Trophic importance of benthic microalgae to macrozoobenthos in coastal bay systems in Korea: dual stable C and N isotope analyses

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ABSTRACT: The role of benthic microalgae as the source of primary organic matter for the macro-zoobenthos community was examined in 3 bay systems of the south coast of the Korean peninsula using stable carbon and nitrogen isotope ratios (δ^{13}C and δ^{15}N) as a dual tracer. The δ^{13}C and δ^{15}N of riverine particulate inputs, primary producers and macrozoobenthos collected from the intertidal and subtidal habitats of the bays were measured and compared with those from adjacent offshore waters. Extensive intertidal flats occurred with wide marsh plains (primarily *Phragmites australis*) at the uppermost part of the intertidal zone in all 3 bay systems, but different hydrologic features were exhibited among bay systems. There were no systematic variations in δ^{13}C for the same plant taxa, but different producer groups were clearly separated by their δ^{13}C values. Benthic microalgae and macroalgae, which had similar δ^{13}C values, were separated by their δ^{15}N values. The δ^{13}C values of macrozoobenthos collected from the offshore areas were similar to those of phytoplankton. Macro-zoobenthos collected from all 3 bay habitats had similar δ^{13}C ranges, and their δ^{13}C values (means of all consumers, feeding types and species) were less negative than those of the offshore macro-zoobenthos. Isotopic linkage between sources and benthic consumers, based on the documented trophic fractionation for C and N, indicated that benthic microalgae and phytoplankton are the major sources of organic matter supporting macrobenthic consumers in the bay systems. A 2-source mixing model revealed that pelagic feeders in both the intertidal and subtidal habitats subsisted in equal shares on marine phytoplankton and benthic microalgae, whereas the food source of benthic feeders was derived predominantly from benthic microalgae. *Phragmites* or riverine particulate inputs appeared to have made little contribution to the diets of consumers in the bay systems. Our collective isotopic data set suggested that benthic microalgae, along with phytoplankton, constituted the organic matter that forms the trophic base of pelagic as well as benthic food webs in the coastal bays, despite differing vegetational composition and hydrology.

KEY WORDS: Stable isotope ratios · Food webs · Benthic microalgae · Tidal flat · Macrozoobenthos · Korean coast

INTRODUCTION

Benthic consumers in shallow coastal environments may have food sources of terrestrial, limnic and marine origin, and the relative importance of those sources may vary temporally and spatially. Our knowledge on the trophic base of food webs in coastal embayments is still limited, due to difficulties in determining the relative role of each food source for benthic invertebrate diets. Stable isotope studies on coastal benthic consumers and their potential food sources have revealed the importance of locally produced food sources for the

benthic consumers (Peterson et al. 1985, Ruckelshaus et al. 1993, Deegan & Garritt 1997, Riera et al. 1999). In this respect, much attention has been paid to the role of benthic microalgae for food webs of coastal embayments, where a high standing crop of benthic microalgae occurs in the surface sediments (Schwinghamer et al. 1983, Riera & Richard 1996, Herman et al. 2000, Riera et al. 2000). Since resuspended benthic microalgal biomass can often exceed that of phytoplankton in the tidal flat ecosystems (Cadée 1971, Baillie & Welsh 1980, de Jonge & van Beusekom 1992, Prou et al. 1994), it is hypothesized that organic matter from benthic microalgae along with phytoplankton may support both benthic and pelagic food webs in the intertidal and adjacent subtidal areas of shallow bay systems.

Coastal bays in Korea might be good examples to identify the importance of benthic microalgae to nearshore food webs, because intertidal flat areas comprise about 2900 km^2 along the western and southern coastline of the Korean peninsula. Since large areas of the tidal flats have been destroyed by reclamation and dredging for agricultural and industrial purposes since the 1900s, a conflict between development by reclamation and conservation of the intertidal flats has recently emerged. The full range of disturbance effects caused by these anthropogenic activities on bay ecosystems is unknown. Characterization of the trophic base of coastal benthic communities may provide novel insight for an integrated management of coastal resources. If benthic microalgae play an important role as a food source for consumers in the systems, the extensive disturbance of tidal flats may change the balance of organic matter sources and the availability of food in the ecosystems. Therefore, it is essential to understand the flow of energy through benthic food webs, and thereby assess the importance of benthic microalgae as a diet for consumers in coastal food webs.

Studies of stomach contents of fishes from the southern coasts of Korea do not offer information on ultimate sources of dietary materials (Park & Cha 1995, Park et al. 1995, Huh & Kwak 1998a,b,c). A recent stable carbon isotope study of consumers in Kwangyang Bay revealed the dominant contribution of benthic microalgae to benthic consumer tissue carbon (Kang et al. 2001). However, information on the roles of potential food sources is still insufficient to establish the importance of benthic microalgae to the southern coastal bay systems of Korea, because of variations in hydrologic conditions, and vegetal and sedimentary composition among bay systems. In the present study, we analyzed stable C and N isotopes as a dual tracer to characterize the food base for benthic communities in 3 coastal bays that have a wide intertidal zone along with a large river discharge, and large stands of *Phragmites*, or without these limno-terrestrial sources.

During the past decade, stable isotope analysis has been used to examine trophic interactions and food web relationships in aquatic habitats (Fry & Sherr 1984, Michener & Schell 1994). The δ^{13}C and δ^{15}N values of consumers reflect those of their diets. Relatively slight ($\leq 1\permil$) fractionation of the C isotope between a consumer and its diet gives the consumer a similar δ^{13}C value to its diet (DeNiro & Epstein 1978, Fry & Sherr 1984). In contrast, higher trophic fractionation of nitrogen compared to carbon occurs with an increase of 2 to 4$\permil$ per trophic level (DeNiro & Epstein 1981, Minagawa & Wada 1984). Therefore, isotopic comparison between consumers and their potential food sources can be used to trace the flow of organic matter through food webs if different food sources are isotopically distinct.

The objectives of this research were to identify organic matter sources that support benthic consumers, and to assess the extent to which materials derived from benthic microalgae are used for benthic invertebrate production within 3 different coastal bay systems of Korea. Since δ^{13}C values of benthic microalgae are readily distinguishable and less negative compared with those of salt marsh, terrestrial vascular plants and phytoplankton (Currin et al. 1995, Riera et al. 1999, Kang et al. 2001), we precluded that δ^{13}C values of consumers of benthic microalgae-based food webs would be less negative than those in marine food webs that are supported by other primary producers. We compared isotopic composition of benthic invertebrates in coastal bay ecosystems with those in offshore systems where phytoplankton are major primary producers. When the main food sources of an animal were identified, the relative importance of each source to the animal diet was calculated through the isotopic mixing model (Fry & Sherr 1984).

