



# Trophic niche overlap in coralline algae- and coral-dominated rocky-bottom subtidal communities

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## ABSTRACT

We investigated trophic structures in rocky subtidal ecosystems transitioning from canopy-forming to barren states across coastlines with varying oceanographic conditions. We examined stable isotopes and functional traits of common invertebrate and fish taxa to understand the food-web consequences. We hypothesized that resource exploitation patterns of functional guilds would result in distinct isotopic niches, defining trophic diversity and niche.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ranges of invertebrate functional groups differentiated pelagic from benthic trophic pathways, reflecting flexible dietary use in the absence of macroalgae. Fish production relied on prey using pelagic and benthic basal resources. Trophic redundancy among consumers within functional guilds contributed to intrinsic trophic structure in barren ecosystems. The resulting community-wide trophic diversity has led to consistent niche widths and overlapping niche space. Overall, our findings highlight the crucial roles of consumers that persist with diverse functional guilds in conferring the adaptability of barren rocky ecosystems following habitat disturbance.

## 1. Introduction

Coastal zones are subject to multiple and massive pressures from both human activities and natural forces, leading to potential ecosystem-wide changes such as biodiversity loss and altered ecosystem functioning (Mineur et al., 2015; He and Silliman, 2019). Monitoring climate change impacts on marine ecosystems is crucial for understanding and mitigating its effects (Brierley and Kingsford, 2009). Climate-induced changes can reshape benthic communities, potentially causing declines in populations of species that cannot adapt (Harley et al., 2006; Przeslawski et al., 2008). The loss of keystone species can disrupt associations between benthic organisms (Bolam et al., 2002; Hooper et al., 2005; Eisaguirre et al., 2020), a problem exacerbated by species introductions from tropical regions, contributing to the “tropicalization” of high-latitude communities (Vergés et al., 2014; Lee et al., 2022). In benthic ecosystems, space limitation affects sessile flora and fauna, especially large canopy-forming kelps and fucoids, which are key ecosystem engineers (Shelamoff et al., 2019; Westerborn and Koivisto, 2022). Human activities and global warming have led to the decline of

these species globally, causing phase shifts from canopy-forming states to barren grounds (Mineur et al., 2015; Krumhansl et al., 2016; Thibaut et al., 2017). Such shifts raise concerns about the trophic structure of food webs and the broader ecological consequences of multiple stressors on complex natural rocky ecosystems (Eisaguirre et al., 2020).

The subtidal rocky bottom ecosystems along the southern coast of Korea have experienced significant changes, particularly the transition from productive kelp forests to less productive coralline barrens. Canopy-forming kelp and algal turf communities, once dominated by genera like *Undaria*, *Ecklonia*, *Laminaria*, and *Sargassum*, have vanished from many subtidal areas (Chung et al., 1998; Kang, 2010; Kwon et al., 2010; Kim et al., 2013; KOEM, 2022). Instead, coralline barrens or bare substrates now constitute a substantial portion of these habitats, with one-third of rocky habitats affected from the 1990s to the 2000s (Kang, 2010; Park and Lee, 2023). This shift has been linked to factors like excessive grazing pressure (Jeon et al., 2015; Hong et al., 2021), eutrophication (Coleman et al., 2008), ocean warming (Kang, 2010; Hwang et al., 2017), and combinations of these factors (Chung et al., 1998). Although restoration efforts, such as artificial reef building, have

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seen some success (Jung et al., 2022; Park and Lee, 2023), subtidal hard-bottom communities have largely been replaced by calcareous coralline algae- and coral-dominated communities (Jeon et al., 2015; Hwang et al., 2017; KOEM, 2022; Lee et al., 2022, 2024). Despite the widespread phase shift and collapse of foundational species, few studies have explored the food-web effects of these disturbances (Kang, 2010).

The southern coastal systems of Korea provide a unique setting to explore the effects of new phases on trophic structures and in food webs, focusing on the persistence of functional roles within faunal assemblages in less complex habitats. We used stable isotope analysis ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) to unravel these dynamics, identifying dietary types, trophic levels, and niche specialization or generalization (Bearhop et al., 2004; Layman et al., 2007, 2012). This method has been applied across various ecosystems, such as macroalgal beds (Kang et al., 2008; Kim et al., 2022), coral reefs (Zhu et al., 2019), artificial reefs (Kang et al., 2021), and maerl beds (Grall et al., 2006) to distinguish benthic and pelagic food web pathways, extending the niche concept to community-level trophic diversity and complexity (Layman et al., 2007; Jackson et al., 2011).

We examined the trophic structures of food webs in subtidal barren rocky bottom ecosystems along the southern coast of Korea by analyzing  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of dominant flora and fauna across diverse locations with varying conditions, including warming, eutrophication, and upwelling. Our main goal was to identify common characteristics in the food web structures of coralline algae- and coral-dominated communities in temperate coastal zones. We predicted that despite biodiversity loss, these communities would retain diverse floral and faunal elements (Chung et al., 1998; Kang et al., 2008; Kwon et al., 2010; Lee et al., 2024). Consequently, we hypothesized that trophic compartments, defined as functional feeding groups in food webs, would lead to differentiated isotopic niches based on primary production sources. This differentiation would ultimately determine the trophic diversity and niche widths of communities. To test this, we compared the isotopic composition and niche metrics of functional feeding groups and also at

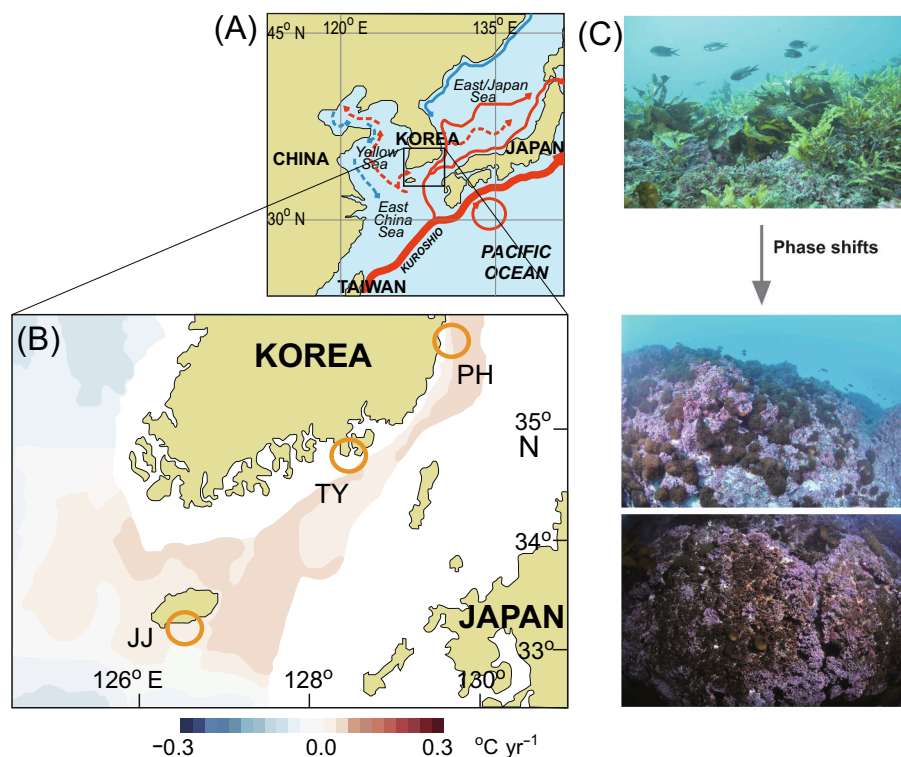
the community level across locations. Our final goals were to assess trophic diversity, complexity, and redundancy in these communities.

