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RESEARCH ARTICLE

Food web structure of a restored macroalgal bed in the eastern Korean peninsula determined by C and N stable isotope analyses

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Abstract Loss of macroalgae habitats has been widespread on rocky marine coastlines of the eastern Korean peninsula, and efforts for restoration and creation of macroalgal beds have increasingly been made to mitigate these habitat losses. Deploying artificial reefs of concrete pyramids with kelps attached has been commonly used and applied in this study. As a part of an effort to evaluate structural and functional recovery of created and restored habitat, the macroalgal community and food web structure were studied about a year after the establishment of the artificial macroalgal bed, making comparisons with nearby natural counterparts and barren ground communities. Dominant species, total abundance, and community structure of macroalgal assemblage at the restored macroalgal bed recovered to the neighboring natural bed levels during the study period. The main primary producers (phytoplankton and macroalgae) were isotopically well separated. δ^{13}C and δ^{15}N values of consumers were very similar between restored and natural beds but varied greatly among functional feeding groups. The range of consumer δ^{13}C was as wide as that of primary producers, indicating the trophic importance of both producers. There was a stepwise trophic enrichment in δ^{15}N with increasing trophic level. A comparison of isotope signatures between primary producers and consumers showed that, while suspension feeders are highly dependent on pelagic sources, invertebrates of other feeding guilds and fishes mainly use macroalgae-derived organic matter as their ultimate nutritional sources in both macroalgal beds, emphasizing the high equivalency of trophic structure between both beds. Isotopic signatures of a few mollusks and sea urchins showed that they use different dietary items in macroalgal-barren grounds compared with macroalgal beds, probably reflecting their feeding plasticity according to the low macroalgal biomass. However, isotopic signatures of most of the consumers at the barren ground were consistent with those at the macroalgal beds, supporting the important trophic role of drifting algae. Our results revealed the recoveries of the macroalgal community and trophic structure at the restored habitat. Further studies on colonization of early settlers and the following succession progress are needed to better understand the process and recovery rate in the developing benthic community.

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Introduction

Macroalgae have an enormous productivity on various coasts and play a significant role as a direct food source of herbivores and as a detritus source entering detrital food chains (Rosenthal et al. 1974; Dunton and Schell 1987; Duggins et al. 1989; Fredriksen 2003; Nybakken and

Bertness 2005; Bode et al. 2006). In addition to their role as primary producers, they provide habitats for many other organisms including invertebrates, fishes, and marine mammals (Moore 1986; Vadas and Elner 1992). Accordingly, because macroalgal beds support high biodiversity and complex food webs in coastal zones, global and local destruction of macroalgal beds, in particular kelp beds, has recently emerged as an important issue with respect to the collapse of coastal ecosystems (Mann 2000; Jackson et al. 2001; Steneck et al. 2002).

Macroalgal beds on rocky marine coastlines of eastern and southeastern Korea are one of the most threatened communities worldwide, having lost over 20% (about 70 km^2 of a total of 330 km^2) of their historical area (NFRDI 2006a; http://www.lib.noaa.gov/korea/wildstock_enhancement). Macroalgae grow only in narrow coastal bands where plants receive enough light for photosynthesis; loss of this habitat appears to be widespread on the coast of the Korean peninsula and are almost gone at some localities. The term "*isoyake*" was used for the decrease of macroalgae in the Japanese coastal zones (Yendo 1902). Steneck et al. (2002) described different patterns and processes of algal decline or kelp deforestation at different geographical regions, including physiological stress and thereby disease, under oceanographic anomalies in temperature, salinity or nutrients, grazing by herbivorous sea urchins, ocean-climate change, trophic cascade effects due to changes in coastal biodiversity, and decline in water quality etc. The massive losses of macroalgal habitats on the coast of Korea have also been explained by these different causes and interactions among the various processes at different localities (MOMAF 2002; NFRDI 2006a).

Efforts towards restoration and creation of macroalgae beds have increasingly been made to mitigate these habitat losses on the coast of Korea (MOMAF 2002; NFRDI 2006a). Various techniques for the construction of artificial macroalgal beds have been developed and commonly used on Korean coasts (http://www.lib.noaa.gov/korea/wildstock_enhancement). These pioneer studies on macroalgal restoration demonstrated the recovery of abundance and diversity in benthic invertebrates and nekton in restored macroalgal beds as barren grounds slowly returned to macroalgal habitats. They also showed that the gut contents of fish from both natural and restored macroalgal habitats are largely composed of benthic invertebrates inhabiting macroalgal beds. Restoration efforts are designed to restore barren grounds to the ecosystem structure and function of natural macroalgal beds. Therefore, along with community structure, a major axis in the recovery of ecological function of macroalgal beds includes trophic support and/or trophic transfer from producers to consumers (see Currin et al. 2003; Moseman et al. 2004). Despite their ecological importance, there is little information on organic matter flow through food webs in the restoration process of macroalgal beds.

While the traditional method using the analysis of gut contents has difficulty in identifying primary organic matter sources of consumers, the carbon and nitrogen stable isotope technique has been widely used in tracking ultimate carbon sources and food web structure because tissue isotope signatures of consumers reflect those of assimilated dietary sources (DeNiro and Epstein 1978; Fry and Sherr 1984; Hobson and Welch 1992). Particularly, this technique has been successfully applied to identification of trophic/functional recovery of macrofaunal and fish communities in the process of coastal marsh restoration (Talley 2000; Currin et al. 2003; Moseman et al. 2004; Wozniak et al. 2006). These approaches were based on consumer isotope composition that was closely related to distinct isotope signatures of dominant marsh species, and concluded that monitoring consumer isotope signatures along with dominant primary producers provides a reasonable indication of how food web support functions change in response to restoration.

Consequently, measurement of isotope signatures for a macroalgal bed community was expected to provide valuable information on the recovery of ecological function in restored macroalgal systems. Macroalgal $\delta^{13}C$ values are known to be quite variable but distinct from those of other primary producers such as phytoplankton (Fry and Sherr 1984; Stephenson et al. 1986; France 1995). Numerous studies showed that many consumer organisms inhabiting macroalgal beds have isotope values similar to those of macroalgae, indicating the great importance of organic matter originating from macroalgae as a dietary source to animals (Dunton and Schell 1987; Duggins et al. 1989; Jennings et al. 1997; Kaehler et al. 2000; Pinnegar and Polunin 2000; Fredriksen 2003).

The present study examined carbon and nitrogen stable isotope ratios of dominant consumers (macroinvertebrates and fish) and primary producers to identify food web support and trophic pathways in a restored macroalgal bed community on the eastern coast of Korea. It also makes comparisons with a nearby natural counterpart and a barren ground community. Their isotope signatures were determined as indicators of trophic structures with the hypothesis that, when the recovery of algal biomass in restored macroalgal beds increases the availability of macroalgal-derived food sources, the isotope signatures of consumers in restored beds change toward those of the natural bed.

Materials and methods

Study site

The study was conducted at the centre of the east coast of Korea (37°21′N, 129°15′E). Along the exposed eastern coastline of Korea, tidal amplitude is very low (less than 30 cm) and macroalgal habitats are well developed on the sublittoral rocky beds. Because the loss of macroalgal habitat was most striking on the eastern coast of the Korean peninsula, artificial reefs have been dropped on the sea bottom to restore and enhance the macroalgal habitat since 2002 (NFRDI 2006a).

The artificial reef we studied was submerged on October 2003 at a depth ranging from 7 to 10 m on a rocky bottom of 100 × 100 m area on the coast of Samchoek City (Fig. 1). A total of 79 sets of artificial reefs were deployed on barren ground in the fall in order to provide 3 months of acclimation prior to establishment of seedling plants. A set of artificial reef consisted of two truncated square concrete pyramids. The faces of the two pyramids were inclined at an angle of 60° and the inner part of the pyramid was opened in order to maximize its stability. The base of the two pyramids had a breadth of 2.6 m and a length of 2 m. Each pyramid had a height of 1.5 m. A 6 m length of longline was hung with leaves of *Saccharina japonica* and deployed between two pyramid reefs, 1 m above the top of the pyramid. Adult leaves of *Eisenia bicyclis*, *Ecklonia cava*, *Ecklonia stolonifera*, *Undaria pinnatifida*, and *Sargassum horneri* were transplanted onto the truncated top of each pyramid in order to lure grazers on barren grounds and thereby lower the grazing pressure on small-sized algal leaves colonizing below. More method details are described elsewhere (NFRDI 2006a, b; http://www.lib.noaa.gov/korea/wildstock_enhancement/ecosystem.htm).

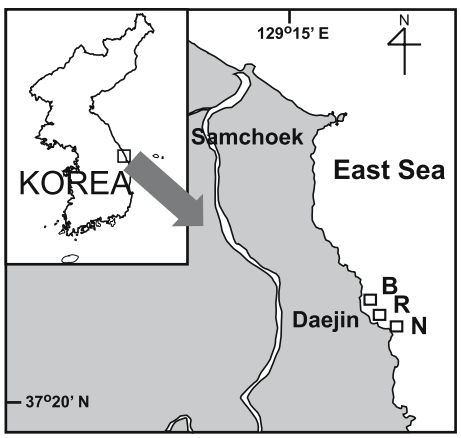

Fig. 1 Map showing the study area. *N* natural macroalgal bed, *R* restored bed, *B* barren ground

The natural macroalgal habitat and barren ground adjacent to the artificially created bed were studied for comparison. Both were located about 500 m from the restored macroalgal bed at a depth of 7–10 m. The natural and restored macroalgal beds and barren ground were separated from one another by sandy substratum.

