

The Importance of Intertidal Benthic Autotrophs to the Kwangyang Bay (Korea) Food Webs: $\delta^{13}\text{C}$ analysis

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The importance of phytoplankton, benthic vegetation, vascular marsh plants (primarily *Phragmites communis* and *Salix gracilistyla*) and riverine particulate inputs to the coastal bay food webs was studied in Kwangyang Bay, Korea using stable carbon isotope ratios. Vascular marsh plants ($\delta^{13}\text{C} = -27.4 \pm 0.8\text{‰}$) and riverine particulates ($-26.0 \pm 0.8\text{‰}$) were isotopically distinct from phytoplankton ($-20.7 \pm 0.8\text{‰}$), microphytobenthos ($-14.2 \pm 0.6\text{‰}$) and seagrass (8.8‰). The $\delta^{13}\text{C}$ values of consumers in the study site ranged from -20.2 to -11.3‰ , suggesting the assimilation of carbon derived from both phytoplankton and benthic vegetation (including algae and seagrass). The relative importance of both pelagic and benthic origins of food sources was likely to vary depending on feeding habit of the consumers. The isotopic difference between pelagic and benthic consumers indicated that plankton-derived carbon was used mostly by pelagic consumers, but the carbon derived from intertidal benthic vegetation was incorporated into food webs through benthic consumers. The $\delta^{13}\text{C}$ values of consumers in the present study differed noticeably from published values of the phytoplankton-based ecosystem, particularly in the ^{13}C enrichment of benthic grazers, deposit-feeders and demersal feeders of fishes. This tendency of the ^{13}C enrichment was also found in suspension-feeding bivalves. Taking the biomasses of benthic vegetation into consideration, benthic microalgae was likely to account for the consumer ^{13}C enrichment. Role of terrestrially derived riverine carbon was limited to the riverine system and was not evident within the bay systems. *Phragmites*, despite their important biomass, appeared to be of little importance as consumer diet.

INTRODUCTION

A rich food supply into estuarine ecosystems can support highly diverse animals. Food availability is an important factor limiting the biomass of estuarine consumers (Herman *et al.*, 1999). Of a variety of food sources for coastal consumers are marsh grasses (Tenore, 1983; Peterson and Howarth, 1987; Deegan *et al.*, 1990; Currin *et al.*, 1995; Schwinhamer *et al.*, 1983; Kwak and Zedler, 1997), phytoplankton and benthic microalgae (microphytobenthos) (Sullivan and Moncreiff, 1990; Currin *et al.*, 1995; Page, 1997), macroalgae (Simenstad and Wissmar, 1985; Jennings *et al.*, 1997), and seagrasses (Fry and Parker, 1979; McConnaughey and McRoy, 1979; McMillan *et al.*, 1980; Nichols *et al.*, 1985). In addition to the autochthonous sources, allochthonous particulate organic matter (POM) from land, river and sea is also highly available food

sources for animals in estuarine habitats and can be significantly incorporated by estuarine bivalves (Incze *et al.*, 1982; Riera and Richard, 1996). Recent studies have pointed out the preferential utilization of locally produced organic matter sources by estuarine consumers (Ruckelshaus *et al.*, 1993; Deegan and Garritt, 1997; Riera and Richard, 1996; Riera *et al.*, 1999).

For the estuarine bay where bare intertidal bed is well developed with high levels of microphytobenthos, numerous studies have demonstrated that resuspended benthic diatoms account for a similar or higher proportion of algal standing crops in the water column compared to phytoplankton (Cadee, 1971; de Jonge and van Beusekom, 1992; Prou *et al.*, 1994; Guarini *et al.*, 1998). Organic matter produced by benthic microalgae in the estuarine intertidal flats may be incorporated directly into the local benthic food webs (Haines and Montague, 1979; Currin *et al.*, 1995; Riera and Richard, 1996), and can also be resuspended and exported to the subtidal zone and deposited elsewhere

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(Baillie and Welsh, 1980; de Jonge and van Beusekom, 1992). Using stable isotope analysis, Hughes and Sherr (1983) showed a significant input of benthic microalgal carbon to subtidal food webs in a Georgia Estuary. Page (1997) reported that suspension-feeding bivalves in tidal channels of a southern California salt marsh utilized resuspended microalgae. Despite the possibility of resuspended benthic diatoms as food for suspension feeders at the whole bay system scale, previous studies did not reveal to what extent resuspended microphytobenthos was utilized actually by estuarine consumers of various feeding groups.