## 2. Materials and methods

### 2.1. Site location and data acquisition

The study area, located in the southern sea of Korea at the north-eastern tip of the East China Sea (Fig. 1), is heavily influenced by the north flowing Tsushima Warm Current, a branch of the Kuroshio. Over the past 55 years (1968 to 2022), this sea has experienced a notable and rapid warming trend, warming by  $1.36^\circ\text{C}$ , which is 2.6 times higher than the global mean of  $0.53^\circ\text{C}$  (Han et al., 2023). The warming phenomenon has been attributed to the weakening of the Siberian High and the East Asian Winter Monsoon in winter, coupled with an increase in transport volume of the Tsushima current in summer. Because of this warming trend, the coastal subtidal zones along the western and northern fringes of the Tsushima trajectory have undergone substantial changes. These areas, initially characterized by expansive rocky bottoms, have transformed into coralline-barren and even coral-covered ecosystems (Kang, 2010; Lee et al., 2022). The rocky bottoms in these locations, which are undergoing a process of rock whitening, now feature a cover of calcareous coralline algae, with dominant species including *Lithophyllum okamurae*, *Corallina* spp. (*C. officinalis*, *C. aberrans*, *C. crassissima*), *Amphiroa beauvoisii*, and *A. anceps*, along with various corals including *Dendronephthya* spp., *Alveopora japonica* (notably in coastal Jeju), *Montipora millepora*, and *Scleronephthya gracillimum*, *Chromonephthya* spp., *Metridium senile*, and *Corynactis viridis* (Chung et al., 1998; Kwon et al., 2010; Kim et al., 2018; KOEM, 2022; Lee et al., 2024).

We conducted field samplings in three contrasting locations: Jeju, Tongyeong, and Pohang (Fig. 1). At each location, we sampled duplicate sites and combined the samples. The environmental conditions varied



**Fig. 1.** Map showing the study area (A) and the sampling locations off the southern coast of Korea (B). Colored contours represent annual increasing rates of sea surface temperature from 2005 to 2021 (data source: Korea Oceanographic Data Center, <https://www.nifs.go.kr/kodc/index.kodc>). JJ, TY, and PH indicate Jeju, Tongyeong, and Pohang sites, respectively. (C) The rocky seabeds in these areas are shifting from ecosystems dominated by canopy-forming kelp to those increasingly characterized by calcareous coralline algae and coral.

across these locations: Jeju experiences warmer and oligotrophic conditions, Tongyeong exhibits low-saline and eutrophic conditions, while Pohang has colder and frequently upwelling conditions (Son et al., 2012; KOEM, 2022; Xu et al., 2022). Given the expected spatial diversity in both benthic and pelagic communities, we chose these three locations to evaluate the general trophic niche across diverse barren-ground communities. In our surveys of rocky bottoms, we observed only small strips of kelp, which were sparsely and individually distributed.

The water temperature in these locations displays distinct seasonality typical of temperate zones. Using the central location, Tongyeong, as the example, winter minima averaged  $4.2 \pm 1.5$  °C during 1963–1986 and  $6.0 \pm 1.0$  °C during 1987–2018, while summer maxima averaged  $25.9 \pm 1.1$  °C during 1963–2016 and  $27.5 \pm 1.1$  °C during 2017–2018, as calculated using daily data from the Korea Oceanographic Data Center (<http://www.nifs.go.kr/kodc/>). Given that stable isotope values in consumer tissues offer a time-integrated assimilation reflecting feeding history over days to months, our sampling occurred in April (spring) and October (autumn) of 2021 in Jeju, 2022 in Tongyeong, and 2023 in Pohang, respectively. This enabled the capture of trophic information of consumers during the preceding winter–spring (cold) and summer–autumn (warm) periods, respectively.

The data included stable isotope ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) values of suspended particulate organic matter (SPOM) as a proxy of phytoplankton, benthic microalgae, benthic invertebrates, and nektonic (fish and invertebrate) samples, randomly collected at water depths ranging from 8 to 20 m at duplicate sites in the three locations. Unless otherwise specified, the data represent means  $\pm$  one standard deviation (SD).

## 2.2. Sample collection and processing

For the measurement of isotope ratios in basal resources, water samples were collected at each site using a 20-L van Dorn water sampler. After collection, the water was prefiltered through a 200- $\mu\text{m}$  mesh net to remove zooplankton and large particles. The filtered water was stored onboard in acid-washed plastic bottles. In the laboratory, SPOM was sorted into two size classes: fine ( $< 20$   $\mu\text{m}$ ) and coarse ( $> 20$   $\mu\text{m}$ ) particles (referred to as FPOM and CPOM, respectively). CPOM—comprising micro-sized phytoplankton (diatoms and dinoflagellates), protozoans (ciliates), and microzooplankton (copepod nauplii)—was collected by sieving approximately 10 L of seawater through a 20- $\mu\text{m}$  mesh net (Kang et al., 2021). FPOM, encompassing nano- and pico-sized plankton, was gathered by filtering the remaining eluate onto precombusted (450 °C for 4 h) Whatman GF/F glass fiber filters with a nominal pore size of 0.7  $\mu\text{m}$ .

Benthic primary sources were sampled by scuba diving to collect five stones and pieces of coralline algae randomly from rocky reefs. Biofilm samples were acquired by gently brushing and rinsing the collected stones and algae with filtered seawater. These biofilms in water were then filtered through a 100- $\mu\text{m}$  mesh net to eliminate epibionts and large particles before being filtered through precombusted Whatman GF/F filters. Although infrequently encountered, a few macroalgal blades were also collected by the divers. These blades were scraped with a razor blade to remove epibionts and then rinsed with deionized water onboard.

In the laboratory, filters containing SPOM (FPOM/CPOM) and biofilms destined for  $\delta^{13}\text{C}$  analysis were placed overnight in a desiccator saturated with concentrated HCl fumes to effect decarbonation. Acid treatments were avoided for  $\delta^{15}\text{N}$  measurements to prevent alterations to nitrogen isotope ratios (Schlacher and Connolly, 2014). Finally, the filter samples were air dried at 50 °C for 48 h. Additionally, macroalgal samples were freeze dried then pulverized using a ball mill (Retsch MM200 Mixer Mill, Hyland Scientific, Stanwood, WA, USA).

For the measurement of isotope ratios in faunal communities, macrobenthic invertebrates were collected from the surface of five areas (each 0.0625 m<sup>2</sup>) at each duplicate site at the three locations. Collection involved encasing them in polyester bags (250- $\mu\text{m}$  mesh), gently

scraping them clean with a stainless-steel knife, and securing the bag opening with a cable tie. This method ensured the inclusion of almost all microhabitats present at each location. The invertebrate samples were placed on ice and transported to adjacent workstations where they were sorted live under a dissecting microscope and kept alive overnight in filtered seawater from the sampling site to evacuate gut material. We, thus, obtain specimens for stable isotope analysis. Only live and intact organisms were collected and immediately sorted to minimize contamination from other material. Fish were collected using a three-layer gill net (2 m high and 30 m long) set around each sampling site for approximately 12 h. After transportation on ice to adjacent workstations, white muscle tissues from the dorsal region were collected. All tissue samples of animal specimens were crushed in glass tubes using a glass grinding rod.

Specimens of each small arthropod species were pooled to collect sufficient material for isotope analysis. While most macroinvertebrate tissues were not acid-treated, small invertebrates such as crustaceans, gastropods, and bivalves underwent decalcification using a 10 % HCl solution until CO<sub>2</sub> bubbling ceased to eliminate potential carbonate effects. However, tissues from small invertebrate intended for  $\delta^{15}\text{N}$  analysis were not subjected to acid treatment. Due to species-specific variability in lipid concentrations, it is essential to correct for  $\delta^{13}\text{C}$  values in lipids, which are isotopically lighter than proteins. Although mathematical correction models based on tissue C:N ratio (Sweating et al., 2006) are available to account for lipid effects, actual  $\delta^{13}\text{C}$  values of lipid-free tissues significantly differ from those derived through mathematical correction. To address this, lipids were extracted from fish tissue samples using a methanol, chloroform, and water mixture (2:1:0.8 v/v/v) (Bligh and Dyer, 1959), and lipid-free tissues were used for  $\delta^{13}\text{C}$  measurements. However, lipid extraction was not performed on invertebrate tissues due to inconsistent differences in  $\delta^{13}\text{C}$  values among invertebrates and their inherently low lipid content. Additionally, since lipid extraction can influence  $\delta^{15}\text{N}$  values (Mintenbeck et al., 2008), a separate set of fish samples intended for  $\delta^{15}\text{N}$  measurements were prepared without lipid extraction. Finally, samples of invertebrates and fish were freeze-dried and homogenized using a ball mill.