Sample collection and processing

Macroalgae, epilithic microalgae, benthic invertebrates and fish were sampled seasonally throughout 2005 at three sites from the natural and restored macroalgal beds and barren ground. Macroalgae were collected by SCUBA divers, in triplicate using 0.5 × 0.5 m stainless steel quadrats. The samples were washed with filtered seawater on board and the contents sieved onto a 1 mm screen to sort attached fauna. After transporting to the laboratory, macroalgae were rinsed with milli-Q water, sorted, air-dried, weighed, and then ground with a mortar and pestle. The biomass of macroalgae was converted into g dry weight m^{-2}. SCUBA divers carried out a few small-sized rocks on board and then epilithic microalgae were sampled by scraping the rock surface using a gentle toothbrush. Materials scrapped were prefiltered through a 100 μm sieve to remove large particles, and epilithic microalgae were collected on precombusted (450°C for 4 h) Whatman GF/F filters (0.70 μm nominal pore size), and treated following the procedure of POM samples as described later.

Benthic macrofauna were collected by hand, by a SCUBA diver scraping the rocky substratum using a stainless steel knife. Macrofauna were sorted live under a dissecting microscope and kept alive overnight at the laboratory in filtered seawater from the sampling site to evacuate gut contents. Only live and intact organisms were collected and immediately dissected to minimize contamination with other material. Zooplankton was sampled by towing a handheld plankton net (mesh size: 200 μm) for approximately 10 min. Fish were captured using a gill net (2 m high × 25 m long) anchored on the sea bottom for about 12 h. Muscle tissue from the dorsal region was defatted in a solution of methanol, chloroform, and water (2:1:0.8) according to the method of Blight and Dyer (1959). Defatting was carried out in order to avoid variations in the $\delta^{13}C$ because of the species' differences in the concentration of isotopically lighter lipids (Focken and Becker 1998). Animal tissue samples were rinsed with milli-Q water and kept frozen in the laboratory until subsequent treatment.

Isotope signatures of phytoplankton were taken from isotopic data for suspended particulate organic matter (POM), collected at an offshore site adjacent to the studied macroalgal beds. Duplicate samples for POM were

collected at monthly intervals from February to November 2005. A known volume (about 20 l) of water was filtered through prewashed and precombusted (450°C for 4 h) Whatman GF/F filters (0.70 μm nominal pore size). Before filtering, the water was prefiltered through a 100 μm sieve to remove large particles and zooplankton. The POM samples were immediately acid soaked with several drops of 1 N HCl, rinsed with distilled water, and then kept frozen until later treatment. Samples for nitrogen isotopes were not acid-treated. For chlorophyll *a* analysis, 2 l of the surface water was filtered using the same procedure as for the POM samples for isotope analysis. The extraction and analytical procedure following the HPLC techniques are described elsewhere (Kang et al. 2006).

Stable isotope analysis

All materials collected for isotope analysis were freeze-dried and mill-ground into a homogeneous powder. After grinding, samples containing inorganic carbonates were acidified with 1 N HCl, rinsed with distilled water, and then oven dried for 48 h at 50°C. Small quantities from each sample were weighed into tin combustion cups. Capsulated samples were combusted at high temperature (1,030°C) in an automated elemental analyzer (Eurovector 3000 Series) and the resultant gas was analyzed for stable carbon and nitrogen isotope ratios, using a continuous flow-through inlet system attached to an isotope ratio mass spectrometer (CF–IRMS, Micromass Isoprime). When samples were to be acidified, $^{15}N/^{14}N$ ratios were measured before acidification because of significant modification of $^{15}N/^{14}N$ after HCl addition (Bunn et al. 1995). $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios were expressed as conventional delta (δ) notation in parts per thousand, or per mill (‰), relative to the Pee Dee Belemnite (PDB) and atmospheric N_2 standards for carbon and nitrogen, respectively, derived from the equation

$$\delta X(‰) = \left[\left(R_{sample}/R_{standard}\right) - 1\right] \times 10^3,$$

where X is ^{13}C or ^{15}N and R is the $^{13}C/^{12}C$ or $^{15}N/^{14}N$. IAEA CH-6 (sucrose, $\delta^{13}C = -10.4 \pm 0.2‰$) and IAEA-N1 (ammonium sulfate, $\delta^{15}N = +0.4 \pm 0.2‰$) of known relation to the international standard were used as reference materials. Standard deviations of repeated measurements of internal peptone and urea standards were less than 0.2‰ for $\delta^{13}C$ and 0.3‰ for $\delta^{15}N$, respectively.

Statistical analyses

All the data were tested for normality using the Kolmogorov–Smirnov test and then homogeneity using the Levene test. If the data showed a normal distribution and were homogeneous, differences between parameters were tested using a *t* test or analysis of variance (ANOVA) without prior transformation of the data. If not, comparisons were tested using the Mann–Whitney test or Kruskal–Wallis ANOVA. Macroalgal assemblages between restored and natural macroalgal beds were compared using a non-metric multidimensional scaling ordination (MDS) based on the similarity (PRIMER statistical package, Clark and Warwick 1994). A hierarchical cluster analysis (Bray–Curtis dissimilarity, average grouping methods) was conducted on the average $\delta^{13}C$ and $\delta^{15}N$ values of each species to determine trophic groups of consumers. The groups were compared using an ANOSIM permutation test. Differences in the average $\delta^{13}C$ and $\delta^{15}N$ values among the groups were tested using *t* test for the macroalgae, and a one-way ANOVA followed by the Tukey HSD multiple comparison test for consumers.

Results

Composition and abundance of macroalgae

Thirty-seven macroalgal taxa composed of five green, eight brown, and 24 red algae were found at three sites during the study period (Table 1). The eight top-ranked macroalgal species were very similar at natural and restored bed sites based on their relative contribution to total biomass. Of macroalgal assemblages found at both natural and restored bed sites, the most important species was a brown alga, the sea mustard *U. pinnatifida*, with an abundance of over 100 g dry weight m^{-2} in February and April. Although less frequent, considerable *S. horneri* was also found in natural and restored beds. While green algae were rare at both sites, a few red algal genera such as *Grateloupia elliptica*, *Chondrus ocellatus*, *Prionitis cornea*, *Lomentaria catenata*, and *Acrosorium yendoi* were commonly collected.

A marked seasonal pattern was detected in total biomass of macroalgae in both natural and restored beds, with much higher values in February and April and lower values in August and November (Fig. 2a). However, there was no difference in total biomass of macroalgae between sites in each sampling month (*t* test, $P > 0.099$ for all cases on the four sampling dates). MDS analysis of the complete data set revealed a tight clustering of macroalgal assemblages in February and April away from those in August and November, exhibiting no distinct spatial separation between the natural and restored beds (Fig. 2 b). This indicated a similar pattern of seasonal succession in macroalgal assemblages in the natural and restored beds.

Table 1 Seasonal changes in biomass (g dry weight m^{-2}) of macroalgae in barren ground, natural bed, and artificial bed

Species	Restored bed				Natural bed				Barren ground			
	Feb	Apr	Aug	Nov	Feb	Apr	Aug	Nov	Feb	Apr	Aug	Nov
Chlorophyta												
Codium arabicum		+	6.4 (4.1)			+	+	+		+		
Codium fragile				+			+					
Ulva prolifera									+			
Ulva conglobata		+										
Ulva pertusa		+	+	+								
Phaeophyta												
Colpomenia sinuosa		1.8 (1.0)			1.2 (0.6)	1.5 (1.0)			+	+		
Desmarestia viridis		1.0 (0.8)	0.1 (0.1)			+				+		
Myagropsis myagroides					+	+						
Sargassum hemiphyllum					+							
Sargassum horneri	5.4 (0.6)	28.2 (7.4)			7.2 (2.9)	30.4 (2.8)						
Undaria pinnatifida	112.4 (82.7)	235.2 (52.6)		9.0(7.4)	102.4 (57.1)	133.5 (14.6)		18.0(11.2)				
Saccharina japonica		7.8 (4.0)	+									
Hizikia fusiformis									+			
Rhodophyta												
Acrosorium yendoi	1.1 (0.4)	1.6 (0.9)		6.1 (4.3)	+	3.44 (0.7)						
Amphiroa ephedraea							+					
Carpopeltis affinis			0.8 (0.1)					0.7 (0.2)			+	
Ceramium kondoi									+			
Chondracanthus tenellus			10.9 (0.1)			+	7.1 (2.6)					
Chondrus ocellatus	4.9 (0.19)	0.8 (0.4)	11.9 (0.2)	+	5.8 (0.7)	3.4 (0.8)	1.7 (0.6)	0.2 (0.2)				
Chondrus yendoi						+						
Delesseria serrulata					+							
Dumontia simplex			+									
Gelidium amansii				6.9 (2.4)		+	0.2 (0.1)				+	
Gelidium pacificum	+											
Grateloupia elliptica	7.3 (3.8)	+	20.1 (16.8)	+	3.6 (0.2)	11.0 (7.4)	+		+			
Gloiopeltis tenax									+			
Gloiosiphonia capillaris						+						
Gracilaria gigas		+										
Grateloupia filicina			+				+					
Heterosiphonia japonica				+	+							