MATERIALS AND METHODS

Description of study bays. Our study bays and adjacent offshore area are located at the centre of the southern coast of the Korean peninsula (Fig. 1). The 3 bays contain large and bare intertidal flats. Kwangyang Bay is affected by river runoff and has large nutrient inputs from freshwater discharge (annual mean 72.9 m^3 s^{-1}) from the Seomjin River, which drains ca. 5×10^3 km^2 of agricultural and forested land (Kwon et al. 2002). The sediment of the intertidal flats consists of sandy mud (Park et al. 1984) and the upper estuarine supralittoral area is lined with common reed *Phragmites australis* communities. Although most of the dense *Zostera marina* beds, which previously occurred in the entire bay, have disappeared, some patches still exist along the low tide line. A few macroalgal mats were also found on the
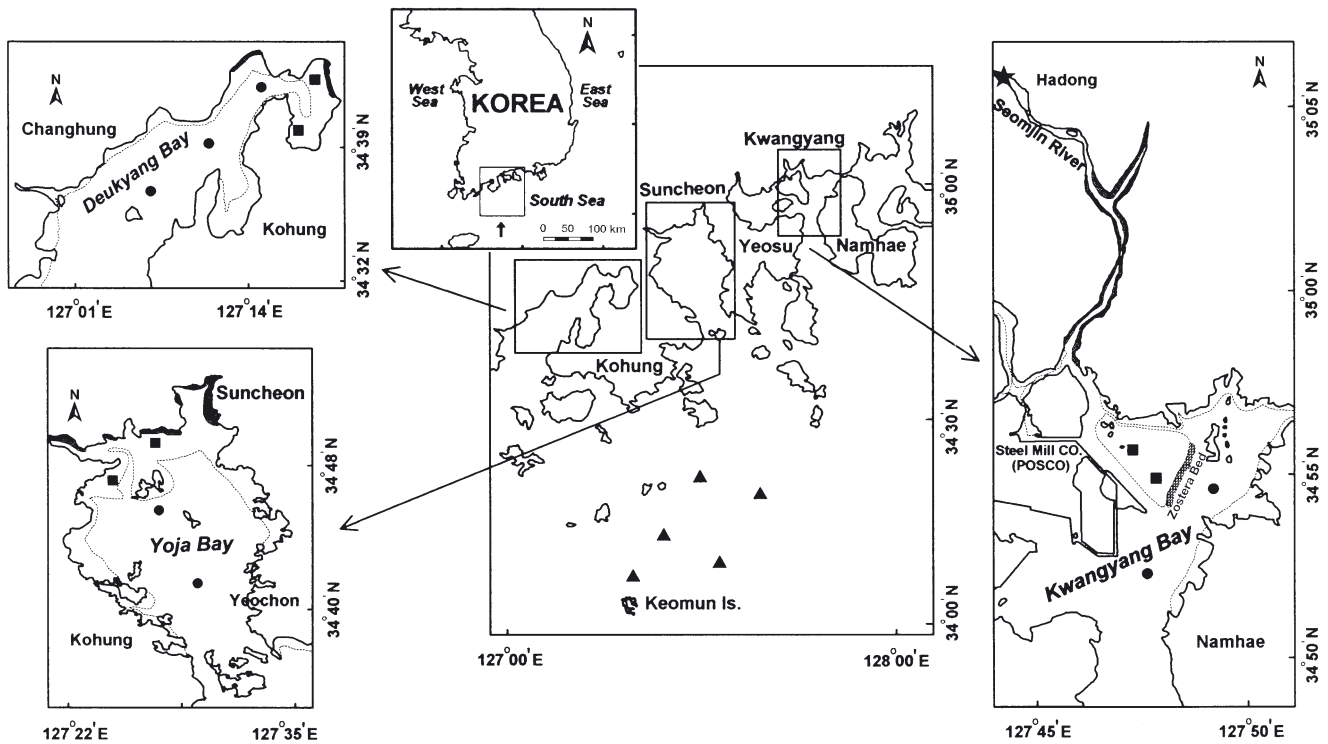
Fig. 1. Map of study area on the southern coast of the Korean peninsula, showing sampling sites in Kwangyang Bay, Yoja Bay, Deukryang Bay and offshore area. Dashed line indicates low water line of tidal flats. Dark black areas are dominated entirely by *Phragmites australis*. (■) Intertidal sites; (●) subtidal sites; (▲) offshore sites; (★) riverine particulate organic matter (POM) collection site

tidal flats. The 2 neighboring bays, Yoja and Deukryang Bays, however, are free from river runoff and the sediments consist entirely of mud (Kong & Lee 1994). In Yoja Bay, the uppermost part of the intertidal zone is covered by broad (~10 km^2) marsh plains of *Phragmites australis*. In Deukryang Bay, the marsh is narrower than that of Yoja Bay, but *Phragmites* still covers restricted areas of the upperintertidal zone, and few macroalgal mats are found on the tidal flats. Surface sediments of the bay are deposited from offshore, and nutrients are mainly supplied by an inflow of coastal waters (Kong & Lee 1994, Yang et al. 1995).

The bay systems are shallow, with a mean depth of ca. 10 m, and are semienclosed. The tidal cycle is semidiurnal, with a maximum tidal amplitude of ~4.0 m on spring tides. Salinities in the surface waters range from 29.3 to 33.5 psu in Kwangyang Bay, from 27.8 to 33.4 psu in Yoja Bay, and from 31.4 to 33.7 psu in Deukryang Bay (National Fisheries Research and Development Institute 2002). Benthic microalgal mats were commonly visible on the intertidal beds in all 3 bays (5 to 44 µg chl *a* g^{-1} dry sediment in this study). A large quantity of commercial clams have been harvested from natural beds and are also cultured intensively on the tidal flats. Detailed descriptions of macro-

zoobenthic communities in these bays are presented by Je et al. (1991), Lim et al. (1991), Jung et al. (1997) and Shin & Kim (2002). Approximately 21 km^2 (ca. 10% of the total bay area) of the intertidal flats in Kwangyang Bay have been reclaimed during the past 20 yr. More recently, reclamation to construct a new port and dredging to ensure access for shipping has also reduced the area of the tidal flats. A large-scale reclamation of the innershore for agricultural purpose is in progress in Deukryang and Yoja Bays.

Sample collection and treatment. Potential food sources and benthic invertebrate macroconsumers were collected from May to July 2001 from 2 intertidal sites and 2 subtidal sites within each bay, and from 5 offshore sites (Fig. 1).

Riverine suspended particulate organic matter (riverine POM) for stable isotope analyses was collected at a site 16 km north from the mouth of the Seomjin River. A total of 20 l of water was pumped and prefiltered with a 63 µm screen to remove large particles, and then the particulates in this prefiltered water were concentrated onto precombusted Whatmann GF/F filters.

Suspended POMs were collected at the entrances of the 3 bays and at 2 offshore sites during flood tide by

the same precedure as for riverine POM, to obtain pure marine particulates. Phytoplankton for stable isotope analyses was collected using a 0.5 m diameter net fitted with a 20 µm mesh and a nonfiltering cod end. Several vertical tows were conducted at the same sites where POM samples were collected. Sediments were obtained using a gravity corer with 5 cm diameter, and surface sediments were subsampled for stable isotope analyses of sedmentary organic matter (SOM) at the 2 subtidal sites inside the bays.

Benthic microalgae were collected by scraping the visible mats of benthic diatoms on the sediment surface at 2 intertidal sites within each bay at low tide. The diatoms were mainly *Navicula* sp., *Cylinderutheca closterium* and *Pleurosigma angulatum*. The method applied to extract benthic diatoms was slightly modified from Couch (1989), and the more detailed procedure is described by Riera & Richard (1996). Seagrass *Zostera marina* and macroalgae *Ulva pertusa* and *Enteromorpha compressa* were collected by hand near the low tide line of Kwangyang Bay and cleaned carefully to remove epibionts. Black pussywillow *Salix gracilistyla*, which is one of the most common shrubs in the riverine system of Kwangyang Bay, was collected by hand at the same site where the riverine POM collection was made. Common reed *Phragmites austalis* was sampled at the upper estuarine site in Kwangyang Bay and at the upper parts of intertidal flats in Yoja and Deukryang Bays. Vascular plants were rinsed with distilled water to remove adhering particles or sediments.