## 2.3. Stable isotope analysis

Filters containing basal resources, SPOM and biofilms, were wrapped in tin plates. Powdered macroalgae and animal samples ( $\sim 1.5$  mg dry weight) were placed into tin cups and encapsulated. These wrapped tissues were then subjected to high-temperature oxidation (1030 °C) in an elemental analyzer (Vario Micro Cube, Elementar, Langensfeld, Germany). Subsequently, the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in the volatiles were determined using a continuous flow isotope ratio mass spectrometer (IsoPrime, GV Instruments, Manchester, UK) coupled with the elemental analyzer. To ensure accuracy and precision, three capsules of the International Atomic Energy Agency standards CH-6 (sucrose) and N1 (ammonium sulphate) were analyzed at the start of each series of measurements to calibrate the instrument, along with an internal laboratory urea standard. Additionally, after every 10 samples, two capsules of urea were analyzed to maintain precision by correcting for any potential machine drift. The isotopic data are presented using conventional  $\delta$  notations relative to the standard gases of Pee Dee Belemnite for carbon and atmospheric N<sub>2</sub> for nitrogen, then reported as parts per thousand (‰). The analytical precision, based on 20 replicates of urea, was  $< 0.1$  ‰ for  $\delta^{13}\text{C}$  and  $< 0.2$  ‰ for  $\delta^{15}\text{N}$ .

## 2.4. Functional group identification

To characterize functional feeding groups and present an overall picture of the trophic web structure of coralline-barren and coral-dominated communities, we conducted a hierarchical cluster analysis—using Euclidean distance and the group averaging method—on the mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of each consumer taxon (Anderson et al.,

2008). Prior to the cluster analysis, both isotope values were scaled to the 0–1 range. A graphical representation of trophic groups was then generated on  $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$  biplots to facilitate comparison among the tested groups. The trophic groups assigned were identified based on previously established feeding traits (<http://eol.org>; <http://www.fishbase.org/search.php>; <http://www.uniprot.org>; Hong et al., 2006; Jumars et al., 2015), including suspension feeders (SF), deposit feeders (DF), grazers (GR), omnivores (OM), predators (PR), and scavengers (SC).

We estimated the trophic position (TP) of predators using the following formulas (Post, 2002):

$$TP_{\text{consumer}} = [(\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{baseline}}) / \text{TEF}] + \lambda_{\text{baseline}},$$

where  $TP_{\text{consumer}}$  and  $\delta^{15}\text{N}_{\text{consumer}}$  represent the TP and  $\delta^{15}\text{N}$  value of the tested consumer, respectively;  $\delta^{15}\text{N}_{\text{baseline}}$  and  $\lambda_{\text{baseline}}$  denote the  $\delta^{15}\text{N}$  value and TP (= 2 in this study) of the baseline organisms (SF, DF, or GR), respectively; and TEF is the trophic enrichment factor (=  $3.3 \pm 0.26$  ‰).

## 2.5. Data analysis

To examine the differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values across basal resources, we conducted a Permutational Multivariate Analysis of Variances (PERMANOVA, based on Euclidean distance) on a three-factor design: resource group (fixed with CPOM, FPOM, biofilms, and macroalgae), location (fixed with three levels of Jeju, Tongyeong, and Pohang), and season (fixed with spring and autumn) (Anderson et al., 2008).

To assess significant differences between trophic groups of consumers, we conducted a PERMANOVA test using a one-factor design, subsequently performing pairwise comparisons between groups. According to the observed differences between cluster groups, we performed separate univariate PERMANOVA analyses on individual  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values using the same factor levels, followed by post-hoc pairwise comparisons for significant factors. We then examined temporal variabilities in isotope values within cluster groups of consumers (pelagic-, benthic-affinity invertebrate groups, and fish group) using a one-way PERMANOVA analysis at individual locations. Finally, we used a two-way PERMANOVA design to determine the spatial and temporal variability in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of consumers at the entire community level. To reduce potential bias from unbalanced sample sizes ( $N$ ) among species, we used the mean isotope values of each species. We set the significance level at  $P < 0.05$ , and computed  $P$  values based on 9999 permutations of residuals with unrestricted permutation of raw data.

## 2.6. Stable isotope metrics

To assess trophic diversity, we employed four community-wide isotope-based metrics. The ranges (CR and NR) of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values serve as indicators of the overall realized niche width, capturing both horizontal (reflecting diversity of dietary resources) and vertical (indicative of trophic lengths) dimensions within the  $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$  biplot space. These metrics, thus, provide comprehensive community-wide measures of trophic diversity (Layman et al., 2007). Further, as a holistic measure of trophic diversity incorporating CR and NR, we estimated both the volume of the  $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$  space (represented as a convex hull-shaped total area (TA) encompassing all assemblages) and the sample size-corrected standard ellipse area (SEAc; Jackson et al., 2011). We hypothesized that CR and NR of each functional group would demonstrate consistency in both seasons across diverse locations, resulting in a close overlap in SEAc within the isotopic niche space. To test the presumed generality of the trophic niche across diverse barren-ground communities, we evaluated trophic niche overlap both at the functional group level and the whole community level using the TA and SEAc measures. This analysis was conducted by assessing the percentage

overlap of the whole ellipse's surface for SEAc (Jackson et al., 2011) and the isotopic nestedness (INes) of the smaller ellipse's surface for TA (Cucherousset and Villéger, 2015). We computed TA and SEAc for individual communities of invertebrates and fish, as well as for whole communities, using the Stable Isotope Bayesian Ellipses in R (SIBER; Jackson et al., 2011).

We then calculated the probabilistic density of niche overlap between seasons and locations at the community level to validate the patterns observed in SEAc and INes, using the nicheROVER package (version 1.1.0, Swanson et al., 2015) in R. The probability of overlap between niche pairs based on  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values was assessed using 10 randomly generated niche regions for each group. Posterior distributions of niche regions were obtained from 10,000 uninformative random permutations to derive niche overlap metrics. We report the posterior mean and 95 % credible intervals (CI) for all niche overlaps, along with directional estimates of niche overlap (e.g., communities A vs. B and B vs. A).

## 2.7. Bayesian stable isotope mixing model

To quantify the proportional contribution of basal resources to functional feeding guilds, we employed the Bayesian stable isotope mixing model in R (MixSIAR, version 3.1.12; Stock and Semmens, 2016). This approach requires isotope data from both consumers and distinct resources alongside TEF values. Employing the functional groups determined by the abovementioned cluster analysis, we conducted the mixing model based on their isotope values, treating community (SF, DF/GR, OM, PR/SC, and fish, individually) as a random factor and location as a fixed factor. Due to significant differences in  $\delta^{13}\text{C}$  values between primary consumers (SF vs. DF/GR), which align with pelagic and benthic origins of basal resources, respectively, we grouped these consumers into two categories representing isotopic baselines of pelagic and benthic pathways. We utilized previously published TEF values from a meta dataset:  $1.3 \pm 0.3$  ‰ for  $\delta^{13}\text{C}$  and  $3.3 \pm 0.26$  ‰ for  $\delta^{15}\text{N}$  (McCutchan Jr. et al., 2003). To achieve a more comprehensive understanding of resource flow through trophic pathways, we adjusted consumer isotope values using TEF to accommodate multiple trophic steps before data input. The model was fitted using Markov Chain Monte Carlo and model convergence was assessed through Gelman–Rubin and Geweke diagnostics. We estimated the median source proportions of the community trophic base, accompanied by 95 % credibility intervals based on the posterior density distribution for each case.