Table 1 continued

Species	Restored bed				Natural bed				Barren ground			
	Feb	Apr	Aug	Nov	Feb	Apr	Aug	Nov	Feb	Apr	Aug	Nov
Lomentaria catenata		2.4 (1.4)			7.0 (1.1)	9.8 (5.9)						
Plocamium telfairiae	6.1 (0.7)	+	+	+	4.3 (2.1)	+	+	+				
Prionitis cornea	1.2 (0.2)	0.7 (0.2)			3.6 (3.6)	12.3 (2.4)		+				
Prionitis divaricata					+							
Pterocladiella capillacea					+							
Spatoglossum pacificum	+	+				+						
Symphyocladia latiuscula					+				+			

Data represent mean and 1 SD in parenthesis. + Rare abundance of less than 0.1 g dry weight m^{-2} in biomass

Isotope signatures of primary producers

The three main primary producers (macroalgae, phytoplankton, and epilithic microalgae) considered in this study had distinct combinations of $\delta^{13}C$ and $\delta^{15}N$ (Table 2). No significant differences in $\delta^{13}C$ and $\delta^{15}N$ values of macroalgae were found between the sampling dates (in the case of *C. ocellatus*, Kruskal–Wallis ANOVA, $\chi^2 = 2.577$, $P = 0.276$ for $\delta^{13}C$; $\chi^2 = 5.692$, $P = 0.058$ for $\delta^{15}N$) and the two sampling sites (Mann–Whitney test, $U = 18.000$, $P = 1.000$ for $\delta^{13}C$; $U = 12.000$, $P = 0.394$ for $\delta^{15}N$). No interaction between the sampling dates or sites was detected for other macroalgae species. High intraspecies variability in $\delta^{13}C$ value was likely to be due to the difference between young and old plants (cf. Fredriksen 2003). The 30 macroalgal species analyzed fell into two distinct groups due to a significant difference in their $\delta^{13}C$ values (*t* test, $t_{28} = 10.862$, $P < 0.0001$). One group, which consisted of species accounting for most of the macroalgal biomass, had distinctly different $\delta^{13}C$ values from those of phytoplankton, averaging $-17.2 \pm 3.3‰$ ($n = 108$) with a range from $-20.4‰$ for *Gloiopeltis tenax* to $-10.3 \pm 2.0‰$ for *Codium arabicum*. The other group, which consisted of only a few red algae species, was isotopically much lighter, with $\delta^{13}C$ values from $-34.8‰$ for *Delesseria serrulata* to $-25.5‰$ for *Gracilaria gigas*. The two macroalgal groups had similar ($P = 0.203$) average $\delta^{15}N$ values of $3.2 \pm 1.3‰$ ($n = 105$) and $3.0 \pm 1.0‰$ ($n = 26$).

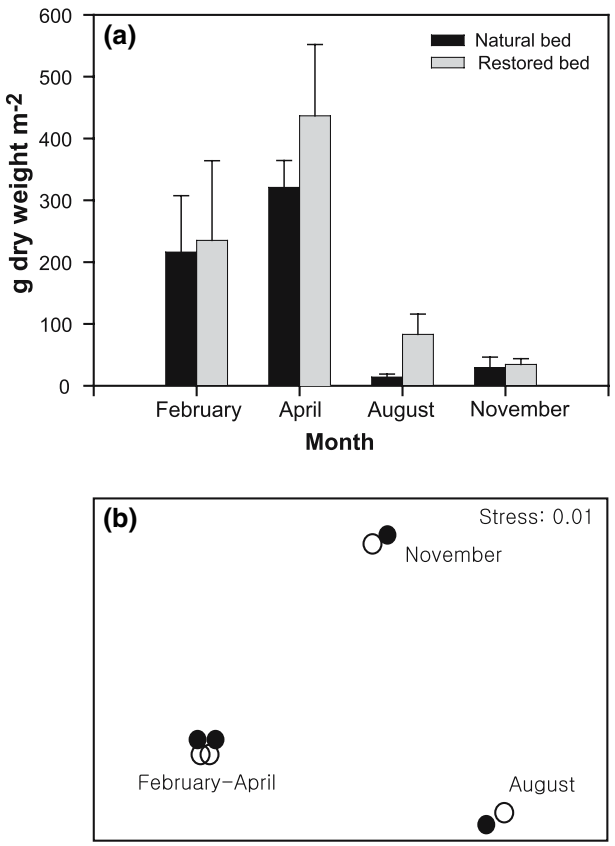

Fig. 2 Total biomass of macroalgae in restored and natural beds (**a**) and comparison of macroalgal assemblages using multidimensional scaling (MDS) analysis (**b**). *White circle* restored bed, *black circle* natural bed

Values of POM from the 3 km offshore site were obtained to represent pure phytoplankton. Values for $\delta^{13}C$ and $\delta^{15}N$ of phytoplankton averaged $-22.1 \pm 1.3‰$ (SD, $n = 20$) and $4.3 \pm 0.7‰$ ($n = 20$), respectively (Table 2). There were no significant differences in either $\delta^{13}C$ or $\delta^{15}N$ values among the ten sampling months (Kruskal–Wallis ANOVA, $\chi^2 = 16.657$, $P = 0.054$ for $\delta^{13}C$; $\chi^2 = 6.026$, $P = 0.737$ for $\delta^{15}N$).

Values for $\delta^{13}C$ and $\delta^{15}N$ of epilithic microalgae averaged $-18.8 \pm 1.8‰$ ($n = 5$) and $6.6 \pm 1.1‰$ ($n = 5$),

Table 2 δ^{13}C and δ^{15}N isotopic signatures of primary producers collected from restored and natural macroalgal beds of the Samchoek coast

	δ^{13}C(‰)		δ^{15}N(‰)		*n*
	Mean	SD	Mean	SD	
Chlorophyta					
Codium arabicum	−10.3	2.0	3.8	1.2	4
Ulva prolifera	−11.8		4.2		1
Ulva conglobata	−16.7		3.7		1
Ulva pertusa	−18.3	0.1	2.8	1.3	2
Phaeophyta					
Colpomenia sinuosa	−12.9	2.1	3.6	1.1	6
Desmarestia viridis	−28.7	1.6	3.8	0.4	6
Hizikia fusiformis	−14.5	0.5	3.0	0.9	3
Laminaria japonica	−19.4	2.0	2.4	0.9	5
Myagropsis myagroides	−16.3	1.8	2.7	1.4	4
Sargassum confusum	−14.3		3.8		1
Sargassum hemiphyllum	−19.8		2.5		1
Sargassum horneri	−18.9	3.1	2.8	1.3	10
Undaria pinnatifida	−19.6	1.8	2.0	1.4	8
Rhodophyta					
Acrosorium yendoi	−31.5	2.7	3.3	0.8	7
Chondracanthus tenellus	−18.8	1.2	2.2	0.3	3
Chondrus ocellatus	−18.6	3.3	4.0	0.9	12
Delesseria serrulata	−34.8		0.9		1
Gelidium amansii	−16.8	1.3	4.7	1.0	5
Grateloupia elliptica	−14.8	2.2	4.4	1.1	11
Gloiopeltis tenax	−20.4		2.2		1
Gloiosiphonia capillaries	−17.4		3.3		1
Gracilaria gigas	−25.5		3.9		1
Heterosiphonia japonica	−33.1		1.7		1
Lomentaria catenata	−19.8	1.2	3.1	1.2	5
Plocamium telfairiae	−33.7	0.7	2.7	0.5	9
Prionitis cornea	−16.0	2.9	3.6	0.4	9
Prionitis divaricata	−18.3	4.1	3.6	0.4	2
Pterocladiella capillacea	−18.1		3.3		1
Spatoglossum pacificum	−18.5	1.7	2.8	0.4	4
Symphyocladia latiuscula	−18.8	0.7	2.9	0.2	2
Phytoplankton	−22.1	1.3	4.3	0.7	20
Epilithic microalgae	−18.8	1.8	6.6	1.1	5

ranging from −20.9‰ (November) to −16.1‰ (September) and from 5.2‰ (November) to 7.4‰ (February), respectively. It should be noted that monthly data for epilithic microalgae were gathered on pooled samples and we have no indications of the variability in isotope values of this source. Although epilithic microalgae displayed δ^{13}C values close to those of dominant macroalgal groups, δ^{15}N values allowed clear separation of these two primary producers.

Isotope signatures of consumers

The ranges of average δ^{13}C and δ^{15}N values of consumers were nearly identical at the three habitats: −21.5 to −15.0‰, −21.5 to −15.0‰, and −21.5 to −15.0‰ for δ^{13}C, and 6.0–12.1‰, 6.0–12.3‰, and 7.0–12.2‰ for δ^{15}N in the restored and natural beds and the barren ground, respectively (Table 3; Fig. 3). From the cluster analysis based on average δ^{13}C and δ^{15}N values, species at natural macroalgal bed were regrouped into two main groups and each group was divided into three to four subgroups (Fig. 4). Isotope signatures of consumers significantly differed among subgroups, being related more to their feeding mode of consumers, postulated from the literature data, than to their taxonomic relationship or habitat characteristics (Fig. 5, ANOSIM test, $P < 0.001$).