Dominant food source in a coastal ecosystem varies spatially. Even within a single estuary, organic carbon sources are probably different along the estuarine gradient and consumers may utilize different food sources spatially (Incze *et al.*, 1982; Ruckelshaus *et al.*, 1993; Riera and Richard, 1996; Deegan and Garritt, 1997; Riera *et al.*, 1999). Furthermore, different trophic groups may use different food sources. Deegan and Garritt (1997) reported that benthic and pelagic consumers use different mixes of food sources. Geomorphologic and hydrological features and dominant vegetation of the coastal bay systems, and also feeding habits of the various consumers in the ecosystem serve as important factors in determining the base of estuarine food webs.

Stable isotopes have been successfully applied to carbon flow and food web structure studies in aquatic ecosystems as powerful tools in tracking carbon sources (see reviews by Fry and Sherr, 1984; Michener and Schell, 1994). Various plants have distinct carbon isotopic ratios because they fix carbon through different photosynthetic pathway and use various dissolved inorganic carbon pools that have different $\delta^{13}\text{C}$ in ambient environments (Benedict, 1978; Wong and Sackett, 1978; Goerike *et al.*, 1994; Lajtha and Marshall, 1994). Carbon isotopic fractionation during trophic transfers is small and predictable, and $\delta^{13}\text{C}$ of a consumer reflects its diet (DeNiro and Epstein, 1978). Therefore, stable carbon isotope enables us to identify carbon sources actually assimilated over time by the consumer (Fry and Sherr, 1984; Peterson and Fry, 1987).

This study aimed to determine the major sources of organic carbon for macroconsumers in the Kwangyang Bay ecosystem. Specific goals were to examine the importance of microphytobenthos as a food component and to identify trophic linkage between intertidal autotrophs and consumers in both intertidal and subtidal habitats. The result of this study will provide

essential information for proper management and conservation of the intertidal zone in the estuarine ecosystems. Although most *Zostera* beds disappeared from Kwangyang Bay, locally small beds still patches along the lower boundary of the intertidal flat. Since the bay system receives a large river runoff, organic matter would be provided from multiple sources. The relative roles of the potential food sources in food webs of the bay system remain still unclear. We used stable carbon isotope analysis to clarify the relative importance of food sources for consumers of various feeding modes in both intertidal and subtidal food webs of the bay system.

MATERIALS AND METHODS

Study area

This study was conducted in Kwangyang Bay, a 230 km² estuarine bay situated on the southern coast of Korea (Fig. 1). The bay is shallow with the depth around 5 m at the inner bay and 20 m at the central

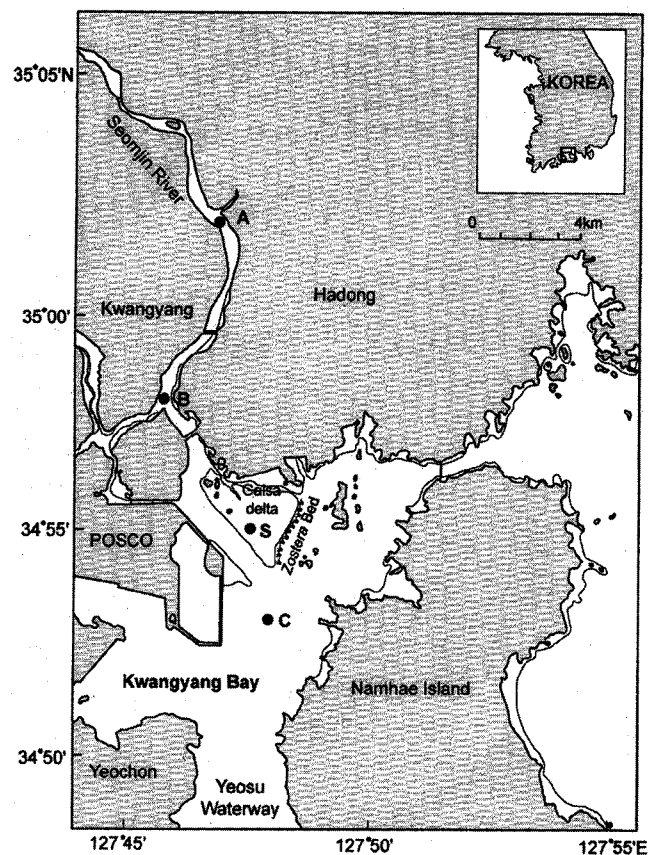


Fig. 1. Map of the Kwangyang Bay system and the sampling stations. Dotted line shows the limit of the intertidal flats and land areas are shaded.