## 3. Results

### 3.1. Isotope signatures of basal resources

The mean  $\delta^{13}\text{C}$  values of potential basal resources (i.e., CPOM, FPOM, biofilms, and macroalgae) analyzed in this study ranged from  $-10.8 \pm 0.3$  ‰ (*Pachyarhron cretaceum*) to  $-21.7 \pm 0.5$  ‰ (FPOM) (Fig. 2; Table S1). Their mean  $\delta^{15}\text{N}$  values also spanned  $3.9 \pm 0.2$  ‰ (*Sargassum* spp.) to  $12.2 \pm 1.0$  ‰ (*Pachyarhron cretaceum*). Basal resources exhibited distinct isotope profiles (three-way PERMANOVA, Pseudo- $F_{3,71} = 34.06$ ,  $P = 0.001$ ), with significant interactions observed between Resource  $\times$  Location ( $P = 0.003$ ) and Resource  $\times$  Season ( $P = 0.001$ ) (Table S2). Pairwise comparisons further differentiated the isotope profiles of resources within locations ( $P < 0.010$ ) and seasons ( $P = 0.001$ ). Further, the mean  $\delta^{13}\text{C}$  values of potential basal resources differed significantly (univariate PERMANOVA, Pseudo- $F_{3,71} = 54.28$ ,  $P = 0.001$ ), with notable interactions of Resource  $\times$  Location ( $P = 0.001$ ) and Resource  $\times$  Season ( $P = 0.021$ ) (Table S3).

Specifically, a clear distinction was observed between pelagic and benthic resources (CPOM and FPOM vs. biofilms and macroalgae) within locations and seasons ( $P < 0.023$ ). The  $\delta^{13}\text{C}$  ranges were as follows:  $-20.7 \pm 0.5$  to  $-18.9 \pm 0.3$  ‰ for CPOM,  $-21.7 \pm 0.5$  to  $-20.6 \pm$

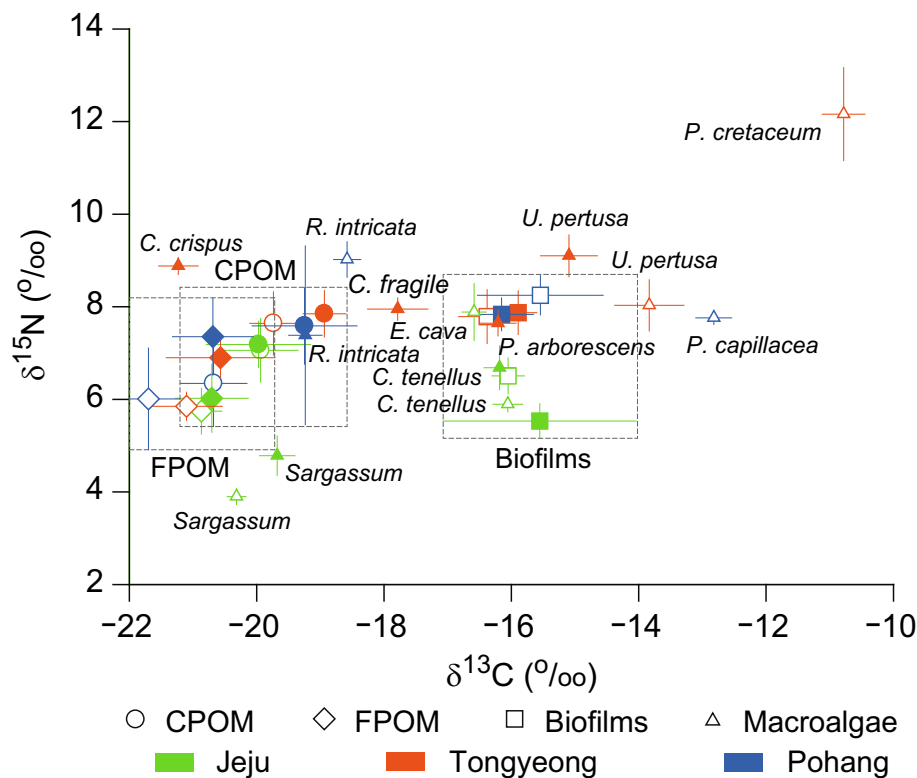


Fig. 2. Bi-plots illustrating the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of basal resources sampled from the Jeju, Tongyeong, and Pohang locations. Each data point corresponds to a different source, distinguished by unique symbols. Values are mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values (‰  $\pm$  1 SD, standard deviation). Dashed-line boxes represent the ranges of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of respective resource types.

0.9 ‰ for FPOM, and  $-16.4 \pm 0.4$  to  $-15.5 \pm 1.0$  ‰ for biofilms (Table S1). Similarly, significant differences were observed in the mean  $\delta^{15}\text{N}$  values among the basal resources (univariate PERMANOVA, Pseudo- $F_{3,71} = 6.421$ ,  $P = 0.001$ ), with strong interactions of Resource  $\times$  Location ( $P = 0.001$ ) and Resource  $\times$  Season ( $P = 0.001$ ). However, these values fell within a narrow range of  $6.3 \pm 0.9$  to  $7.8 \pm 0.5$  ‰ for CPOM,  $5.7 \pm 0.5$  to  $7.4 \pm 0.8$  ‰ for FPOM, and  $5.5 \pm 0.4$  to  $8.2 \pm 0.4$  ‰ for biofilms, with some overlaps between them. It should be noted that the isotope profiles of macroalgae were species-specific, and due to their limited availability, we excluded them from our isotope mixing model.

### 3.2. Food web structure

During each sampling event, we identified and examined a total of 36 to 55 invertebrate and fish species combined (Tables S4–S6). Across all locations, these species displayed average  $\delta^{13}\text{C}$  values spanning  $-21.9$  ‰ (*Halocynthia roretzi*) to  $-13.3$  ‰ (*Phyllidiella pustulosa*), covering the entire spectrum of basal resource values. Their  $\delta^{15}\text{N}$  values ranged from 6.4 ‰ (*Perampithoe* spp.) to 14.7 ‰ (*Neoditrema ransonnetii*), indicating an increase compared with CPOM, FPOM, and biofilms. Cluster analysis based on  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values depicted a clear alignment with the presumed feeding behaviors of different trophic groups (Figs. S1–S3), revealing two overarching clusters within each sampling unit. This analysis delineated the SF group (designated as Group I) from other invertebrate (DF/GR, OM, and PR/SC) and fish groups (Group II) (Fig. 3), which could be further divided into two subgroups: invertebrates (Group IIa) and fish (Group IIb).