In natural and restored beds, consumers exhibited very similar configurations of groupings based on their C and N stable isotope ratios (Fig. 5a, b). The differences among subgroups were significant for both δ^{13}C and δ^{15}N at both habitats (one-way ANOVA, $P < 0.001$ for both cases). The Tukey HSD test ($P = 0.05$ level) revealed a clear trend toward increasing δ^{15}N from plants through suspension feeders, grazers, herbivores, deposit feeders (primary consumers) and benthic omnivores and predators (secondary consumers) to fish. Primary consumers had an average δ^{15}N value of 7.3 ± 0.7‰ while secondary consumers averaged 9.5 ± 0.7‰, and fish averaged 11.5 ± 0.5‰ at both restored and natural beds. Interestingly, a few gastropods, clustered in subgroup 2c of the natural bed, had an average δ^{15}N value of 9.3 ± 0.6‰, similar to that of the secondary consumers.

δ^{13}C values allowed the separation of primary consumer groups at the natural bed. Subgroup 1a of both beds exhibited the lowest δ^{13}C values, falling within the ranges for phytoplankton. The ranges of δ^{13}C and δ^{15}N of these suspension feeders were well consistent with those of pelagic zooplankton (−21.8 ± 1.2‰). Subgroup 1b, comprising two suspension-feeding bivalves and three grazers, had intermediate δ^{13}C values between those of phytoplankton and macroalgae. Subgroup 1c of the restored and natural beds included consumers from diverse feeding strategies such as herbivores, deposit feeders, detritus feeders, and omnivores. Subgroups 1d of the natural bed had less negative δ^{13}C values than those of the other consumers, consisting mainly of herbivores. Members constituting subgroup 1c and 1d had δ^{13}C values corresponding to the δ^{13}C range of macroalgae. Although there were slight differences in δ^{13}C values of some invertebrates (e.g., the sea urchin *Hemicentrotus pulcherrimus*) between habitats, primary consumer groups at the restored bed were also separated into four subgroups, with similar δ^{13}C ranges with those of the natural bed. As a

Table 3 $\delta^{13}C$ and $\delta^{15}N$ (‰) of invertebrates and fish collected from restored and natural macroalgal beds, and barren ground

Species	Common name	Restored bed			Natural bed			Barren ground			Feeding strategy
		$\delta^{13}C$	$\delta^{15}N$	*n*	$\delta^{13}C$	$\delta^{15}N$	*n*	$\delta^{13}C$	$\delta^{15}N$	*n*	
Porifera											
Demospongia	Sponge				−22.1 ± 0.8	7.3 ± 0.8	3	−20.6	7.9	1	S
Cnidaria											
Acnthopleura japonica	Rock anemone				−18.0	8.6	1				O
Annelida											
Lysidice collaris	Eunicidae worm							−17.4 ± 0.8	9.4 ± 0.9	5	P
Halosydna brevisetosa	Short-scaled worm	−17.4 ± 1.1	9.1 ± 0.7	3	−18.8 ± 0.2	8.8 ± 1.1	2				O
Nereis spp.	Nereid worm				−18.8 ± 0.3	10.3 ± 1.2	3				O
Sabellastarte japonica	Feather worm	−20.1 ± 1.1	6.7 ± 0.2	2							S
Mollusca											
Polyplacophora											
Lepidozona albrechtii	Albrecht's chiton	−18.3	7.1	1	−19.9	7.2	1	−14.2 ± 0.2	8.8 ± 0.6	2	O
Rhyssoplax kurodai	Kuroda's chiton				−17.4	9.9	1	−17.9	8.2	1	O
Gastropoda											
Aplysia kurodai	Korean common sea hare	−18.3 ± 1.9	7.0 ± 0.4	4	−18.7	8.0	1	−18.3 ± 0.4	7.5 ± 0.1	2	H
Aplysia parvula	Tiny sea hare				−16.1 ± 0.5	7.4 ± 0.6	2				H
Cantharidus jessoensis	Hokkaido jewel top	−19.1	8.0	1	−16.6 ± 2.0	7.9 ± 0.7	3	−14.7 ± 0.1	9.2 ± 0.6	2	H
Mitrella bicincta	Variegated dove shell	−16.5 ± 1.1	9.9 ± 0.3	2	−17.4 ± 0.1	9.9 ± 0.3	2	−15.8 ± 0.7	10.3 ± 0.5	2	Sc/P
Calliostoma multiliratum	Multi-lined top							−18.2	8.7	1	H
Ceratostoma burnetti	Burnett's murex							−16.7 ± 0.5	9.1 ± 0.1	2	P
Omphalius pfeifferi carpenteri	Black truban shell				−15.6	8.9	1	−16.0 ± 0.1	8.6 ± 0.6	1	H
Acmaea pallida	Snowy limpet	−15.9	8.6	1	−16.4 ± 1.2	8.7 ± 0.7	2	−14.9 ± 1.5	10.0 ± 1.4	3	H
Searlesia modesta	Modest buccinum	−17.6 ± 0.7	9.4 ± 0.3	3	−17.0 ± 0.6	9.5 ± 0.2	2				P
Homalopoma nocturnum	Nocturnal top shell	−15.8	8.5	1	−16.4 ± 1.9	9.3 ± 0.9	4				H
Kelletia lischkei	Lischke's buccinum				−15.8	10.2	1				P
Lirularia iridescens	Iridescence top shell	−19.1	7.5	1	−18.2 ± 0.4	7.4 ± 0.2	2				H
Cellana toreuma	Common intertidal limpet				−16.1	6.8	1				H
Umbonium costatum	Sand snail	−15.0	7.3	1							D
Nucella heyseana	Japanese dogwhelk	−18.7	11.5	1							P
Ceratostoma inornatum	Japanese oyster drill	−16.8	8.8	1							P
Bivalvia											
Mytilus galloprovincialis	Mediterranean mussel	−19.9 ± 0.7	6.5 ± 0.9	3				−20.2 ± 0.6	7.3 ± 0.4	3	S
Barbatia virescens	Blood clam							−19.3	8.0	1	S
Arca boucardi	Kobelt's ark shell				−19.6	6.0	1				S

Table 3 continued

Species	Common name	Restored bed			Natural bed			Barren ground			Feeding strategy
		$\delta^{13}C$	$\delta^{15}N$	*n*	$\delta^{13}C$	$\delta^{15}N$	*n*	$\delta^{13}C$	$\delta^{15}N$	*n*	
Arthropoda											
Ligia exotica	Wharf roach				−21.7 ± 1.3	8.0 ± 0.6	2	−18.7 ± 0.04	7.5 ± 0.02	2	D/O
Pagurus sp.	Hermit crab	−18.5 ± 0.1	7.3 ± 1.9	2	−18.4 ± 0.8	8.6 ± 1.6	4	−16.3 ± 1.2	9.6 ± 0.7	3	G/Det
Amphipods (mixed)	Gammaridian amphipod	−19.4 ± 1.4	7.0 ± 1.1	3	−20.8 ± 1.3	7.2 ± 0.3	2	−19.2 ± 0.8	7.0 ± 0.7	3	G/Det
Caprella sp.	Skeleton shrimp	−20.6 ± 1.6	6.9 ± 0.3	3	−20.2 ± 1.7	6.5 ± 0.3	3	−18.5 ± 1.0	7.5 ± 0.3	3	G/Det
Hyastenus elongatus	Longhorn decoration crab	−21.4	7.6	1	−21.2	7.6	1				D
Ovalipes punctatus	Warty swimming crab	−16.7 ± 0.1	11.5 ± 1.6	2							?
Echinodermata											
Crinoidea	Feather star	−20.3 ± 1.2	7.1 ± 1.2	4	−19.8 ± 0.8	7.7 ± 0.4	4	−20.5 ± 0.5	7.5 ± 0.5	3	S
Stelloridea											
Asterina pectinifera	Bat seastar	−17.7 ± 1.4	8.6 ± 1.4	8	−18.5 ± 0.8	9.4 ± 1.1	4	−17.1 ± 1.0	9.3 ± 0.7	5	O
Asterias amurensis	North Pacific seastar	−17.5 ± 1.7	9.8 ± 1.0	6	−18.6 ± 0.3	10.3 ± 0.4	2	−18.6 ± 1.7	11.2 ± 1.7	2	P
Echinodea											
Strongylocentrotus nudus	Globular sea urchin	−19.4 ± 0.7	6.2 ± 0.8	2	−19.5 ± 0.8	6.9 ± 0.4	2	−17.2 ± 2.0	11.5 ± 0.03	2	H
Hemicentrotus pulcherrimus	Korean common sea urchin	−19.7	6.0	1	−17.5	7.3	1	−19.7	11.2	1	H
Strongylocentrotus intermedius	Intermedial sea urchin	−18.8	6.6	1				−19.3	11.6	1	H
Clypeaster japonicus	Japanese sand dollar	−17.0	8.5	1							D
Holothuroidea											
Cucumaria chronhjelmi	Black sea cucumber							−20.9	7.4	1	S
Stichopus japonicus	Japanese sea cucumber	−17.5	10.3	1	−18.2	8.0	1	−17.5	8.9	1	D
Chordata											
Halocynthia roretzi		−21.2 ± 1.6	7.2 ± 0.1	2	−21.0 ± 0.5	7.7	3				S
Styela clava		−22.5	5.9	1	−22.5 ± 1.9	7.5	3				S
Fish											
Ditrema temmincki	Sea chub	−16.4	10.7		−16.1 ± 0.1	11.2 ± 0.4	2	−17.0 ± 0.1	10.2 ± 0.1	2	Df
Sebastes schlegeli	Schlegel's black rockfish	−17.5 ± 1.1	11.3 ± 0.6	5	−17.5 ± 0.5	12.3 ± 0.7	3	−16.3 ± 0.1	11.5 ± 0.1	2	Df
Hexagrammos agrammus	Spotty belly greenling	−17.2 ± 1.2	10.8 ± 0.4	3	−16.5 ± 0.7	11.6 ± 0.6	4	−16.8 ± 0.1	10.8 ± 0.2	2	Df
Sebastes pachycephalus	Spotbelly rockfish	−17.0 ± 0.2	12.0 ± 0.4	4	−16.9 ± 0.3	11.9 ± 0.5	4	−16.5 ± 0.3	11.9 ± 0.8	4	Df
Sebastes minor	Minor rockfish				−17.9 ± 0.2	11.8 ± 0.2	2	−15.7 ± 0.1	12.2 ± 0.5	2	Df
Hexagrammos otakii	Greenling	−16.8 ± 0.6	11.6 ± 0.4	8	−16.9 ± 0.8	11.3 ± 0.9	4	−16.6 ± 0.3	10.6 ± 0.4	2	Df
Pleurogrammus azonus	Atka mackerel	−19.4	11.0	1				−19.7 ± 0.1	10.5 ± 0.2	2	Pl
Sebastes oblongus	Oblong rockfish	−16.6	12.0	1	−17.1 ± 0.7	12.3 ± 0.6	2	−16.2 ± 0.3	11.8 ± 1.4	3	Df
Sebastes vulpes	Fox jacopever							−16.0	11.5	1	Df
Liopsetta obscura	Black plaice	−16.6	11.5	1	−17.1	10.5	1				Df