channel. Tidal cycle is semidiurnal, maximum tidal range is 3.4 m and the highest tidal current velocity is from 50 to 80 cm s⁻¹ in the central part. Marine waters enter by the southern entrance (Yeosu Hae-Man). Freshwater flows into the bay mainly from Seomjin River at the northern end of the bay (mean flow of 120 m³s⁻¹ and annually 5.8 to 8.7×10⁸ tons). Sandy mud delta is well developed in the northern part of the bay. About 15 km² intertidal flat located north of Myodo Island was reclaimed for Kwangyang Steel Mill Company (POSCO) in the beginning of 1980s. Additional 6 km² intertidal flat east of the Works was also reclaimed in 1988. Large area of the northern intertidal delta remains. The Korean Government is planning large-scale conservation projects for the Kwangyang Bay environments and ecosystems. Further physical, biological and sedimentary features for the bay are described in detail by Park *et al.* (1984), Choi and Goh (1984) and Jung *et al.* (1997).

Kwangyang Bay is rather closer to the 'European-type' estuaries which are dominated by large, relatively bare intertidal sandy mudflats than the American-type estuaries which are dominated by large stands of the marsh grass *Spartina*. Reed grass, *Phragmites communis*, forms large masses of vegetation at the edges of Seomjin River and the estuary, but most of the grass is confined to the supralittoral zone of the estuary. Rocky substrates are limited only to the vicinity of small islands within the bay. Most of the substrates consist of mud or sandy mud. A few macroalgal (mostly *Enteromorpha compressa* and *Ulva pertusa*) mats were found from the intertidal and subtidal flats of the estuary. Benthic microalgal mats were commonly visible on the intertidal beds of Galsa delta (ca. 15 µg Chl *a* · mg⁻¹ dry sediment, unpubl. data). The dominant microalgae in the flats were *Navicula* sp., *Cylindrotheca closterium*, *Pleurosigma angulatum*, *Achnathes* sp., *Rhizosolenia alata*, *Rhaphoneis amphiceros* and *Melosira* sp. etc. Most of the dense eelgrass (*Zostera marina*) beds which were well developed in the whole bay disappeared recently and only a tenth part of the previous bed area exists along the lower intertidal flat boundary of Galsa delta now (Yun *et al.*, 1997).

Field collection and processing

Samples of potential food sources (POM and primary producers) were collected in November 1999, February and May 2000. Consumers (invertebrates and fishes) for stable isotope analyses were collected in

November 1999 and May 2000. Samplings were conducted from an intertidal flat and three subtidal stations (Fig. 1). While Station A was located at the upper estuary, Station B was located at the mouth of the estuary and Station C at the central bay channel. The intertidal flat (Galsa delta) near the mouth of the estuary was dominated by entirely bare sandy mud sediments. Samples of POM were collected at the three subtidal stations and a riverine station 16-km north from the mouth of the estuary. To examine the role of terrestrial organic matter, additional sampling for a brackish water clam *Corbicula* sp. was carried out along an estuarine gradient.

About 20 l of water was pumped from each of the four sampling sites for analysis of suspended particulate matter. The water was prefiltered with a 63 µm screen to remove any zooplankton and large particles and then POM was filtered on precombusted Whatmann GF/F filters. Phytoplankton was collected by horizontal tows of plankton net (20 µm mesh size) at the Stations B and C, and then centrifuged in the laboratory. Two dominant vascular marsh plants (*Phragmites communis* and *Salix gracilistyla*) were collected by hand at the mid-estuary and the zone upstream of the upper estuary. Macroalgae (*Enteromorpha compressa*, *Ulva pertusa* and *Chondrus ocellatus*) and leaves of seagrass (*Zostera marina*) were collected by hand from intertidal and subtidal zones and cleaned up carefully to remove epibionts. Benthic microalgae were sampled on the large mudflat of Galsa delta and separated through a procedure slightly modified from the method of Couch (1989). The microalgae were extracted from sediments, which were collected by scraping the upper 2 mm in areas of dense microalgal mats, and finally kept on the precombusted GF/F filters. More detailed procedure for the extraction of benthic microalgae is well described by Riera and Richard (1996).