Intertidal benthic invertebrates were collected by sieving sediment cores through 500 µm mesh screens. Sediment samples for benthic consumers from offshore and subtidal sites were collected using a 0.12 m^2 van Veen grab. Organisms found in the sediment samples were cleaned of epibionts and identified. While all POM, sediment and plant materials were stored on ice in the field, the collected benthic invertebrates were kept alive overnight in filtered sea water from the sampling sites to evacuate gut contents. All collected materials were kept frozen in the laboratory until subsequent treatment. Muscle tissue was dissected carefully from thawed specimens of bivalves, crabs and shrimps, and whole tissues of polychaetes were used for isotopic analysis.

Stable isotope analysis. SOM, plant and animal tissue samples were treated with 10% HCl to remove inorganic carbonates. The samples were then rinsed with deionized distilled water to remove the acid. All samples were freeze-dried and then ground with a mortar and pestle. All the powdered samples were kept frozen (–70°C) until analysis. Carbon and nitrogen isotope ratios were determined using continuous-flow isotope mass spectrometry. Dried samples (ca. 1 mg for animal tissues and 5 mg for plant tissues)

were combusted in an elemental analyzer (EuroVector 3000 Series) and the resultant gas (CO_2 and N_2) was introduced to an isotope ratio mass spectrometer (Micromass IsoPrime) in a continuous flow using a He carrier. Data are expressed as the relative per mil (‰) difference between sample and conventional standards of Pee Dee Belemnite carbonate (PDB) for carbon and air N_2 for nitrogen, according to the following equation:

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

where X is ^{13}C or ^{15}N and R is the $^{13}C{:}^{12}C$ or $^{15}N{:}^{14}N$ ratio. Secondary standard of known relation to the international standard was used as a reference material. The standard deviations of $\delta^{13}C$ and $\delta^{15}N$ for 20 replicate analyses of the internal peptone standard were ±0.1 and ±0.2‰, respectively.

Statistical analyses and isotope mixing model. All statistical procedures were carried out using SPSS software (SPSS 1999). Normality of distributions was tested using the Shapiro-Wilk procedure for normality. Because all data were judged not to deviate significantly from a normal distribution, ANOVA and unpaired *t*-tests were performed without any prior transformation of the data. Homogeneity of variances was tested using Levene's test. One-way ANOVA tests were used to determine equality of isotopic values between potential food sources (producer groups, POM and SOM) from the 3 bays. When variances were homogeneous in the cases of Levene's homogeneity-of-variance tests, Duncan multiple comparison tests were subsequently used to determine where the significant differences occurred among variables. A 2-tailed, 2-sample *t*-test was also performed to test for significant differences in the isotopic signatures of macrozoobenthos between the coastal bay systems and the offshore sites, and between benthic and pelagiac feeders. To prevent overrepresentation of a single species in the ANOVA and *t*-tests due to replicate sampling, replicate values of the same consumer species from a habitat were averaged, and the average values were used in ANOVA and *t*-tests.

We used dual stable isotope plots of $\delta^{13}C$ and $\delta^{15}N$ to compare the stable isotope values of consumers with those of potential food sources within the study bays. In this step, we identified the trophic relationship by subtracting literature values for trophic fractionation of 1 and 2 to 4‰ per trophic level for $\delta^{13}C$ and $\delta^{15}N$, respectively, from isotope values of consumers (DeNiro & Epstein 1978, 1981, Fry & Sherr 1984, Minagawa & Wada 1984, and also McClelland & Valiela 1998, Riera et al. 1999). The proportional role of benthic microalgae as a food source for each consumer was estimated using a simple 2-source mixing model with phytoplankton and benthic diatoms as end-members. The

generalized mixing equation based on mean $\delta^{13}C$ values for a producer and consumer group was:

$$\% \text{ benthic microalgae} = \frac{\delta^{13}C_{consumer} - \delta^{13}C_{phytoplankton} - f}{\delta^{13}C_{benthic\ microalgae} - \delta^{13}C_{phytoplankton}} \times 100$$

where $f = +1‰$ for primary consumers, the average enrichment of animal carbon relative to their diet (DeNiro & Epstein 1978, Fry & Sherr 1984), and $f = +2‰$ for predators and omnivores because of a double trophic enrichment in $\delta^{13}C$. However, we did not consider the trophic effect for tertiary consumers feeding on other predators, because a further enrichment in tertiary consumers would not be expected due to their consumption of a diverse spectrum of prey items from both primary and secondary consumers (Junger & Planas 1994, Deegan & Garritt 1997).

RESULTS

Isotopic composition of primary producers, POM and SOM

Mean $\delta^{13}C$ values for dominant primary producers and riverine POM from Kwangyang Bay varied with a relatively wide range, between -28.9 and $-11.5‰$ (Appendix 1; www.int-res.com/journals/suppl/Kang_appendices.pdf), showing a substantial variation among plant taxa (Duncan multiple comparison test, p < 0.05). There were no significant differences among bays in $\delta^{13}C$ for the same food sources (ANOVA, p > 0.1 for *Phragmites*, phytoplankton and benthic diatoms, Table 1). Accordingly, most of the plant groups (i.e. *Phragmites*, phytoplankton, macroalgae, benthic diatom and seagrass) and riverine POM were easily differentiated by their $\delta^{13}C$ signatures, with -26.7 (±1.8), -20.8 (±1.1), -14.5 (±1.5), -14.1 (±0.4), -11.5 (±0.1), and -23.7 (±0.5)‰, respectively (Table 1, Appendix 1; www.int-res.com/journals/suppl/Kang_appendices.pdf). The $\delta^{15}N$ values of the same plant taxa were not significantly different among bay systems either (ANOVA, p = 0.315, 0.115 and 0.890 for *Phragmites*, phytoplank-

ton and benthic diatom, respectively). Despite a narrower range (6.1 to 14.2‰) relative to that of $\delta^{13}C$ values, mean $\delta^{15}N$ values tended to be separated distinctly into 3 different groups, i.e. *Phragmites* (7.4 ± 1.5‰) and riverine POM (8.6 ± 1.1‰), benthic diatom (11.0 ± 0.9‰) and phytoplankton (11.4 ± 0.9‰), and macroalgae (14.2 ± 1.0‰) and seagrass (14.1 ± 0.1‰). Although benthic diatoms and macroalgae overlapped in their ranges of $\delta^{13}C$ values, macroalgae had heavier $\delta^{15}N$ values than benthic diatoms, and thus a dual isotope plot of $\delta^{13}C$ and $\delta^{15}N$ distinguished more clearly between these primary producers.

Suspended POM from the waters at the entrances of the bays had quite constant $\delta^{13}C$ values with a mean value of $-20.4‰$ (±1.1) among different bay systems (ANOVA, p = 0.689, Table 1). The $\delta^{13}C$ values ($-20.7 \pm 0.1‰$) of the suspended POM from the offshore waters were comparable to those of phytoplankton ($-20.0 \pm 0.5‰$). The mean $\delta^{15}N$ value of suspended POM from the mouths of the 3 bays was 11.3‰ (± 0.9), corresponding to the isotopic range for phytoplankton. While mean $\delta^{13}C$ values of offshore phytoplankton and POM were similar to those from the bays (*t*-test, p = 0.063 and 0.689 for phytoplankton and POM, respectively), mean $\delta^{15}N$ values of phytoplankton and suspended POM (9.5 ± 0.7‰ and 8.8 ± 1.4‰, respectively) were slightly lighter in offshore than in the bay systems (*t*-test, p < 0.001). Mean $\delta^{13}C$ and $\delta^{15}N$ values of SOM were similar among the 3 bay systems with overall mean values of $-19.5‰$ (±0.9) and 10.5‰ (±0.7), respectively (ANOVA, p = 0.925 and 0.850 for $\delta^{13}C$ and $\delta^{15}N$, Table 1).