Table 3 continued

Species	Common name	Restored bed			Natural bed			Barren ground			Feeding strategy
		δ^{13}C	δ^{15}N	*n*	δ^{13}C	δ^{15}N	*n*	δ^{13}C	δ^{15}N	*n*	
Thamnaconus modestus	Black scraper	−19.5 ± 0.02	10.1 ± 0.9	2	−18.7 ± 0.5	9.7 ± 0.9	2				Pl
Alcichthys elongatus	Elkhorn sculpin	−15.9 ± 0.7	12.1 ± 0.03	2	−16.9 ± 0.1	10.9 ± 0.5	2				Df
Stichaeus grigorjewi	Long shanny				−17.7	12.0	1				Df
Paralichthys olivaceus	Flatfish	−17.7 ± 0.5	11.8 ± 0.5	4							Df
Seriola lalandi	Yollowtail amberjack	−17.6	12.0	1							Df
Mugil cephalus	Striped mullet	−18.6	10.0	1							Al
Halichoeres poecilopterus	Multicolorfin rainbowfish	−17.3	10.9	1							Df
Pseudorhombus pentophthalmus	Fivespot flounder	−17.0 ± 0.4	11.4 ± 0.1	2							Df
Limand herzensteini	Brown sole	−17.6 ± 0.8	10.8 ± 1.1	2							Df
Paraplagusia japonica	Black tonguefish	−16.6	11.2	1							Df

Data represent mean ± 1 SD

H herbivore, *S* suspension feeder, *D* deposit feeder, *O* omnivore, *P* predator, *Df* demersal fish, *Pl* planktivore, *Al* algivore, *G/Det* grazer/detritus feeder, *Sc/P* scavenger/predator

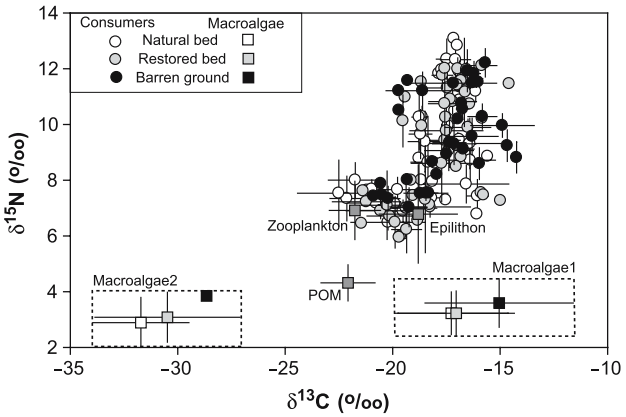

Fig. 3 Dual plot of average of δ^{13}C and δ^{15}N values for food sources and consumers in three different habitats. *Vertical* and *horizontal bars* represent standard deviations. *POM* suspended particulate organic matter

result, consumers of the same feeding modes were assigned to subgroups of similar δ^{13}C ranges at both the natural and restored beds.

Most of the benthic predators and omnivores were clustered into subgroups 2a and 2b at the natural bed. The δ^{13}C range of these feeding groups at the restored bed intervened between the two subgroups of the natural bed. The δ^{13}C values (on average −17.3 ± 0.3‰ in the restored bed and −18.1 ± 0.7‰ in the natural bed) of these consumers fell within the range for macroalgae. Their δ^{15}N values (on average 9.0 ± 0.5‰ in the restored bed and 10.0 ± 0.4‰ in the natural bed) suggest that they occupy a higher trophic level than the above-mentioned subgroups. Subgroup 2b of the natural bed also included other herbivores, exhibiting heavier δ^{13}C and δ^{15}N values (on average −16.2 ± 0.5‰ and 9.3 ± 0.6‰) compared with other herbivores. Subgroup 2c, comprised of the fish in the natural bed, had the heaviest δ^{15}N corresponding to the top predators at these habitats and similar δ^{13}C (−17.0 ± 0.5‰) to those of predator and omnivore subgroups. Lastly, most the fishes of the restored bed were similar in their δ^{13}C and δ^{15}N ranges with those of the natural bed while planktivorous and algivorous fishes formed another subgroup, which had more negative δ^{13}C range than the fish groups. The stable isotope ratios of one predatory gastropod (the dog whelk *Nucella heyseana*) were close to those of planktivorous and algivorous fishes.

At the barren ground, isotopic distributions of suspension feeders, herbivores/grazers and omnivores, and fish were similar to those at the restored and natural beds (Fig. 5c). However, some benthic consumers exhibited different features from those in the macroalgal beds. The noticeable difference was attributed to isotopic shifts in a few consumers assigned to omnivorous and herbivorous subgroups in the natural and restored beds.

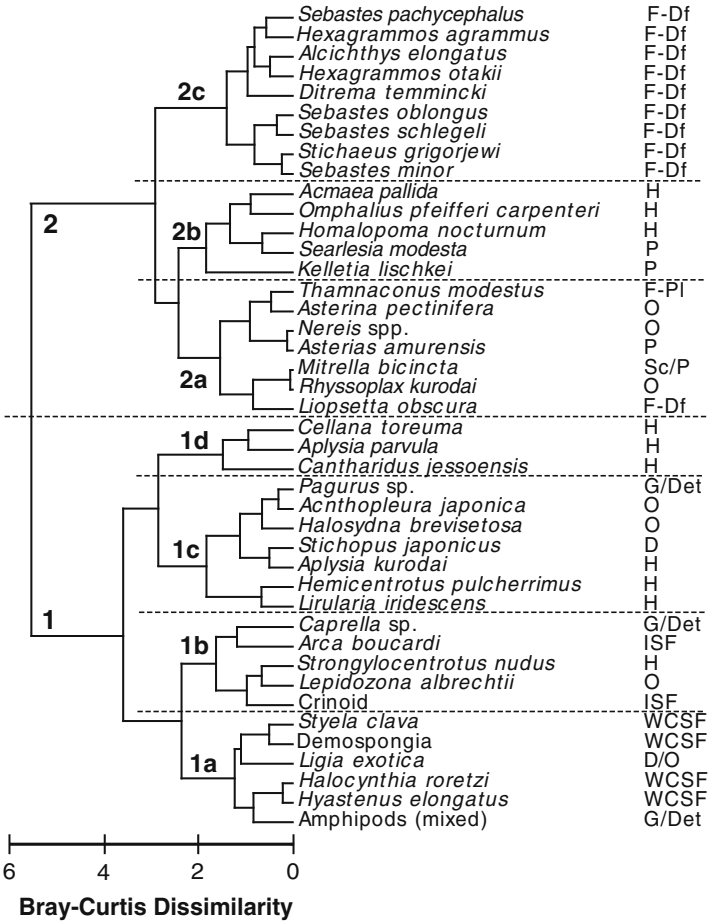

Fig. 4 Hierarchical clustering of the average $\delta^{13}C$ and $\delta^{15}N$ values for invertebrates and fish in natural beds using Bray–Curtis dissimilarity. Trophic groups: *WCSF* water column suspension feeders, *ISF* interface suspension feeders, *G/Det* grazers/detritus feeders, *D* deposit feeders, *H* herbivores, *O* omnivores, *P* predators, *Sc/P* scavengers/predators, *F-Pl* planktivore fish, *F-Al* algivore fish, *F-Df* demersal fish

Discussion and conclusions

Restoration of benthic communities

The subtidal macroalgal assemblage on exposed rocky areas on the eastern coast of Korea is likely to be dominated by a few giant brown algae. The dominant taxa in this study were *U. pinnatifida* and *S. horneri*. The various phytogeographical studies of subtidal rocky habitats in this region also report that these dominant brown algal species (*U. pinnatifida* and *Sargassum* spp.) appear to account for the macroalgal biomass at depths from 6 to 12 m (Lee et al. 1982; Choi et al. 2006). Because of limited sampling depths and sites (only three sites), the number of taxa (36 species) found in this study was relatively low compared to those previously reported in comparable studies (95 species, MOMAF 2002; 46, NFRDI 2006a; 87, Choi et al. 2006). As suggested by MOMAF (2002) and Choi et al. (2006) on the occurrence of the "rock whitening" event on the eastern coast of the Korean peninsula, abnormal conditions, such as warming water temperature, high grazing pressure by herbivores, and resource exploitation by humans, would lead readily to a decrease in the biomass of the predominant macroalgal species, simplifying macroalgal assemblages. Yoo et al. (2004) also demonstrated in the coastal zone adjacent to the study area that high predation of invertebrate predators on sea urchins in natural macroalgal beds reduced their density, whereas elevated sea urchin density on the barren grounds resulted in lasting deforestation.