Zooplankton samples were collected using a 0.5 m diameter net fitted with a 220 µm mesh and a non-filtering cod end. Several vertical tows were conducted at each station. Specimens were sorted and gently transferred in the filtered water from the sampling site. Only copepods were analyzed in the present study because plankton samples of other classes were too small for isotope analyses. Benthic copepods (haracticoids) were collected from 2 l of superficial sediment, using a method based on a migration characteristic with which they are attracted to the light (Couch, 1989). Pelagic and benthic copepods were held in the filtered water for 12 h to evacuate gut con-

tents.

Various macroconsumers (crustaceans, bivalves, gastropods, cephalopods, ascidians, echinoderms, polychaetes and a variety of fish species) were collected by hand or using dredges, seines, trawls and gill nets. Invertebrates were kept alive overnight at the laboratory in filtered water from the sampling site to evacuate gut contents. Live and intact organisms were chosen to minimize contamination with other material and were frozen immediately. While only muscle tissues were needed for most crustaceans, bivalves, gastropods, ascidians and fish species, whole organisms were used for small invertebrates, such as copepods, amphipods and isopods, echinoderms and polychaetes. Tissues of each animal species were pooled for stable analysis.

All POM, floral and faunal samples for stable carbon isotope analysis were acidified in 10% v:v HCl to remove carbonates, quickly rinsed three times with distilled water and kept frozen (-80°C) until analysis. The freeze-dried samples were ground to a fine powder with a mortar and pestle.

Analytical method

Isotopic composition of the samples was determined using continuous-flow isotope mass spectrometry. Dried samples (about 1 mg for animals and 5–10 mg for plants) were combusted and the resultant gas (CO_2) was introduced to a single inlet dual-collector mass spectrometer [Automated NC Analysis (ANCA) SL 20-20; PDZ Europa]. Two samples of an internal reference material (leucine for animals, citric acid/leucine for plants) were analyzed after five tissue samples in order to calibrate the system and compensate for drift with time. Isotope data were expressed as the relative per mil (‰) difference between the sample and conventional standard of Pee Dee Belemnite carbonate (PDB) as follows:

$$\delta^{13}\text{C} = \left[\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right] \times 1000 \text{ (‰)}$$

Where R_{sample} and R_{standard} are the $^{13}\text{C}/^{12}\text{C}$ ratios of sample and standard, respectively. Experimental precision based on the standard deviation of replicates of the internal standard was $\pm 0.12\text{‰}$.

Procedures for chlorophyll *a* analysis followed the method described by Parsons *et al.* (1984). Particulate organic carbon (POC) and nitrogen (PON) concentrations were analyzed using a Perkin-Elmer CHN elemental analyzer after filtration of 500 ml seawater

on 25 mm diameter GF/F filter. Salinity was measured using a SeaBird type CTD meter.

RESULTS AND DISCUSSION

Sources of organic matter in Kwangyang Bay

Primary producers: The stable carbon isotope ratios of dominant primary producers within the bay system showed no marked differences between sampling dates and between stations (Kruskal-Wallis ANOVA, $p=0.954$), but differed greatly among vegetal groups (Kruskal-Wallis ANOVA, $p<0.001$) (Table 1). C_3 marsh plants displayed the most negative $\delta^{13}\text{C}$ values compared with the other producers sampled. The two dominant marsh plants, *Salix gracilistyla* and *Phragmites communis*, had mean $\delta^{13}\text{C}$ values of $-26.8 (\pm 0.9)\text{‰}$ and $-27.8 (\pm 0.5)\text{‰}$, respectively. These are comparable to values measured for these species from the Hyungsan river estuary in the southeastern coast of Korea (Kang *et al.*, 2000).