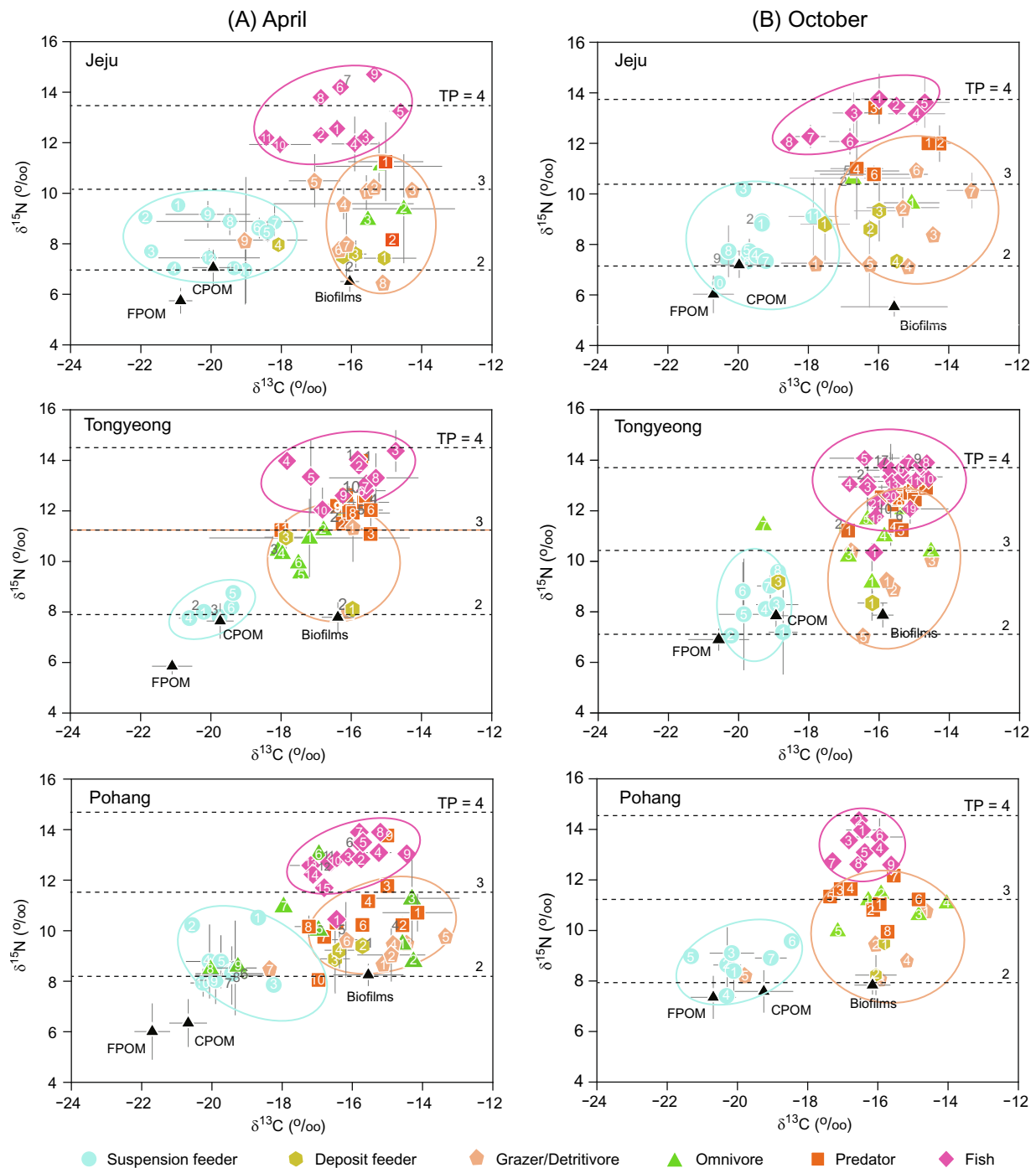
A one-way multivariate PERMANOVA indicated significant differences between trophic groups in terms of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values ( $P = 0.001$ ) for all six sampling units. Subsequent univariate PERMANOVA revealed significant differences for both  $\delta^{13}\text{C}$  ( $P = 0.001$ ) and  $\delta^{15}\text{N}$  values ( $P = 0.001$ ) across all sampling units (Table S7). Pairwise comparisons of  $\delta^{13}\text{C}$  values between cluster groups revealed significant

distinctions between Group I (overall range:  $-21.9$  to  $-17.0$  ‰) and Group IIa ( $-18.1$  to  $-13.3$  ‰) ( $P = 0.001$ ), as well as between Group I and Group IIb ( $-18.4$  to  $-14.5$  ‰) ( $P = 0.001$ ). However, no significant differences were observed between Group IIa and Group IIb ( $P > 0.16$ ) at all locations during both seasons. Regarding  $\delta^{15}\text{N}$  values, significant distinctions were observed between trophic groups ( $P < 0.012$  for all sampling units), except for Group I vs. Group IIa ( $P = 0.170$ ) at the Jeju location in April, with overall ranges of 6.5 to 10.5 ‰, 6.4 to 13.4 ‰, and 11.7 to 14.7 ‰ for Group I, Group IIa, and Group IIb, respectively.

The estimation of trophic positions of consumers identified similar food chain lengths (trophic levels  $\sim 4$ ) across all sampling units (Fig. 3). The trophic levels of each functional group were nearly identical, with invertebrates SF, DF, and GR occupying mean levels 2–3, omnivorous invertebrates (OM) at mean levels 2.6–3.1, predatory invertebrates (PR) at mean levels 2.7–3.6, and fish at mean levels 3.4–3.9 as top predators. Based on the proximity of  $\delta^{13}\text{C}$  values of Group I and Group IIa to pelagic and benthic basal resources, respectively, along with their estimated trophic position, we refer to Group I (SF group) as the pelagic-affinity group and Group IIa as the benthic-affinity group.

### 3.3. Seasonal and spatial dynamics of consumer isotopic niches

The isotopic niche metrics of both pelagic-affinity and benthic-affinity invertebrate groups (Groups I and IIa) showed no notable seasonal variation across all locations (Fig. 4A–C). Neither community displayed clear directional seasonal trends in TA and SEAc between April and October at the three locations (Fig. 4D–E), reflecting close overlaps in both horizontal and vertical niche axes (i.e., CR and NR). Notably, except for the  $\delta^{13}\text{C}$  values at Tongyeong (Pseudo- $F_{1,15} = 5.852$ ,  $P = 0.030$ ; Pseudo- $F_{1,44} = 11.39$ ,  $P = 0.002$ , respectively), neither  $\delta^{13}\text{C}$  nor  $\delta^{15}\text{N}$  values of invertebrate Group I and IIa showed significant differences between months (Pseudo- $F < 3.0$ ,  $P > 0.1$  for all the remaining cases; Table S8). Although Tongyeong exhibited significant seasonal



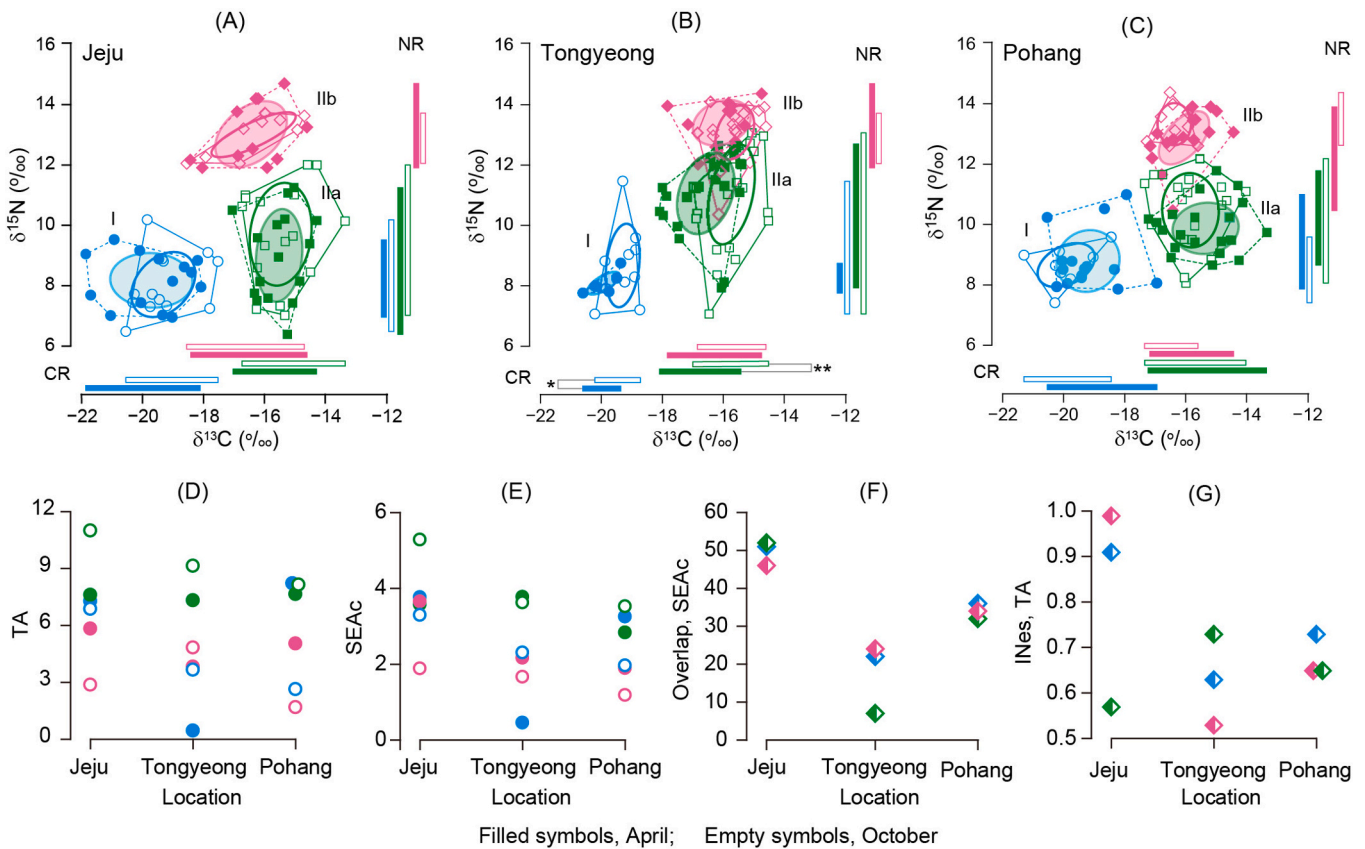
**Fig. 3.** Bi-plots displaying the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of macroinvertebrate and fish taxa collected from Jeju, Tongyeong, and Pohang in April (A) and October (B). Consumer classifications are derived from a hierarchical cluster analysis based on the Euclidean distances calculated from the average  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for each taxon. Dashed lines indicate the estimated mean trophic positions (TPs) of consumers, using  $\delta^{15}\text{N}$  values as proxies. Species code numbers are provided in Supplementary Figs. S1–S3.