About an year after establishment of the artificial macroalgal bed in the study area, dominant species, total abundance and community structure of the macroalgal assemblages in the artificially restored macroalgal bed were very similar to those at the neighboring natural bed at equivalent depth (Fig. 2). Although, additional time series data are needed to better understand recovering processes of macroalgal communities, our findings suggest that the decayed bare substratum has been successfully restored to a common macroalgal habitat by deploying artificial reefs of concrete pyramids with kelps attached. NFRDI (2006b) described the mechanism by which barren grounds are restored to dense macroalgal beds. When artificial reefs were deployed on barren grounds, grazing herbivores such as sea urchins and sea hares move to artificial reefs from the barrens, feeding on *Saccharina* leaves suspended 1 m

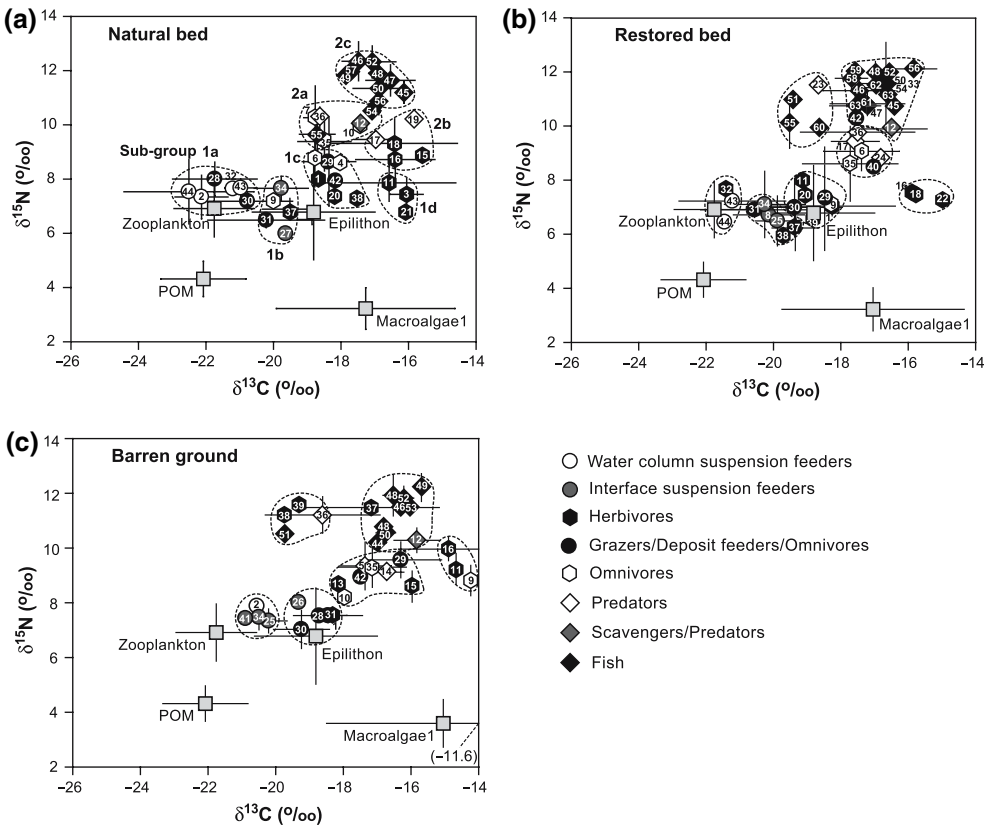

Fig. 5 Dual plot of average δ^{13}C versus δ^{15}N values of invertebrates, fish, and primary producers in **a** restored, **b** natural beds, and **c** barren ground. *Vertical* and *horizontal bars* represent standard deviations. The groups of taxa (*dotted circles*) were chosen from the hierarchical cluster analysis. **Invertebrates**: 1 *Aplysia kurodai*, 2 Demospongia, 3 *Aplysia parvula*, 4 *Acnthopleura japonica*, 5 *Lysidice collaris*, 6 *Halosydna brevisetosa*, 7 *Nereis* spp., 8 *Sabellastarte japonica*, 9 *Lepidozona albrechtii*, 10 *Rhyssoplax kurodai*, 11 *Cantharidus jessoensis*, 12 *Mitrella bicincta*, 13 *Calliostoma multiliratum*, 14 *Ceratostoma burnetti*, 15 *Omphalius pfeifferi carpenteri*, 16 *Acmaea pallida*, 17 *Searlesia modesta*, 18 *Homalopoma nocturnum*, 19 *Kelletia lischkei*, 20 *Lirularia iridescens*, 21 *Cellana toreuma*, 22 *Umbonium costatum*, 23 *Nucella heyseana*, 24 *Ceratostoma inornatum*, 25 *Mytilus galloprovincialis*, 26 *Barbatia virescens*, 27 *Arca boucardi*, 28 *Ligia exotica*, 29 *Pagurus* sp., 30 Amphipods (mixed), 31 *Caprella* sp., 32 *Hyastenus elongatus*, 33 *Ovalipes punctatus*, 34 Crinoid, 35 *Asterina pectinifera*, 36 *Asterias amurensis*, 37 *Strongylocentrotus nudus*, 38 *Hemicentrotus pulcherrimus*, 39 *Strongylocentrotus intermedius*, 40 *Clypeaster japonicus*, 41 *Cucumaria chronhjelmi*, 42 *Stichopus japonicus*, 43 *Halocynthia roretzi*, 44 *Styela clava*; **Fish**: 45 *Ditrema temmincki*, 46 *Sebastes schlegeli*, 47 *Hexagrammos agrammus*, 48 *Sebastes pachycephalus*, 49 *Sebastes minor*, 50 *Hexagrammos otakii*, 51 *Pleurogrammus azonus*, 52 *Sebastes oblongus*, 53 *Sebastes vulpes*, 54 *Liopsetta obscura*, 55 *Thamnaconus modestus*, 56 *Alcichthys elongatus*, 57 *Stichaeus grigorjewi*, 58 *Paralichthys olivaceus*, 59 *Seriola lalandi*, 60 *Mugil cephalus*, 61 *Halichoeres poecilopterus*, 62 *Pseudorhombus pentophthalmus*, 63 *Limand herzensteini*, 64 *Paraplagusia japonica*

above the top of the pyramid reefs by underwater longline and other macroalgal leaves transplanted onto the truncated top of each pyramid. A substantial recruitment of macroalgae occurs on the barren grounds because of reduced grazing intensity. In addition, gametophytes released from algae attached to the top of the pyramid are also recruited onto the surrounding rock surface, growing there and then increasing the macroalgal biomass. Nybakken and Bertness (2005) and Steneck et al. (2002) reviewed similar phenomena during the establishment of barren grounds due to urchin grazing and/or hydrographic effects, and the reestablishment of macroalgal beds under natural conditions.

The concrete pillars of the pyramids and the neighboring rocky beds had rapidly become occupied by diverse benthic organisms, including animals and macroalgae (NFRDI 2006a, b). These studies demonstrated that the total macrofaunal density and diversity in artificially created macroalgal beds recovered to natural bed levels about an year after establishment of the artificial macroalgal bed, and were much higher than those at barren grounds. They also showed that there were similarities in macrofaunal community patterns between the restored and natural macroalgal beds, and disparities between the two types of macroalgal beds and the barren grounds. In effect, the restored and natural beds showed relatively high densities of gastropods and annelid worms compared to the barren grounds, which were dominated by gammarid amphipods. As shown by the previous comparative studies between

artificial and natural macroalgal beds, this study also confirms a rich and diversified faunal composition of diverse functional roles (Table 3).

