbon strategies [75]. Nevertheless, they certainly serve as a significant carbon sink [33]. Estimates of global carbon sequestration by all macroalgae are very high, ranging from 61 to 268 Tg C year^{−1} [76,77]; thus, seaweed habitats, typically kelp forests, may hold considerable carbon stocks in coastal areas, and their role as carbon sinks has become a major focus of international attention [31]. In this study, total C incorporation by seaweed was 110.2 tons in May and 71.3 tons in October. Among macroalgal species, *E. cava*, a large brown alga, incorporated the most C in both May and October. This result is attributable to the morphological characteristics and life cycle of *E. cava*. In temperate regions, most algae generally decline, or disappear completely, during the summer when the water temperature increases and then reappear during September and October; their biomass and productivity are especially high during the spring season [34,78,79]. By contrast, *E. cava* is a large perennial species and thereby maintains high biomass in the subtidal zone in autumn. Thus, *E. cava* beds play a vital role as standing stocks of organic carbon and are key components of organic carbon cycling off the coast of Jeju Island, considering that *E. cava* is the dominant species forming kelp forests and the major habitat-forming organism in subtidal areas.

Coralline algae act as a carbon dioxide sink via photosynthesis and CaCO₃ dissolution; the potential estimate of global carbon sequestration by erect and crustose coralline alga is 1.6×10^9 tons C year^{−1} [80]. In this study, erect coralline algae incorporated the second-highest amount of C annually due to high biomass in the UI and S2 zones and morphological characteristics. In addition, crustose coralline algae may incorporate a considerable amount of carbon into their skeleton. A few studies presented that the increase in atmospheric CO₂ results in a reduction in seawater pH, which inhibits the growth of erect and crustose coralline algae [65,66]. However, elevated water temperature under low seawater pH enhances the growth of coralline algae [66]. These coralline algae prefer ammonium rather than nitrate as nitrogen sources [81]. The growth rate and calcification of encrusting coralline algae are considerably enhanced when they are exposed to high ammonium concentrations under ambient and high-pCO₂ environments [82]. The effluent from land-based fish farms has relatively high concentrations of total ammonia nitrogen (ammonia + ammonium) as well as total oxidized nitrogen (nitrite + nitrate) [32]. Thus, the growth of coralline algae is maintained by high ammonia concentrations and the increase in water temperature. This indicates that coralline algae may play an important role as a carbon sink.

Similar to its incorporation of total C, *E. cava* also incorporated the most total N and P, with average values of 1,642.6 and 221.5 kg, respectively. Erect coralline algae showed low total N incorporation due to low tissue N content. Remarkably, *Ulva* spp. incorporated more total N (942.8 kg) in May, although the area covered by this species was low in the entire study area. *Ulva* species are green-tide-forming macroalgae that exhibit a high affinity for nutrients [83,84]. They are widely used as nutrient (especially N) biofilters for effluents from land-based integrated aquaculture systems due to their high N uptake rate, growth, and tissue N content [11,32,85]. Green tides caused by *Ulva* blooms have been observed off the southern coast of Korea during the winter–spring season [86,87]. In this study, *Ulva* spp., which had a high cover and biomass in the intertidal zone in May, were directly affected by the fish farm discharge. Moreover, *Ulva* spp. had a high tissue N content ($4.27 \pm 0.10\%$), reflecting the high N concentration in the water column. This implies that *Ulva* spp. contribute to improving water quality by acting as a nutrient

sink; because these species incorporate very large amounts of nutrients, they may play an ecologically important role in nutrient cycling in coastal ecosystems.

5. Conclusions

Fish farm effluent with high nutrient concentrations distinctly impacted macroalgal community structure in the intertidal zone. Overall, *Ulva* spp. characterized by high growth at high nutrient concentrations and rapid nutrient uptake rates dominated the intertidal zone; only four species had a cover of more than 1%. By contrast, the macroalgal community structure in the subtidal zone was only slightly affected by the discharge from land-based aquaculture. Perennial algae such as *E. cava*, erect coralline algae, and *P. caulifera* had high cover and biomasses in the subtidal zone. This indicates that the assemblage structure and composition of intertidal macroalgae are conspicuously affected by fish farm effluent. *Ecklonia cava* incorporated the most total C, N, and P in May and October due to its high biomass and characteristics as a perennial alga. In particular, *Ulva* spp. appear to play an important role as a nutrient sink that removes anthropogenically generated nutrients from over-enriched discharge, such as that from fish farms during the spring. However, further work is required to elucidate the contribution of the macroalgal community to the carbon budget and nutrient cycling in coastal areas.

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