differences in invertebrate  $\delta^{13}\text{C}$  values, the CR of both invertebrate groups highly overlapped between months, indicating minimal variations.

Similarly, the isotopic metrics of the fish community (Group IIb) did not exhibit any discernible seasonal trends. There were no seasonal fluctuations in the sizes of TA and SEAc observed across all locations (Fig. 4D–E), with their CR and NR overlapping consistently between months. Additionally, there were no significant differences in the fish  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values between months at the three locations (Pseudo- $F < 2.6$ ,  $P > 0.1$  for all cases; Table S8). The isotopic niches of both

invertebrate and fish communities exhibited considerable overlap between months, with SEAc percentages ranging from 46 to 52 %, 7 to 24 %, and 24 to 36 % at Jeju, Tongyeong, and Pohang, respectively (Fig. 4F). Moreover, seasonal overlap in community isotopic niches was particularly notable in the isotopic nestedness of TA (INes of the convex hull area), ranging from 0.57 to 0.99, 0.53 to 0.73, and 0.65 to 0.73 at Jeju, Tongyeong, and Pohang, respectively (Fig. 4G).

Community-wide (invertebrates and fish combined) trophic diversity (TA and SEAc) remained relatively consistent across the three locations (Fig. 5A). A two-way PERMANOVA revealed that the ranges of  $\delta^{13}\text{C}$  and



**Fig. 4.** Isotopic niche areas ( $\text{‰}^2$ ) for each cluster group of invertebrates and fishes (cluster group I: suspension feeders; IIa: deposit feeders/grazers/omnivores/predators of invertebrates; IIb: fishes) illustrated by the total area (TA, convex hull area) and standard ellipse area (SEAc, circles) in Jeju (A), Tongyeong (B), and Pohang (C) in April (solid lines and empty circles) and October (dotted lines and filled circles). The ranges (NRs and ARs) of the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of individual cluster (functional) groups are provided for each sampling month. Comparisons of TA (D), SEAc (E), overlaps in TA (F), and overlaps in SEAc (G) of each cluster group between seasons.

$\delta^{15}\text{N}$  values within the entire faunal assemblages were almost identical between seasons (Pseudo- $F_{1,255} = 0.409$ ,  $P = 0.619$ ), but significant differences were observed between locations (Pseudo- $F_{2,255} = 6.072$ ,  $P = 0.001$ ), with no significant interaction effect between both factors (Pseudo- $F_{2,255} = 0.589$ ,  $P = 0.624$ ; Table S9). Further univariate PERMANOVA indicated that the spatial variation in isotopic ranges was primarily attributed to differences in consumer  $\delta^{15}\text{N}$  values among locations (Pseudo- $F_{2,255} = 10.07$ ,  $P = 0.001$ ; pairwise comparisons,  $P < 0.04$  for the three cases). However, although disparities in the number of fish species with higher  $\delta^{15}\text{N}$  values influenced spatially distinct mean  $\delta^{15}\text{N}$  values of the entire community, both CR and NR showed significant overlap across locations. Consequently, isotopic niche overlap metrics revealed considerable overlaps in the  $\delta$ -space of communities among locations (ranging from 33 to 61 % in SEAc; 0.86 to 0.99 in INes), indicating minimal changes in the community isotopic niches. NicheR-OVER estimates at the whole community level indicated a high degree of isotopic niche overlap between seasons, with a mean probability exceeding 90 % (Fig. 5B). Similarly, the overlap between locations was substantial, with mean probabilities ranging from 75 % to 96 % (Fig. 5C), corroborating the overlap patterns observed in SEAc and INes.

### 3.4. Mixing model calculation of dietary proportions

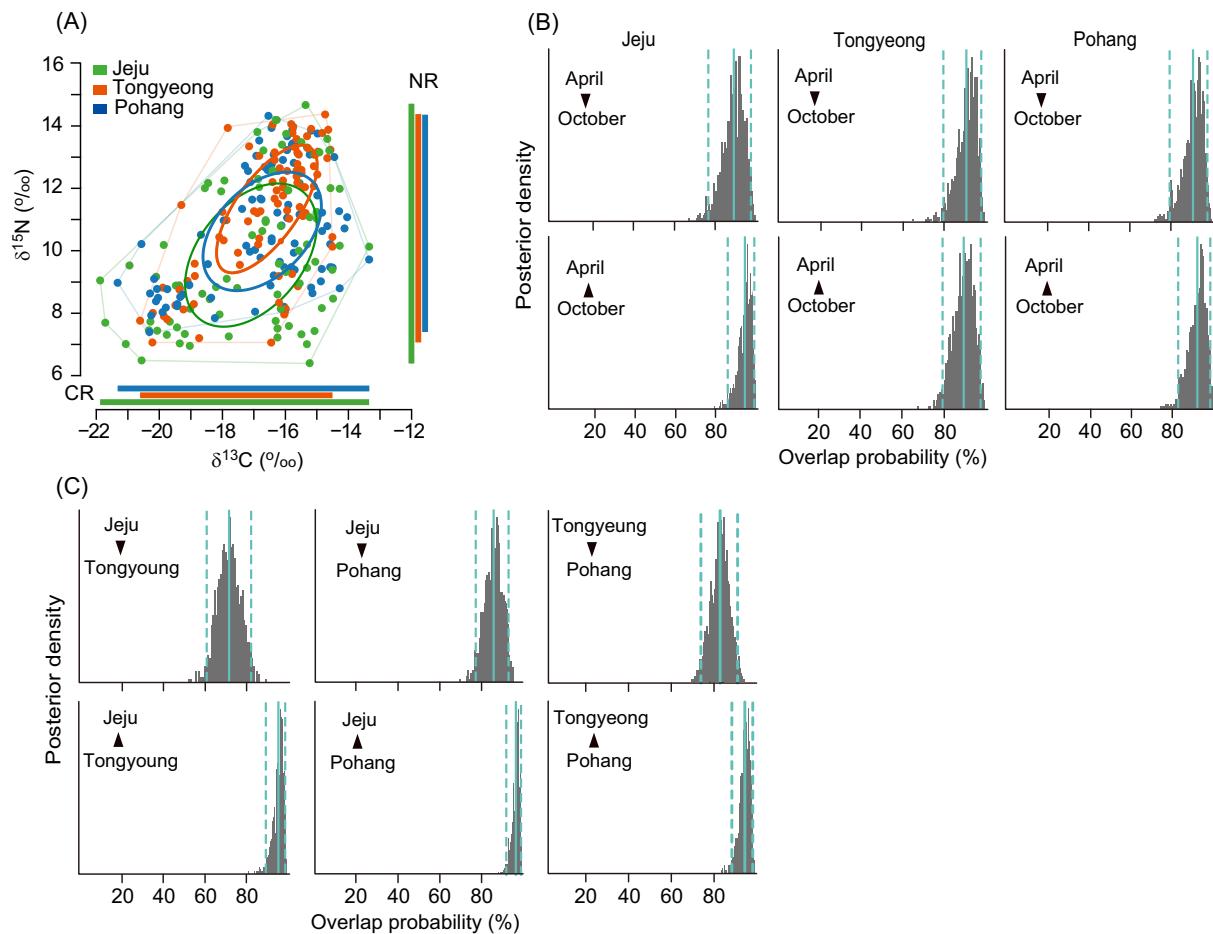
The  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of SF (Group I) and DF/GR (Group IIa) groups followed expected patterns, indicating their consistent reliance on pelagic and benthic sources for basal resources throughout their feeding history. These values served as end-member values representing isotopic baselines of food web pathways in the MixSIAR mixing model. The mixing-model estimation revealed that the DF/GR (benthic-affinity)