Sources of organic matter and their isotopic signatures

There are two main primary producers at subtidal macroalgal habitats on the eastern coast of the Korean peninsula: macroalgae and phytoplankton. In this study, macroalgae can be divided into two groups based on their $\delta^{13}C$ values (Table 2). The broad $\delta^{13}C$ range of macroalgae is well recognized (Dauby 1989). As shown in this study, various red algae were found to have strongly negative $\delta^{13}C$ values of around −30‰ (Dauby 1989; Fredriksen 2003). The total amount of carbon produced by some species of red algae (in particular *A. yendoi*, *Plocamium telfairiae*, *Heterosiphonia japonica*, *D. serrulata* and *G. gigas*) with such a negative $\delta^{13}C$ value is likely to be negligible in this system (Table 1; also Chung et al. 1991; MOMAF 2002; Choi et al. 2006). This is supported by little contribution of these red algal species to the dietary sources of grazing herbivores, as indicated by the much less negative $\delta^{13}C$ values of consumers than that of the $\delta^{13}C$ of the red algae species. As a result, another macroalgal group, which constitutes the main fraction of biomass and has an average $\delta^{13}C$ value of -17.2 ± 3.3‰, can be considered representative of macroalgal production in this system.

Samples representing phytoplankton in this study were taken about 3 km from the macroalgal bed sites. In consideration of their seasonal variability in isotopic ratios (Goering et al. 1990), phytoplankton samples were collected at monthly intervals from February to November. Offshore pelagic zooplankton trawled simultaneously with phytoplankton samples had an average $\delta^{13}C$ value of -21.8 ± 1.2‰, close to the -22.1 ± 1.2‰ of phytoplankton. Consequently, the latter value is considered the carbon value for pure phytoplankton, falling within the range generally found for phytoplankton in temperate coastal waters (Fry and Sherr 1984; Stephenson et al. 1986; Goering et al. 1990).

The stable isotope compositions of these two main primary producers in the study area were clearly distinguished. Nevertheless, it was difficult to determine the relative contribution of these sources to the sestonic and sedimentary organic matter pool because sinking particles could not be collected because of the shallow water depth and rocky substratum. The macroalgal productivity in this area has been shown to be around 6 kg wet weight m^{-2} $year^{-1}$ (MOMAF 2002; NFRDI 2006b). According to a wet:dry weight ratio of 3:1 (Fredriksen 2003), these values correspond to about 2 kg dry weight m^{-2} $year^{-1}$. The CHN elemental composition of 29 macroalgal species analyzed during this study showed carbon content of dry weight averaged 36.5% (±8.7 SD, $n = 76$, unpublished results). From this, we can infer an annual macroalgal productivity of 700 gC m^{-2} $year^{-1}$. Such productivity is close to the worldwide range reported by Mann (1973), from 800 to 2,000 gC m^{-2} $year^{-1}$. This figure is 3× the productivity of phytoplankton (around 200 gC m^{-2} $year^{-1}$, Hahm and Kim 2001), indicating that macroalgae-derived carbon is an important source for animals inhabiting the macroalgal bed system. Indeed, phytoplankton biomass in the water column of the study area was relatively low compared to levels generally found in other temperate coastal areas, monthly chlorophyll *a* concentrations ranging from 0.30 to 0.79 μg l^{-1} (average 0.56 μg l^{-1}, ± 0.19 SD, $n = 14$, unpublished results).

Among the other possible sources of organic matter are epilithic microalgae. Production and biomass of epilithic microalgae were not measured in this study because of the incapacity to accurately separate them. The contribution of this source to primary production in this rocky environment was expected to be low compared to that of the two above-mentioned primary producers. However, the importance of epilithic microalgae to primary consumers was likely to be higher in the barren grounds free of macroalgae. The $\delta^{13}C$ values (average -18.8 ± 1.8‰) of epilithic microalgae overlapped those of dominant macroalgae but the $\delta^{15}N$ values (average 6.6 ± 1.1‰) were about 3.5‰ higher than those of macroalgae and phytoplankton, allowing separation from these two primary producers.

Food web structure

The $\delta^{13}C$ and $\delta^{15}N$ values of consumers varied greatly between functional feeding groups rather than taxonomic groups or habitat characteristics, the overall $\delta^{13}C$ range being as wide as that of primary producers. This result suggests that consumers have a different dietary composition and thereby use ultimately different origins of organic matter depending on their feeding strategy. Since the $\delta^{13}C$ values of macroalgae showed a broad range and thus the variance about the mean value for fauna is often greater than the difference between mean values of the end members, the relative contribution of primary producers via mixing model calculations are not quantitative estimates.

In the restored and natural beds, suspension feeders, including the ascidians *Halocynthia roretzi* and *Styela clava*, the sponge Demospongia, and the crab *Hyastenus elongatus* had $\delta^{13}C$ signatures close to phytoplankton, indicating that phytoplankton are their sole source of nutrients. Their similar $\delta^{13}C$ and $\delta^{15}N$ ranges to pelagic zooplankton confirm that their primary consumption is the

same as that of offshore pelagic zooplankton using exclusively phytoplankton of pelagic origin, given a 3–4‰ trophic enrichment in δ^{15}N (DeNiro and Epstein 1981; Minagawa and Wada 1984; Vander Zanden and Rasmussen 2001). Ascidians and sponges have a nonselective feeding mechanism and favorably consume small organic particles such as nanoplankton or bacteria (Pile et al. 1996; Bone et al. 2003; Petersen 2007). Little and Kitching (1996) reported that the importance of detritus as a food source on rocky shores will vary greatly with wave exposure. In this respect, Bode et al. (2006) showed that suspension feeders use phytoplankton at exposed beaches similar to the study area, but macrophytes contributed to half of their diet in sheltered areas. Dunton and Schell (1987) also reported a high dependence on phytoplankton of sessile suspension feeders (bryozoans and hydroids) in an Arctic kelp forest.

Grall et al. (2006) demonstrated a slight difference in isotopic composition between those water column filter feeders that have closer C and N isotope values to suspended POM, and interface filter feeders, which have much less negative δ^{13}C values, reflecting the use of subsidiary ^{13}C-enriched carbon sources in an Atlantic maerl bed. At the three habitats of this study, another suspension-feeding group, which can be classified as interface filter feeders (cf. Grall et al. 2006), had also slightly more ^{13}C-enriched values than those of water column suspension feeders. Of this group were two bivalves, *Mytilus galloprovincialis* and *Arca boucardi*, one tubicolous polychaete, *Sabellastarte japonica*, and one crinoid. These species live within crevices of rocks or beneath the holdfasts of macroalgae. Their δ^{13}C values were between those of phytoplankton and macroalgae, suggesting that their carbon originated from a mixture of both sources. Epilithic microalgae can be considered as another possible candidates for a ^{13}C-enriched source. However, considering the trophic fractionation effect of 3.4‰ in δ^{15}N, similar δ^{15}N values between the interface filter feeders and epilithic microalgae reject this as an important contribution to this microalgae-derived organic matter source in the diets of the interface filter feeders. Our conclusion is supported by Little and Kitching (1996) who stated that the suspension-feeding invertebrates of rocky shores could gain enough energy to explain their growth rates by feeding on a combination of macroalgal detritus and phytoplankton. In addition, this result indicates that sediment-derived macroalgal detritus may still be available as a dietary source for suspension feeders on the boundary of the water–rock interface.

Isotope values of the skeleton shrimp *Caprella* sp. were also clustered into this category, indicating consumption of a mixed diet of pelagic and macroalgal origins. The caprellid species appear to be opportunist feeders, consuming the most readily available organic material (Keith 1969). They implement a number of feeding strategies (browsing, filter feeding, predation, scavenging, and scraping) in their natural habitat. Gonad δ^{13}C values of sea urchins *Strongylocentrotus nudus* (at both beds) and *H. pulcherrimus* (at the restored bed) were similar to those of the interface suspension feeders but closer to the most negative limit of macroalgal values. Sea urchins are considered to be a key role species in grazing macroalgae in this study area. Yoo et al. (2007) presumed that grazing pressure of sea urchins is very large (grazing potential by a mean density of three individuals m^{-2} may exceed the mean production of seaweed cultured in domestic coastal waters of Korea). Slightly more negative δ^{13}C values found in sea urchin gonads than those of muscle tissue of other grazers might reflect either (1) a high grazing activity of the sea urchins on macroalgal species with comparatively negative δ^{13}C values (e.g., *U. pinnatifida* and *S. horneri* etc.) or (2) higher gonadal-lipid contents, which have a lighter δ^{13}C value than proteins and carbohydrate (Focken and Becker 1998). Although gammarid amphipods are also known to be an important grazer group in macroalgal beds (Yoo et al. 2007), a lack of data at species level makes it difficult to analyze their detailed dietary sources in this study.

Isotope signatures of consumers from diverse feeding strategies suggest that diverse macroalgal groups are used by these consumers in the restored and natural beds. These consumers were divided into two groups by their δ^{13}C values. The first group included four herbivores (the gastropods *Aplysia kurodai*, *Cantharidus jessoensis*, and *Lirularia iridescens*), one deposit feeder (the holothurian *Stichopus japonicus*), and one detritus feeder (the hermit crab *Pagurus* sp.). Consumers belonging to the second group were four herbivores (Porifera *Aplysia parvula*, three gastropods, *C. jessoensis*, *Acmaea pallida*, and *Homalopoma nocturnum*), one surface grazer (the gastropod *Cellana toreuma*) and one deposit feeder (the gastropod *Umbonium costatum*). The broad δ^{13}C range (−19.1 to −15.0‰) of these consumers corresponded to the δ^{13}C ranges of macroalgae, strongly suggesting that diverse macroalgal groups are used by consumers in both the restored and natural beds. Their δ^{15}N values, about 4‰ higher than those of macroalgae, further confirmed that these consumers occupy around the second trophic level, given a 3−4‰ trophic enrichment, and use macroalgae directly or in the form of detritus. Yoo et al. (2007) demonstrated, from laboratory experiments using 29 benthic invertebrates of subtidal macroalgal habitats, that these consumers have high grazing rates on macroalgae. Explanation for the difference in δ^{13}C values between the two consumer groups is unclear in this study. The δ^{13}C shifts between the consumer groups probably reflect their dependence on particular macroalgal species and availability (density) of the particular algal species within their habitats (Fredriksen 2003).