Isotopic composition of macrozoobenthos

The $\delta^{13}C$ values of macrozoobenthos collected from the bay systems were uniformly less negative and somewhat more variable than those collected from the adjacent offshore area (Fig. 2). The bay consumers had a range of $\delta^{13}C$ values from -17.8 to $-10.0‰$, whereas the offshore consumers ranged from -20.5 to $-16.4‰$ (Appendices 2 & 3; www.int-res.com/journals/suppl/Kang_appendices.pdf). The $\delta^{15}N$ values of consumers

Table 1. ANOVA tests for differences in the $\delta^{13}C$ and $\delta^{15}N$ values of primary producers and suspended particulate and sedimentary organic matter (POM and SOM, respectively) among bays

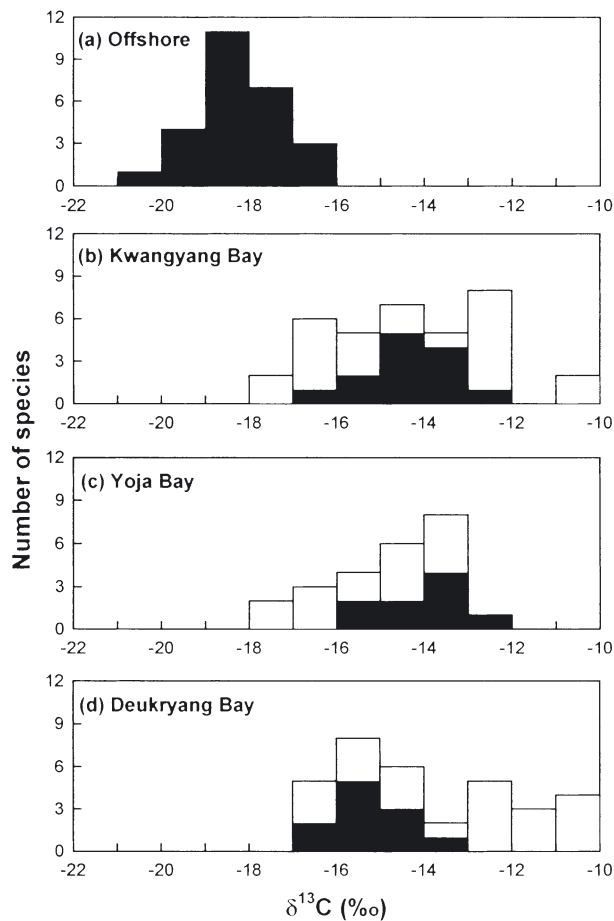|	$\delta^{13}C$				$\delta^{15}N$			
	F	df	p	Mean (±SD) ‰	*F*	df	p	Mean (±SD) ‰
Phragmites	4.764	2, 4	0.087	-26.7 (±1.8)	1.561	2, 4	0.315	7.4 (±1.5)
Phytoplankton	4.547	2, 6	0.063	-20.8 (±1.1)	0.112	2, 6	0.896	11.4 (±0.9)
Benthic diatoms	1.502	2, 12	0.262	-14.1 (±0.4)	0.117	2, 12	0.890	11.0 (±0.9)
POM	0.396	2, 6	0.689	-20.4 (±1.1)	0.089	2, 6	0.916	10.8 (±0.5)
SOM	0.079	2, 10	0.925	-19.5 (±0.9)	0.165	2, 10	0.850	10.5 (±0.7)

Fig. 2. Frequency distribtion of $\delta^{13}C$ values of macrozoobenthos collected in offshore sites, Kwangyang Bay, Yoja Bay and Deukryang Bay. White bar segment: intertidal animals; black bar segment: subtidal animals

thic feeder category, had similar $\delta^{13}C$ values. The division was less clear in the subtidal habitats. No isotopic difference was found between pelagic and benthic feeders in Yoja and Deukryang Bays (*t*-test, p = 0.135 and 0.174, respectively). Mean $\delta^{13}C$ values of benthic feeders were significantly different between bay systems and offshore sites (*t*-test, p < 0.001 for deposit feeder and predator; p = 0.004 for omnivore) (Appendices 2 & 3).

The ranges of $\delta^{15}N$ values for macrozoobenthos were nearly identical in Kwangyang (13.6 to 18.5‰), Yoja (14.1 to 18.5‰) and Deukryang Bays (12.7 to 17.8‰, Appendix 2; www.int-res.com/journals/suppl/Kang_appendices.pdf). The $\delta^{15}N$ values of the consumers and predators were generally higher than those of their potential prey. Primary consumers, such as suspension feeders (mean 14.3 ± 0.5‰, n = 31) and deposit feeders (14.7 ± 0.7‰, n = 29), had significantly (ANOVA, p < 0.001) lighter $\delta^{15}N$ values than predators (17.2 ± 0.7‰, n = 24) and omnivores (17.5 ± 0.6‰, n = 9). This result indicates that there was an isotopic shift in $\delta^{15}N$ from primary consumers to predators, showing heavier $\delta^{15}N$ with increasing trophic level. In the same manner, $\delta^{13}C$ and $\delta^{15}N$ values of producers (phytoplankton) and benthic consumers in the phytoplankton-dominated offshore area also exhibited a clear trophic enrichment, which was estimated to average 1.0 and 3.0‰ per trophic level for C and N, respectively (Appendix 3; www.int-res.com/journals/suppl/Kang_appendices.pdf). Mean $\delta^{15}N$ values of each functional group were also significantly heavier in the bay systems than those in the offshore sites (*t*-test, p < 0.001 for deposit feeder, predator and omnivore) (Appendices 2 & 3; www.int-res.com/journals/suppl/Kang_appendices.pdf).

Isotopic linkage between the potential primary food sources and the bay consumers