group contributed more (median 51 to 77 % and 53 to –85 %, respectively, except for omnivores at Tongyeong in April) to the diets of omnivorous and predatory invertebrate consumers than the pelagic-affinity (SF) group (median 23 to 49 % and 15 to 47 %, respectively) at all locations in both seasons (Fig. 6). In contrast, the dietary contribution of benthic-affinity prey to fish (Group IIb) ranged from approximately 36 to 75 % compared with 25 to 64 % of pelagic-affinity prey on each occasion.

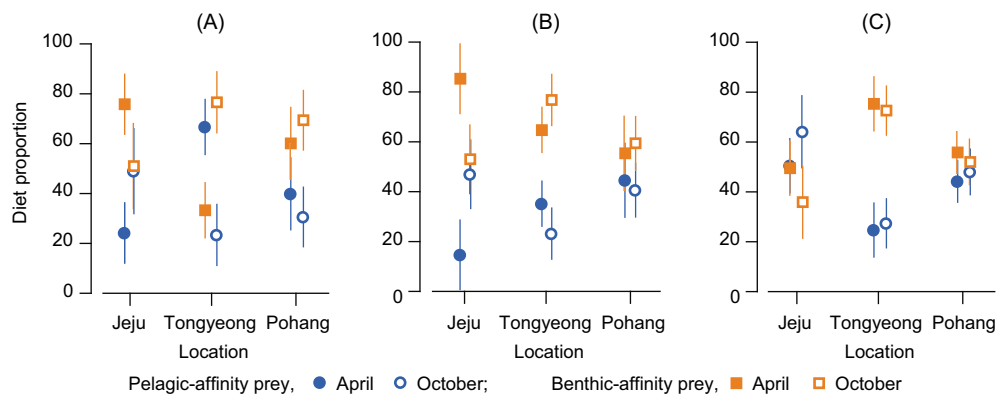
## 4. Discussion

We found that in coralline-barren ecosystems with intermittent coral presence, the food web structure remains relatively stable despite fluctuating oceanographic conditions along the coastline. The maintenance of rich biodiversity is widely acknowledged as crucial for ensuring ecosystem stability and continued functioning, as species with functional redundancy can buffer the impacts of individual species' loss (Biggs et al., 2020). In kelp forests, the decline of keystone species at higher trophic levels—whether due to natural or anthropogenic factors or both—often leads to increased urchin populations, further depleting kelp canopy and understory algal communities (Eisaguirre et al., 2020). However, our findings suggest that even in the absence of palatable macroalgae, barren ecosystems exhibit trophic redundancy, not only within functional guilds but also at the entire community level. Additionally, our results from three locations sampled in different years indicate that expected year-to-year variations in environmental parameters may reduce potential biases when interpreting food web patterns across different locations.

We observed a consistent isotopic niche across the rocky-bottom



**Fig. 5.** Isotopic niche areas for the combined community of invertebrates and fish (A), represented by the total area (TA, convex hull area) and standard ellipse area (SEAc, circles) based on the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ranges (CR and NR) encompassing all consumer taxa collected from Jeju, Tongyeong, and Pohang. Posterior distribution of the probabilistic niche overlap (%) between two seasons in each location (B) and between locations (C). The vertical (see green) solid lines represent posterior means and dotted lines represent 95 % credible intervals. The arrows indicate the directions of niche overlaps between the communities. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 6.** The proportional contribution (median and 95 % credibility intervals) of pelagic- and benthic-affinity prey (suspension feeders and deposit feeders/grazers, respectively) to the diets of higher-level consumers, specifically invertebrate omnivores (A) and predators (B), and fishes (C) in Jeju, Tongyeong, and Pohang in April and October. These estimations are derived using the MixSIAR mixing model.

food webs following transitions from canopy-dominated to barren states. Indeed, community-wide CR, NR, niche area (SEAc, TA), and niche overlaps all remained consistent with time and space. At the functional-guild level, distinct differences in CR between SF and DF/GR groups highlighted their exclusive consumption of pelagic and benthic organic matter, indicating trophic niche partitioning (Jennings et al.,

1997; Kang et al., 2008, 2021). This differentiation underscores the roles of both functional feeding guilds as isotopic baselines for pelagic and benthic food-web pathways, respectively (Post, 2002; Kang et al., 2021), assigning them to pelagic- and benthic-affinity prey for predators. The increase in  $\delta^{15}\text{N}$  values of omnivorous and predatory invertebrates, along with their considerable overlap in CR with the DF/GR group,

suggests a prevalence of trophic transfer through the benthic pathway to higher trophic levels. Despite barren conditions, our site-specific mixing-model estimation supports a substantial consumption of benthic prey by omnivores and predators in most subtidal barren locations.

Fish assemblages sampled from three distinct locations exhibited noticeable variations (Tables S4–6), likely influenced by differing oceanographic conditions. Despite these variances, little seasonal or spatial pattern was observed in their NR and trophic niche areas, indicating similar trophic positions across locations. Moreover, highly overlapping CRs also suggest consistency in their dietary use (pelagic vs. benthic), implying seasonal uniformity in the dietary contribution of pelagic- and benthic-affinity prey to fish predation. However, our mixing-model estimation revealed slight spatial variations in the contribution of pelagic vs. benthic pathways to fish nutrition. This spatial disparity in dietary use of fish may stem from species-specific characteristics in feeding habits (Jennings et al., 1997) or differences in prey abundances and diversity (Wellenreuther and Connell, 2002; de la Vega et al., 2023) influenced by hydrographic conditions impacting invertebrate communities. Our findings underscore the importance of diverse (pelagic and benthic) sources of organic matter as the trophic base in barren rocky-reef ecosystems. Similar high diversity of food sources has been documented in comparable barren ecosystems such as maerl beds (Grall et al., 2006), oyster reefs (Martinez-Baena et al., 2023), coral reefs (Page et al., 2013; Lesser et al., 2022), subtidal soft-bottom habitats (Kang et al., 2020), and other barren rocky reefs (Kang et al., 2008).

Despite some spatial disparities, the shared trophic reliance of fish groups on both pelagic- and benthic-affinity prey underscores the close connection between pelagic and benthic food chains, highlighting the significance of both carbon sources in the functioning of barren rocky-reef ecosystems. Most rocky-reef fish species primarily consume benthic invertebrates of suitable size as their main food sources, with some species feeding on both fishes and invertebrates (Russell, 1983; Howarth et al., 2021). Our mixing-model results indicate heavy foraging by reef fish on epifaunal invertebrates of both functional feeding guilds, which utilize pelagic and benthic food sources. However, predicting predation on abundant SF (e.g., sponges, anthozoans, bryozoans, and ascidians in our systems), with pelagic  $\delta^{13}\text{C}$  signatures, remains challenging due to their low acceptability by fish (Russell, 1983). Nonetheless, certain mollusks and arthropods, along with underexplored zooplankton in this study, serve as feasible dietary resources that facilitate the transfer of pelagic carbon through food web pathways. Additionally, the foraging behavior of motile fish on pelagic or benthic assemblages in soft-bottom habitats adjacent to rocky reefs may result in their tissue  $\delta^{13}\text{C}$  values matching pelagic  $\delta^{13}\text{C}$  signatures (which are more negative than those of reef-derived benthic sources) (Wyatt et al., 2012; Martins et al., 2013). As a result, despite variations in faunal compositions, the observed consistency in CR and NR at the entire community level across barren rocky-reef ecosystems highlights a generalized pattern in niche diversity made by functional groups.