Isotope signatures of three omnivores, including the Cnidaria *Anthopleura japonica*, the polychaete *Halosydna brevisetosa*, and the chiton *Lepidozona albrechtii*, from the natural bed, allow these species to be assigned to the herbivore–deposit feeder group. Their $\delta^{13}C$ values indicate that macroalgae-derived carbon was an important component of their diet. Their $\delta^{15}N$ values were generally higher than those of herbivores and deposit feeders, and very similar to those of the same species or other omnivores in the restored bed, further supporting their use of small invertebrates, young macroalgae, and organic detritus (Hong et al. 2006).

Higher $\delta^{15}N$ values of other herbivorous gastropods, including *Omphalius pfeifferi carpenteri*, *A. pallida*, and *H. nocturnum* in the natural bed, suggest the use of a food resource with a higher $\delta^{15}N$ value than those of macroalgae. Considering a 3–4‰ trophic enrichment, their $\delta^{15}N$ values were two trophic levels higher than macroalgae, corresponding to those of predatory gastropods (*Searlesia modesta* and *Kelletia lischkei*) and other predators. Their $\delta^{13}C$ values were still within the range of macroalgae. Accordingly, the isotopic signatures of these herbivores may reflect considerable consumption of epilithic microalgae as their subsidiary carbon source in the natural bed. This conclusion is supported by the documentation of Barnes (1987) that the marine archaeogastropods, to which these gastropods belong, are largely microphagous, grazing on fine algae, sponges or other organisms growing on rocks and kelps.

The benthic predator and omnivore group in restored and natural beds showed higher $\delta^{15}N$ values than those of primary consumers (zooplankton, benthic suspension feeders, herbivores, and deposit feeders), suggesting that they have carnivorous feeding habits and thus occupy a higher trophic level. The $\delta^{13}C$ values (on average -17.3 ± 0.3‰ in the restored bed and -18.1 ± 0.7‰ in the natural bed) of these consumers were within the range of macroalgae. Despite slight differences between habitats (t test, $t_{11} = 0.043$ and 0.002 for $\delta^{13}C$ and $\delta^{15}N$, respectively), their $\delta^{13}C$ and $\delta^{15}N$ values indicate that these higher level consumers mainly feed on animals that have macroalgae-derived carbon as their carbon sources. The planktivorous fish, the black scraper *Thamnaconus modestus*, in the natural bed was included in this group (discussed later). In this study, nitrogen isotopes of primary consumers displayed significant trophic enrichment, on average 4‰ heavier than that of primary producers. However, the average enrichment of this benthic predator–omnivore group compared with the primary consumers was relatively low (less than 2‰), suggesting the prevalence of omnivory (Kaehler et al. 2000; Bode et al. 2006). Food items and feeding habits of these benthic consumers were well documented from the broad literature data set by Hong et al. (2006). It has also been well established that higher trophic-level consumers of the kelp-associated community are indirectly dependent on the same ultimate food source as the lower level consumers (Jennings et al. 1997; Kaehler et al. 2000; Fredriksen 2003; Bode et al. 2006).

Almost all fish had the heaviest $\delta^{15}N$ values corresponding to the top predators in these ecosystems. However, the average trophic enrichment between secondary (benthic predator–omnivore) and tertiary consumers (fish) was less than 2‰, indicating the consumption of a diverse spectrum of prey items from primary and secondary consumer groups (Deegan and Garritt 1997). Fish may be divided into two groups by their $\delta^{13}C$ values, one with -17.0 ± 0.5‰, similar to those of predator–omnivore groups, and the other with slightly more negative values of -19.1 ± 0.5‰. The similar $\delta^{15}N$ values between these fish groups suggest that almost all fish were feeding at similar trophic levels but the different $\delta^{13}C$ values indicate that trophic pathways supporting fish nutrition may be different. Most the fish species belonged to the former group. Their isotopic signatures suggest that macroalgae provide the majority of organic matter that supports the fish of these macroalgal habitats through trophic linkage between macroalgae, benthic invertebrates, and fishes. Most of the fishes belonging to this group are demersal or resident species, and feed on diverse prey items such as amphipods, decapods, isopods, cephalopods, bivalves, polychaetes, other fishes, etc. (Kim et al. 2004; NFRDI 2006a). In contrast, the planktivorous fish (*T. modestus*, *Mugil cephalus*, and *Pleurogrammus azonus*) constitute the other fish group; their $\delta^{13}C$ values indicating considerable incorporation of organic carbon from pelagic sources. Kim et al. (2004) also documented that the black scraper, *T. modestus*, and the atka mackerel, *P. azonus*, mainly forage for pelagic prey such as zooplankton, and the diet of the striped mullet, *M. cephalus*, includes zooplankton, small benthic organisms and detritus. A gastropod, the dog whelk *N. heyseana*, was a member of this group, reflecting its feeding habit: boring bivalves, barnacles, and other gastropods (Hong et al. 2006). Previous studies have demonstrated that stable isotope signatures can distinguish between benthic and pelagic trophic pathways (Thomas and Cahoon 1993; Jennings et al. 1997; Pinnegar and Polunin 2000). Our data also showed different trophic pathways between ^{13}C-enriched benthic food chains and ^{13}C-depleted planktonic chains, confirming the suggestion of Jennings et al. (1997) that benthic food chains are important to the macroalgal bed communities under conditions of relatively low planktonic production.

Surprisingly, with the exception of a few invertebrates, consumer isotope signatures on the barren ground were very similar to those in restored and natural beds. On the barren ground, a water column suspension feeder,

Demospongia, was clustered into the same category as interface suspension feeders. This result may be indicative of high availability of macroalgal detritus as drifting algae to the diets of suspension feeders (Bustamante and Branch 1996). Although the relatively ^{13}C-depleted values of suspension feeders are indicative of their high dependence on pelagic sources, the δ^{13}C values of other invertebrates and fish corresponding to a range of macroalgae, and the clear trend toward increasing δ^{15}N from macroalgae through these invertebrates to fish suggest that macroalgae-derived organic matter is still important as their ultimate source of food, even on the barren ground (Bustamante et al. 1995; Bustamante and Branch 1996). Isotopic shifts in a few mollusks and sea urchins are most likely to reflect their feeding plasticity according to the low biomass of available macroalgae. For example, the chiton *L. albrechtii* and the gastropod *C. jessoensis* of subgroup 2a on the barren ground were about 3–5‰ and 1–2‰ heavier in δ^{13}C and δ^{15}N than those at the restored and natural beds. Sea urchins *S. nudus*, *H. pulcherrimus* and *S. intermedius* were about 5‰ heavier in δ^{15}N. The chiton has a highly omnivorous feeding strategy (see above discussion). In contrast, sea urchins may lack the morphological structure necessary to capture drifting algae without the aggregation of individuals (Contreras and Castilla 1987). As speculated by Fredriksen (2003), the sea urchins on the barren ground probably eat a large variety of food items ranging from macroalgae and epilithic microalgae to encrusting animals.

In conclusion, about an year after establishment of the artificial macroalgal bed in the study area, the decayed bare substratum had been successfully restored to a common macroalgal habitat by deploying artificial reefs of concrete pyramids with attached kelps. Development of the macroalgal community was likely to contribute to diverse colonization of macrozoobenthos, elevating diversity. The δ^{13}C and δ^{15}N values of consumers varied greatly between functional feeding groups rather than taxonomic groups or habitat characteristics, the overall δ^{13}C range being as wide as that of primary producers. The range of isotope signatures between primary producers (mainly phytoplankton and macroalgae) and consumers (invertebrates and fish) emphasizes that the consumers have different dietary compositions and thereby ultimately use organic matter of different origins depending on their feeding strategy. These trophic characteristics were consistent at all the habitats of restored and natural macroalgal beds, and the macroalgae-barren ground. This result strongly indicates structural and trophic recovery of the restored habitat. Trophic recovery may be further supported by comparisons of the condition of major consumers (data not shown in this study). The condition of sea urchins (*H. pulcherrimus* and *S. nudus*) and a gastropod (*Homalopoma amussitatum*) were similar in the restored and natural macroalgal beds. Their condition on the barren ground was a third (sea urchins) and a half (gastropod) of that at the restored and natural macroalgal beds. Nonetheless, with the exception of the case of suspension feeders, isotope signatures of the remaining consumers further indicate the trophic importance of organic matter of macroalgal origin as a nutritional source even for consumers on the barren ground, supporting the important trophic role of drifting algae in the neighboring ecosystems (Bustamante and Branch 1996; Kaehler et al. 2000; Rodríguez 2003; and references therein). Although, it was evident that the almost complete recovery of faunal composition was achieved at the restored habitat, more detailed time-scale data on colonization of earlier settlers and the following successional progress are needed to better understand the process and recovery rate of the developing benthic community, particularly in restoring populations of functionally important species.

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