Isotopic comparison between potential food sources and benthic consumers was made by subtracting the fractionation values of 1‰ for $\delta^{13}C$ and 3‰ for $\delta^{15}N$ per trophic level from the measured isotope values of consumers (Fig. 3). The biplots of $\delta^{13}C$ and $\delta^{15}N$ values for the dominant producers and consumers showed very similar configurations in the 3 bay systems. The $\delta^{13}C$ and $\delta^{15}N$ values of consumers tended to be aligned between marine phytoplankton and benthic diatom in all the 3 bay systems. Despite Kwangyang Bay being affected by river runoff and having patches of seagrass and macroalgal mats, the alignment pattern of isotopic values of the Kwangyang Bay consumers was similar to those from Yoja and Deukryang Bays. The isotopic signatures of the bay consumers were far from those of *Phragmites* or riverine POM, and were positioned at the opposite end of the plot.
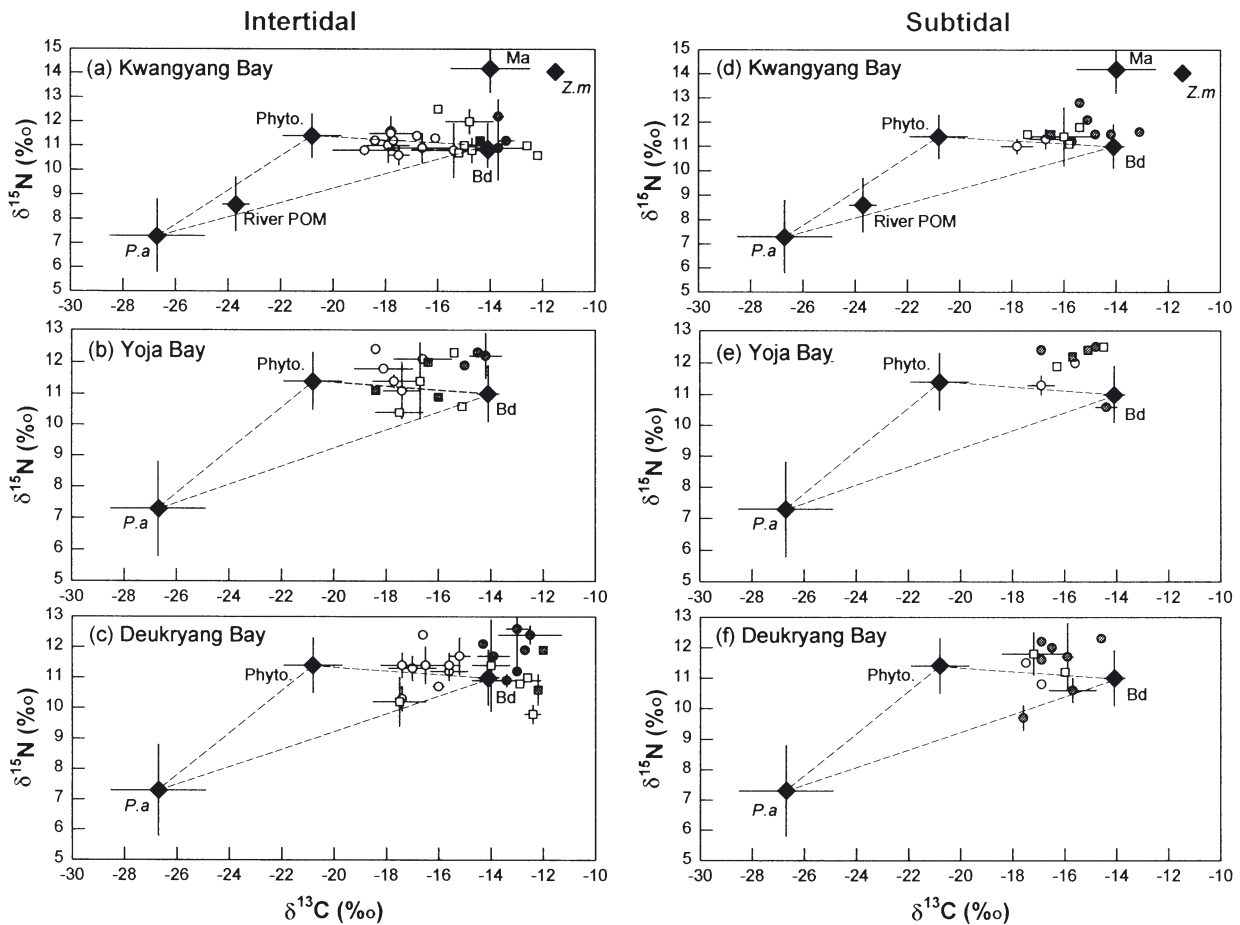
had similar ranges in the bays (12.7 to 18.5‰) and the offshore area (11.2 to 17.3‰).

Macrozoobenthos collected in Kwangyang, Yoja and Deukryang Bays had similar $\delta^{13}C$ ranges of –17.8 to –10.2‰, –17.4 to –12.5‰ and –16.6 to –10.0‰, respectively (Fig. 2, Appendix 2; www.int-res.com/journals/suppl/Kang_appendices.pdf). Macrozoobenthos $\delta^{13}C$ signatures showed similar distribution patterns between intertidal and subtidal habitats in all 3 bays, but were more variable in the intertidal habitats. The $\delta^{13}C$ values of intertidal macrozoobenthos varied markedly according to their feeding zone (strategy). Benthic feeders had less negative $\delta^{13}C$ values than pelagic feeders (*t*-test, p < 0.001 for all 3 bays). Suspension-feeding bivalve species, which were assigned to the pelagic feeder category in this study, usually had more negative $\delta^{13}C$ values, from –17.8 to –14.2‰, than other feeding groups. Deposit feeders (–14.4 to –11.5‰) and predators and omnivores (–16.6 and –10.0‰), which were all assigned to the ben-

Fig. 3. $\delta^{13}C$ and $\delta^{15}N$ values of macrozoobenthos from intertidal (left) and subtidal (right) sites, corrected for trophic fractionation effects and compared to isotopic values of food sources in Kwangyang Bay, Yoja Bay and Deukryang Bay. Primary producers: Phyto. = phytoplankton, Bd = benthic diatom, *P.a = Phragmites australis*, Ma = macroalgae, *Z.m = Zostera marina*. Macrozoobenthos: (O) suspension feeders, (●) deposit feeders, (□) predators, (■) omnivores. To correct for trophic fractionation, 1 and 3‰ were subtracted from the $\delta^{13}C$ and $\delta^{15}N$ values of suspension and deposit feeders, respectively; 2 and 6‰ were subtracted from the $\delta^{13}C$ and $\delta^{15}N$ values of predators and omnivores, respectively. Dashed lines encompass the areas where isotopic values for consumers (corrected for trophic fractionation) are expected when their diets consist of a mix of the dominant producers in the study systems. Error bars are means ± 1 SD

In intertidal habitats, the isotopic signatures of suspension feeders fell between those of phytoplankton and benthic diatoms, whereas the deposit feeders were much more closely aligned with those of benthic diatoms (Fig. 3a–c). With only a few exceptions, the distribution of isotopic values of the predators and omnivores closely matched those of the deposit feeders. Therefore, these alignments of consumer isotope signatures indicate that pelagic feeders in the intertidal habitats obtain their food from a mixture of benthic diatoms and phytoplankton, while benthic feeders use materials derived mostly from benthic microalgae. Such a difference in the isotopic compositions between benthic and pelagic feeders was less amenable for the subtidal consumers (Fig. 3d–f). Isotopic signatures of

the subtidal consumers were closer to benthic microalgae than phytoplankton.