The consistent size of community-wide niches (TA and SEAc) across barren rocky-reef ecosystems indicates a notable functional redundancy within the community. This niche consistency persists irrespective of varying hydrographic conditions, showing no expansion or compression of trophic niches. This functional redundancy is primarily attributed to trophic diversity ensured by niche partitioning. Different groups of invertebrates categorized into feeding guilds, such as SF vs. DF/GR groups, display differentiation in resource use across diverse locations and seasons. Generally, macroalgae within kelp forest ecosystems act as trophic supporters for high secondary production (Duggins et al., 1989; Kang et al., 2008; Kim et al., 2022) and provide habitats for a diverse array of animals, thereby influencing the dynamics of faunal populations (Kwon et al., 2010; Eisaguirre et al., 2020). However, when transitioning to barren conditions, fluctuations in food availability, both seasonally and spatially, could considerably alter the trophic dynamics of populations and communities inhabiting rocky-bottom habitats. Despite the

potential for such changes, the constancy observed in isotopic niche space occupied by different functional invertebrate groups suggests the absence of niche elimination resulting from the loss of specific feeding-guild consumers, or trophic niche homogeneity induced by resource homogenization within these barren ecosystems (Burdon et al., 2020). Our mixing model estimation further accounted for the consumption of both pelagic and benthic baseline consumers, which occupy distinct trophic niches, by higher-level predators (including both invertebrates and fish). This highlights the stable community-wide trophic niches present in barren rocky-bottom ecosystems.

With consistent niche sizes observed, the extensive trophic niche overlaps further underscore trophic redundancy across barren rocky-reef ecosystems. Indeed, TA presented nearly complete overlaps across all locations, while SEAc similarly displayed high overlaps across locations. Despite expected declines in macroinvertebrates of diverse functional feeding groups, coralline-barren communities in subtidal rocky-bottom habitats retain relatively high species diversity, sometimes comparable to kelp-dominated systems (Ojeda and Dearborn, 1989; Kwon et al., 2010). We also found a diverse array of invertebrates and fish in our barren ecosystems. Furthermore, we observed a remarkable uniformity in trophic niches (both area size and  $\delta$ -space occupied) of individual functional groups (defined here as pelagic- and benthic-affinity invertebrate groups, and fish) across all locations, with different groups partitioning their niche space in every location (Fig. 4). Trophic interactions of primary consumers with different feeding habits (SF vs. DF/GR) with pelagic and benthic resources expand the entire community CR. Further, interactions with predators (both invertebrates and fishes) made by different mixes of both prey groups expand the community NR. The consistent niche space observed for each functional group across locations suggests that a diverse array of fauna contributes to species and functional redundancy, thereby resulting in the observed high degree of niche overlap and consistent overall niche space in barren rocky-bottom communities.

Our isotopic analysis provides evidence of primary consumers utilizing both pelagic and benthic resources, followed by their transfer to predators, thus maintaining consistent trophic niches and their overlap across locations. Food webs reliant solely on phytoplankton or specific algae may exhibit narrower trophic niches compared with those supported by multiple basal resources (Quillien et al., 2016; Park et al., 2020). While benthic organic matter, such as macroalgal detritus, can support the secondary production of SF in macroalgal beds (Duggins et al., 1989), the CR of SF groups in these barren grounds indicates their exclusive dependence on phytoplankton. We anticipated that variations in trophic conditions from oligotrophic to eutrophic states would result in a spatial shift from pico/nano to microphytoplankton in community composition and availability (with differing biomasses). However, the resulting spatial patterns in food resource exploitation by SF consumers were unclear due to the proximity of isotope values between CPOM and FPOM. Similarly, the higher  $\delta^{13}\text{C}$  values observed in invertebrates of the DF/GR groups compared with those of the SF group in the absence of macroalgal availability, may indicate high dietary flexibility (Padilla and Savedo, 2013). The herbivory of grazers on kelps can transition to omnivory. For example, sea urchins, the dominant grazers on kelps, can consume a diverse array of food items in the absence of canopy cover, including bivalves, gastropods, crustaceans, sponges, bryozoans, coralline algae, silt and sand particles, and benthic diatoms (Ridder and Lawrence, 1982; Lee et al., 1988). Many grazers can also exploit benthic biofilms formed by microalgae, bacteria, and other microorganisms on rock surfaces (Kang et al., 2021), bivalve shell surfaces (Barillé et al., 2017), and potentially coralline algae surfaces (Fig. 1) common in barren grounds.

Our findings further emphasize the interconnectedness of pelagic and benthic trophic pathways, often coupled with detrital pathways, which stretch from primary resources to apex predatory fish. This phenomenon is widespread across various locations. Doubtless, the trophic signatures of primary consumers we observed indicate their adaptability

(i.e., feeding flexibility) to fluctuating food resources, representing how they convey the redundancy of species within functional groups across different locations, even when faced with varying hydrographic conditions (Gitay et al., 1996). As a result, apex predators (e.g., fishes) with generalist feeding habits maintain their foraging niches based on the acceptability and availability of prey items, effectively linking different trophic pathways. Although our study did not directly investigate food web stability, we noticed a consistent trend in trophic niche processes that contribute to the stability of food webs within barren rocky-bottom ecosystems. Further, the widespread overlap in trophic niches observed across barren rocky-bottom habitats likely arises from the interconnected food-web pathways linking pelagic and benthic sources following transitions from canopy-forming to barren states.

## 5. Conclusion

Our findings shed light on the often-overlooked intricacies of food-web dynamics in disturbed habitats, particularly in rocky subtidal ecosystems undergoing phase shifts (cf. Kang et al., 2008; Kim et al., 2022). Despite commonly observed declines in basal resources and invertebrate prey abundances, our findings reveal a surprising consistency in trophic niche dynamics across barren rocky-bottom ecosystems, even under diverse hydrographic conditions. This uniformity stems from the remarkable trophic equivalence observed among consumers within functional groups across barren locations, providing a high degree of trophic redundancy. Consequently, this redundancy likely facilitates extensive community-wide trophic niche overlaps. Moreover, the presence of species comprising diverse functional feeding guilds, capable of partitioning multiple basal resources (from pelagic to benthic) and creating further food-web pathways to apex predators, may enable rocky-bottom ecosystems to maintain uniform food-web structure and function despite reductions in basal resources. The spatial consistency and overlaps of trophic niches occupied by common rocky subtidal taxa highlight the adaptability of barren communities to the new environmental conditions following phase shifts. This further suggests that the flexibility of food webs following phase shifts creates intrinsic trophic structure in these barren ecosystems. Overall, our findings highlight the crucial roles of consumers that persist with diverse functional feeding guilds in conferring the adaptability of barren rocky-bottom ecosystems following habitat disturbance.

## CRedit authorship contribution statement

**Hee Yoon Kang:** Writing – original draft, Visualization, Investigation, Formal analysis, Data curation, Conceptualization. **Byeong-Gweon Lee:** Writing – review & editing, Supervision, Methodology, Formal analysis, Data curation. **Sang Rul Park:** Writing – review & editing, Visualization, Methodology, Investigation, Formal analysis. **Changseong Kim:** Writing – review & editing, Validation, Investigation, Formal analysis, Data curation. **Jaebin Jang:** Writing – review & editing, Investigation, Formal analysis, Data curation. **Chang-Keun Kang:** Writing – review & editing, Writing – original draft, Supervision, Resources, Funding acquisition, Data curation, Conceptualization.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marpolbul.2024.116997>.

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