A great difference in $\delta^{13}C$ (6.7‰) between benthic microalgae and phytoplankton allowed the application of a mixing equation to identify the relative contributions of the 2 food sources to consumer diets. Differences in $\delta^{15}N$ values between these 2 food sources were too small to be used. Contributions of intertidal benthic microalgae to benthic food webs of the 3 coastal bays were variable among different feeding groups of consumers (Table 2). Pelagic feeders in both the intertidal and subtidal habitats were calculated to have received roughly half of their carbon from benthic microalgal source. This result implies that suspension feeders in the study bays

Table 2. Potential contribution (%) of benthic microalgae to carbon incorporated by macrozoobenthos inhabiting Kwangyang, Yoja and Deukryang Bays. Calculations were based on a 2-source mixing model and fractionation factor per trophic level of 1‰. Data are ranges (mean ± SD, n). Average $\delta^{13}C$ values of the same consumer species from a habitat were used for the model

Bay/habitat	Pelagic feeders	Benthic feeders
Kwangyang Bay		
Intertidal	30–81 (52 ± 15, 11)	72–128 (94 ± 9, 11)
Subtidal	45–61 (53 ± 12, 2)	51–115 (81 ± 17, 11)
Yoja Bay		
Intertidal	36–63 (47 ± 10, 5)	36–99 (73 ± 20, 10)
Subtidal	58–78 (68 ± 14, 2)	58–96 (81 ± 14, 7)
Deukryang Bay		
Intertidal	51–84 (64 ± 12, 9)	49–131 (111 ± 21, 14)
Subtidal	49–58 (54 ± 6, 2)	54–93 (66 ± 13, 9)

subsist with equal shares on marine phytoplankton and benthic microalgae. It was apparent that the food source of the benthic feeders (deposit feeders, predators and omnivores) was derived predominantly from benthic microalgae. The estimated contribution of benthic microalgae to benthic feeders in the intertidal habitats accounted for averages of 94, 72 and 111% of the carbon incorporated into their tissues in Kwangyang, Yoja and Deukryang Bays, respectively, while benthic microalgae constituted on average 81, 81 and 66% of incorporated carbon by benthic feeders in the subtidal habitats, respectively. Marine phytoplankton may explain the remaining proportion.

DISCUSSION

Identification of food sources for macrozoobenthos

The present study provides supporting evidence that the food web in coastal bays, where extensive tidal flats are present, is strongly linked to benthic microalgal production on the tidal flats. The $\delta^{13}C$ values of offshore macrozoobenthos is close to that of phytoplankton, and trophic enrichment of $\delta^{13}C$ and $\delta^{15}N$ clearly suggests that their food base may be phytoplanktonic organic matter. In contrast to the offshore habitat, the $\delta^{13}C$ values of macrozoobenthos in the bay systems were significantly less negative than those of phytoplankton. The mean $\delta^{13}C$ values of macrozoobenthos collected in the 3 bay systems (–14.2‰) was less negative than those collected in Youngil Bay (–18.1‰ for 29 macrozoobenthic species, our unpubl. data), a neighboring estuarine bay lacking tidal flats. This suggests that benthic consumers in the study bays may take a ^{13}C-enriched dietary source

(Fry & Parker 1979). Many studies have demonstrated a shift in the $\delta^{13}C$ signatures of consumers between deep and shallow benthic habitats, suggesting that the difference reflected the utilisation of different dietary sources (Fry & Parker 1979, France 1995, Yoshii 1999). In the present study, mixing model calculations and homogeneity of the isotopic signatures of producers and consumers indicated the important role of benthic microalgae as a basic food source in the intertidal and subtidal zone in the 3 study bay systems. The heavier $\delta^{13}C$ values of consumers in the bay systems, compared to those in the adjacent offshore area or to a neighboring bay without tidal flats, may be explained by the importance of benthic microalgae in the diets of the bay consumers.

Interestingly, a significant difference in $\delta^{13}C$ signatures was found between feeding types, in particular in the intertidal habitat. This isotopic variation probably reflects differential inputs of benthic microalgae in their diets. Deposit feeders utilize food sources derived exclusively from benthic microalgae, whereas suspension feeders use a mixture of benthic microalgae and marine phytoplankton. Differentiation of the carbon isotopic signatures of consumers within the same community due to a respective dependence on phytoplankton or benthic vegetation has been previously reported (France 1995, Deegan & Garritt 1997, Riera et al. 1999, Herman et al. 2000). Less negative $\delta^{13}C$ values in the intertidal benthic feeders in Kwangyang and Deukryang Bays than those in the subtidal indicate a stronger dependence of intertidal benthic feeders on benthic microalgae than subtidal benthic feeders. The less clear separation in $\delta^{13}C$ values of consumers with feeding patterns in the subtidal habitat is likely to result from a more homogenous distribution of organic matter by active mixing of suspended and sedimentary POM (Deegan & Garritt 1997, McClelland & Valiela 1998). The wider range in the dependence of predators and omnivores on benthic microalgae than those of the deposit feeders seems to reflect the more diversified prey components for the higher-level consumers (calculation not shown; see points in Fig. 2). Their $\delta^{13}C$ and $\delta^{15}N$ signatures also indicate that organic matter originated from both benthic microalgae and phytoplankton was transferred to higher trophic positions through benthic food webs, but benthic microalgae were the primary carbon source in this food web.

Phragmites can make an important contribution to aquatic food webs in reed-grass-dominated tidal marshes (Wainright et al. 2000). In the present study, carbon of this marsh plant appeared to make little contribution to our study systems. Based on $\delta^{13}C$ values of consumers in Kwangyang Bay, Kang et al. (2001) suggested that a minor contribution of *Phragmites* detritus

to the subtidal food webs was due to the direct sedimentation of dead *Phragmites* leaves within the marsh, as shown in North Sea salt marshes (Hemminga et al. 1996). Relatively high molar C:N ratios in vascular plants such as *Phragmites* sp. and *Salix* sp. have been measured (e.g. 34 ± 25 in tidal marshes of Delaware Bay, Wainright et al. 2000). Kang et al. (1993) reported that SOM in the study bays had a relatively low molar C:N ratio of <10, indicating a higher contribution from algal sources. The low C:N ratio and δ^{13}C values (–19.5 ± 0.9‰, Table 1) of SOM indicated a low contribution by *Phragmites* detritus to the SOM pool. Additionally, the minor role of *Phragmites* detritus to the consumer diets may be explained by its lower digestibility. Deegan & Garritt (1997) suggested that even though algae and salt marsh vascular plant production are of similar magnitude and equally available, algae will contribute more dominantly to the production of higher trophic levels because of the higher digestibility of most algae compared to vascular plants.

Consumer isotopic signatures indicated that riverine terrestrially derived organic matter is not an important food source even in the Kwangyang Bay system, which has a large river runoff. For this bay, Kwon et al. (2002) showed that the input of terrestrial particulate matter is very low, despite the large freshwater discharge through Seomjin River and a POM concentration in the low salinity zone of the upper estuary that is controlled by the production of phytoplankton. The molar C:N ratio of POM at the Seomjin River estuary varied from 4.6 to 8.5 (Kang et al. 2001, Kwon et al. 2002), corresponding to typical marine particulate matter (Hecky et al. 1993). This suggests a minor contribution of terrestrial-origin POM to the estuarine POM pool. Several studies have concluded that a terrestrial-origin carbon source, even from high turbid systems, is of little importance to estuarine food webs, and its role is limited to the riverine or upper estuarine area because of its poor nutritional quality (Incze et al. 1982, Simenstad & Wissmar 1985, Bunn et al. 1989, Deegan & Garritt 1997, Page 1997).

Although in coastal areas where macroalgae or seagrass are abundant these sources of nutrition can be significant (Fry & Parker 1979, Duggins et al. 1989, Jennings et al. 1997, McClelland & Valiela 1998), we presume that these carbon sources were of minor importance in our study systems because they occur only in small patches in Kwangyang Bay, and are virtually absent in the other 2 bay systems. Measured C:N ratios of macroalgae and seagrasses are 9.8 to 43.8 and 11.1 to 69.4, respectively. Thus, a relatively low contribution of organic matter from these sources to the POM and SOM pool may be inferred from their slightly higher molar C:N ratios than those either of POM or SOM.

Comparison of the 3 coastal bay systems

Considering the different regimes of vegetal composition, hydrology and thereby nutrient and particulate matter supply in the 3 study bays (see references in 'Materials and methods'), we expected to see a shift in the primary food source of macrozoobenthos from marine phytoplankton in Deukryang Bay and *Phragmites* in Yoja Bay to a more complex diet in Kwangyang Bay. Our collective data set rejected this initial hypothesis, but supported the assertion that benthic microalgae, along with phytoplankton, constituted the organic matter that forms the trophic base of the pelagic as well as the benthic food webs in these estuarine bays, as proposed by Baillie & Welsh (1980), de Jonge & van Beusekom (1992) and Guarini et al. (1998). Isotopic evidence indicated that the dietary source of consumers did not vary greatly among bays. The great uniformity in the isotopic ranges of each feeding type in the same habitats of the 3 bays may suggest that these systems are influenced predominantly by shallow water and strong tidal mixing. Flume experiments and field observations have shown variation in the resuspension of benthic microalgae in response to stepwise increases in current velocity or wind speed, local deposition of much of the resuspended biomass, and rapid settling of fine sediment and microalgae at low current or wind speed (de Jonge & van Beusekom 1992, 1995, Blanchard et al. 1997, Widdows et al. 1998, Herman et al. 2000, Lucas et al. 2000). In shallow estuaries, resuspended benthic microalgal biomass explains much of the spatial distribution of chl *a*, and it contributes as much as the true phytoplankton or accounts for most of the chlorophyll *a* in the water column (Shaffer & Sullivan 1988, de Jonge & van Beuskom 1992, 1995, Zurburg et al. 1994, Guarini et al. 1998). The mean chl *a* concentrations in the upper 0.5 cm of sediment ranged from 36.3 to 326.5 mg m^{-2} in the intertidal flats of the study bays (our unpubl. data), values comparable to those in the Ems estuary (The Netherlands, de Jonge & Colijn 1994) and Marennes-Oléron Bay (France, Guarini et al. 1998). These values are roughly 4- to 21-fold higher than the depth-integrated chl *a* concentrations in the overlying waters. Resuspension of benthic microalgae and their deposition elsewhere are occurring in the study bay systems. When considering the limited mobility and small foraging range of macrozoobenthos, benthic consumers are probably dependent on a benthic microalgae-derived food source in the overlying waters, and sediments of both intertidal and subtidal habitats.

The quality, as well as the quantity, of the organic matter also has an influence on the feeding activity of the primary consumers. Algae are a more nutritious food source than marsh or terrestrial macrophytes,

which consist largely of refractory materials (Mann 1986, Newman 1991). The existence of a high benthic microalgal biomass enables consumers to find food of high quality and quantity. On the other hand, a strong tidal exchange with offshore waters may limit the retention of POM within the bays. Extensive water movement by strong tidal currents may lower the residence time of marsh detritus and terrestrial organic matter within the bay.

Stable isotope composition of potential food resources and benthic consumers

Isotopic data for *Salix* and *Phragmites* are limited, but reported values are quite similar to values from the present study (Kang et al. 2000, 2001, Wainright et al. 2000). The $\delta^{13}C$ value of –23.7‰ (±0.5) for riverine POM from the Seomjin River implies a strong contribution of fresh marsh or upland C_3 plant detritus to the riverine POM pool (Kang et al. 2001). Marine phytoplankton collected at the mouths of the 3 bays had similar $\delta^{13}C$ values to previously reported values for phytoplankton at coasts of the Korean peninsula (–20.7‰, Kang et al. 2001) and at the East China Sea (–19.7‰, Tan et al. 1991). Adjacent offshore phytoplankton also had a mean $\delta^{13}C$ of –20.0‰ (±0.5), typical of marine phytoplankton (Gearing et al. 1984). The $\delta^{13}C$ range of benthic diatoms (–14.5 ± 0.6 to –13.7 ± 0.7‰) in the present study was comparable to those from other intertidal mudflats (Couch 1989, Currin et al. 1995, Créach et al. 1997, Page 1997, Riera et al. 1999). The $\delta^{13}C$ values of macroalgae and seagrass *Zostera marina* collected from Kwangyang Bay (mean –14.5 ± 1.5 and –11.5 ± 0.1‰, respectively) fell well within previously reported ranges for the same or similar species in the coasts of the Korean peninsula and elsewhere (see Kang et al. 2001).

Stable isotope signatures of consumers integrate carbon assimilation over time periods corresponding to taxon-specific organic carbon turnover times (Tieszen et al. 1983, Fry & Sherr 1984) and isotopic values of their potential food sources can vary seasonally (Lajtha & Marshall 1994). Indeed, seasonal changes in $\delta^{13}C$ of primary producers are often rapidly reflected in the $\delta^{13}C$ of invertebrates due to a high turnover rate for the assimilated carbon by the animals (Fry & Arnold 1982, Gleason 1986, Georing et al. 1990, Riera & Richard 1997, Zah et al. 2001). The rapidity of change and turnover of stable isotopes in animal tissues has been found even for fish and birds (Hobson & Clark 1992, Hesslein et al. 1993). For example, a remarkable decrease in the $\delta^{13}C$ of oysters *Crassostrea gigas* occurred 1 to 2 mo after the incorporation of terrestrial-origin light carbon at the Charente estuary of

Marennes-Oléron Bay (Riera & Richard 1997). By contrast, the $\delta^{13}C$ values of most taxa of aquatic consumers in a grassland river in New Zealand showed strong increases from summer to autumn (≤3 mo) due to a decrease in the relative availability of terrestrial carbon (Huryn et al. 2001). A previous study in Kwangyang Bay (Kang et al. 2001) and our monthly monitoring data (this study and our unpubl. data) did not show any conspicuous difference in the $\delta^{13}C$ values of either phytoplankton or benthic microalgae between seasons. Therefore, it is reasonable to expect that a probable long-term seasonal effect of $\delta^{13}C$ in food sources on the consumer $\delta^{13}C$ values would be minimized in this study.

The $\delta^{13}C$ range (–20.5 to –16.4‰) of macrozoobenthos collected in the offshore area was consistent with those reported in other phytoplankton-based ecosystems worldwide (Gulf of Mexico, Fry & Parker 1979; Bering Sea, McConnaughey & McRoy 1979a; Narragansett Bay, Gearing et al. 1984; Malaysian offshore waters, Rodelli et al. 1984). The $\delta^{13}C$ values of macrozoobenthos did not differ greatly among bay ecosystems. However, a general pattern of ^{13}C enrichment in the bay macrozoobenthos compared to the offshore areas was evident. Site-dependent variation of consumer $\delta^{13}C$ values by a high contribution of ^{13}C-enriched plant carbon has been previously demonstrated from comparisons between eelgrass bed and eelgrass-free communities (Fry & Parker 1979, McConnaughey & McRoy 1979b, McClelland & Valiela 1998). Riera & Richard (1996) have also shown that less negative $\delta^{13}C$ values in oysters *Crassostrea gigas* of estuarine intertidal habitats compared to those of marine littoral habitats was attributed to preferential use of ^{13}C-enriched benthic microalgae by intertidal oysters in Marennes-Oléron Bay. In spite of a slight shift between feeding types, the $\delta^{13}C$ values of suspension feeders and deposit feeders in the study bays were comparable to reported values for organisms of which the diet was primarily derived from ^{13}C-enriched benthic microalgae (Schwinghamer et al. 1983, Page 1997, Riera et al. 1999). Therefore, the distribution pattern of $\delta^{13}C$ signatures suggested that the ^{13}C enrichment in macrozoobenthos in the study bays reflects an intensive use of benthic microalgae. A few deposit feeders and predators from intertidal habitats had much less negative $\delta^{13}C$ signatures than the $\delta^{13}C$ signature of benthic microalgae, such that they lay outside the end-member value of the mixing equation (Fig. 2). This seems likely to have been caused by taxon-specific differences in fractionation shifts of C and N during assimilation of organic matter (DeNiro & Epstein 1978, McConnaughey & McRoy 1979a). Another explanation for the high $\delta^{13}C$ values in some of the deposit feeders and predators is the existence of an alternative organic

matter source that is more ^{13}C-enriched than benthic diatoms. Blue-green algal-mats, which have δ^{13}C values in the range of −16.5 to −5‰ (Calder & Parker 1973, Fry et al. 1982, Pulich & Scalan 1987, Page 1997) are a potential source because cyanobacterial colonies were often observed on surface sediments in the intertidal flats during the sampling period.

Marsh plant δ^{15}N values were close to values reported for *Phragmites* species in other brackish-marsh ecosystems (Wainright et al. 2000). The δ^{15}N values for benthic diatoms (10.9 ± 0.1‰), marine phytoplankton (11.4 ± 0.3‰ in the bays and 9.5 ± 0.7‰ offshore), macroalgae (14.2 ± 1.0‰) and seagrass (14.1 ± 0.1‰) were slightly heavier than ranges found for the corresponding producers (2.5 to 9.0‰, 3.0 to 12.0‰, 5.0 to 12.0‰ and 4.0 to 8.0‰, respectively) in other coastal environments (Currin et al. 1995, Newell et al. 1995, Maksymowska et al. 2000 and references within). Phytoplankton from the bays displayed a slightly heavier δ^{15}N value than those from the offshore areas. Minagawa & Wada (1986) described the δ^{15}N of marine plankton from the East China Sea of between 5 and 6.5‰ in the shallow continental shelf contiguous to our offshore study sites, and between 1 and 3‰ in the Kuroshio warm current. The δ^{15}N values of primary consumers (14.3 ± 0.5 and 14.7 ± 0.7‰ for suspension and deposit feeders, respectively) collected in the study bays were also heavier than values reported for the corresponding primary consumers in other coastal environments (see ranges in Table 2 in Page 1997). For example, these values are ~6.5‰ higher than a mean δ^{15}N of 7.8‰ (±0.9) reported for primary consumers in Plum Island Sound, Massachusetts (Deegan & Garritt 1997). These heavier δ^{15}N signatures in macrozoobenthos probably reflected a similar ^{15}N enrichment of benthic microalgae and phytoplankton that were identified to be the most important organic matter sources in our study systems. Recently, several studies have pointed out that heavy δ^{15}N signatures in primary producers and animals could be indicative of high availability of land-derived ^{15}N-enriched inorganic nitrogen (Kwak & Zedler 1997, McClelland et al. 1997, Page 1997, Riera et al. 2000). Lee et al. (2001) reported that the main sources of nitrogen in Kwangyang Bay are freshwater runoff and industrial wastewater. Therefore, our nitrogen isotope signatures for plants and macrozoobenthos probably provide evidence of increasing wastewater inputs to these coastal bay ecosystems.

Regional comparison

Several studies of stable plant and animal isotopes in tropical tidal flat ecosystems with extensive mangrove forests in Asia have shown that mangrove detritus constitutes a dominant dietary component for animals in the tidal creeks (Rodelli et al. 1984, Newell et al. 1995, Chong et al. 2001). Instead of mangroves, marsh plants colonize terrestrial boundaries of the temperate tidal flats in the Yellow Sea (Koh 2001). Of the marsh plant species that are present, *Phragmites australis* establishes extensive monospecific stands in the coastal bays of the South Sea of Korea. However, our results revealed that the primary food sources for macrozoobenthos are the benthic and planktonic microalgae in the study bay systems and the role of the vascular plants was negligible.

Most European intertidal mudflats are large and bare of macrophytes. The vascular plants colonize the uppermost areas of the mudflats. Stable isotope studies of primary producers and consumers in these tidal flats suggest that benthic microalgae are the most important source of organic matter supporting food webs in these habitats (Riera & Richard 1996, Créach et al. 1997, Riera et al. 1999, Herman et al. 2000). In contrast to the European coasts, where benthic microalgae are a main primary producer in the mudflats, much of North American tidal flats are covered by large stands of the marsh grass *Spartina*. Traditionally, although part of the marsh production is exported to coastal and offshore waters (Odum & de la Cruz 1967), *Spartina* detritus, after microbial decomposition, has been considered to be the primary source of organic matter supporting the tidal-flat food webs (Haines 1976a,b, Haines & Montague 1979, Peterson et al. 1985, Peterson & Howarth 1987, Currin et al. 1995). It is evident from many studies that, though less nutritious, vascular plants such as mangrove, *Spartina* spp. and *Phragmites* spp. can be incorporated into the coastal food web when detritus derived from these plants is available. However, more recent studies applying multiple stable isotope techniques in the salt marshes of North America suggested that the relative importance of algae and vascular plants changes from system to system (Sullivan & Moncreiff 1990, Deegan & Garritt 1997, Kwak & Zedler 1997). These studies concluded that the relative importance of each group might be influenced by elements of the basic hydrology of the system, such as tidal amplitude. Deegan & Garritt (1997) observed that estuarine food webs with microtidal marshes were dominated by algal organic matter, whereas estuarine food webs with macrotidal salt marshes were dominated by salt marsh plants and benthic microalgae. This was thought to result from the regular tidal flooding that increased the tidal mixing and transport of vascular plant detritus. From this, they hypothesized that a minor role of marsh plants in a weak tidal-range system would be attributed to the disconnection between marsh area and the aquatic food web.

Despite the high tidal range of ~4 m, our study systems do not have food webs dependent on *Phragmites* detritus. Results obtained in our study systems could not be explained by the hypotheses for North American tidal flat food webs, that is, high dependence on marsh organic matter of food webs in areas with large salt marshes (dominance of marsh plants) or variation in relative importance of algae and marsh plants with tidal amplitude (tidal range). The food webs of the coastal bays in the Korean peninsula rather conform to generalizations, which are developed for European coastal mudflat ecosystems. As with the typical European tidal flats (McLusky 1989), *Phragmites* plains cover the uppermost part of the intertidal zone in our study systems and are only flooded by spring high tides. The disconnection between marsh plains and tidal flat ecosystems probably decreases the availability of *Phragmites* detritus to the tidal flat food web.

In conclusion, the stable isotope data from the 3 bay systems in the south coast of the Korean peninsula showed that the macrozoobenthos in the adjacent subtidal within the bays feed, to a large extent, on the tidal flat microphytobenthos, implying a strong food-web linkage between the intertidal microphytobenthos and the adjacent subtidal macrobenthic consumers. Therefore, reducing the areal size of the intertidal zone may severely reduce benthic production in the entire bay system, affecting coastal fisheries on a large scale. On the other hand, the minor contribution of the *Phramites* marsh should be relegated to a side-aspect. We assume these marshes have little resemblance to the *Spartina* marshes on the American Atlantic coast because they are higher up on the shore, and almost limnic to terrestrial, but not intertidal.

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