Marine algae were isotopically distinct from marsh plants. The $\delta^{13}\text{C}$ values of 3 different genera of macroalgae varied from -16.5‰ for *Chondrus ocellatus* at the bay channel to -13.1‰ for *Ulva pertusa* at the Galsa delta with a mean of $-14.9 (\pm 0.9)\text{‰}$, being more ^{13}C -enriched than those of marsh plants. A wide variability in $\delta^{13}\text{C}$ of macroalgae is generally accepted (Currin *et al.*, 1995). Benthic microalgae in the Galsa delta consisted mostly of diatoms. The $\delta^{13}\text{C}$ values of benthic microalgae ranged from -15.1 to -13.2‰ with a mean of $-14.2 (\pm 0.6)\text{‰}$. These values fell into the ranges previously reported elsewhere for benthic diatoms (Currin *et al.*, 1995; Page, 1997). Eelgrass *Zostera marina* was collected once in the bay channel. Its $\delta^{13}\text{C}$ value of -8.8‰ fell well within the range reported for seagrasses (McConnaughey and McRoy, 1979; Fry *et al.*, 1987), being the most positive in the plant species collected.

Four samples of phytoplankton averaged $-20.7 (\pm 0.8)\text{‰}$, typical of marine phytoplankton (Gearing *et al.*, 1984). These values intervened between the values of benthic algae and marsh plants. Similarly, off Kwangyang Bay, phytoplankton $\delta^{13}\text{C}$ value of -19.7‰ was measured in the East China Sea by Tan *et al.* (1991), and also mean $-18.6 (\pm 2.2)\text{‰}$ was reported in the southeastern coast of Korea by Kang *et al.* (2000).

Particulate organic matter: Salinity ranged from 0 psu at the upper stream station to 32.0 psu at the

Table 1. $\delta^{13}\text{C}$ values (‰) of major primary producers in Kwangyang Bay and Soemjin Rive

Species	Site	November 1999	May 2000	Mean \pm SD
Phytoplankton (>20 μm)				-20.7 \pm 0.8
	Mouth of estuary	-21.0	-21.6	
	Bay channel	-19.6	-20.7	
Marsh plants				
<i>Salix gracilistyla</i>	Upper river	-27.4	-26.1	-26.8 \pm 0.9
<i>Phragmites communis</i>	Upper estuary	-28.4	-27.6	-27.8 \pm 0.5
	Mouth of estuary	-27.2	-27.8	
Macroalgae				-14.9 \pm 1.4
<i>Enteromorpha compressa</i>	Mouth of estuary	-15.1		
<i>Ulva pertusa</i>	Intertidal delta		-13.1	
	Intertidal delta	-14.4	-15.8	
	Bay channel		-14.0	
<i>Chondrus ocellatus</i>	Bay channel		-16.5	
Microphytobenthos				-14.2 \pm 0.6
Benthic diatoms	Intertidal delta	-15.1	-14.5	
	Intertidal delta	-13.2	-14.3	
	Intertidal delta	-13.6	-14.4	
	Intertidal delta	-13.8	-14.8	
Eelgrass				-8.8
<i>Zostera marina</i>	Bay channel		-8.8	

Table 2. Salinity, concentrations of suspended particulate matter (SPM), chlorophyll *a*, particulate organic carbon (POC) and nitrogen (PON) from Kwangyang Bay (November 1999, February and May 2000) collected in association with SPM samples analyzed for stable carbon isotope ratio ($\delta^{13}\text{C}$) of particulate organic matter (POM)

Sites	Salinity (psu)	Chlorophyll <i>a</i> ($\mu\text{g l}^{-1}$)	POC ($\mu\text{g l}^{-1}$)	PON ($\mu\text{g l}^{-1}$)	POC:Chl <i>a</i>	C/N	SPM (mg l^{-1})	$\delta^{13}\text{C}$ POM (‰)
Seomjin River	0.0	0.74 \pm 0.16	180 \pm 43	17 \pm 4	319 \pm 71	12.6 \pm 0.4	1.6 \pm 0.5	-26.0 \pm 0.8
A (upper estuary)	22.9 \pm 1.4	3.51 \pm 1.95	394 \pm 210	59 \pm 29	147 \pm 56	7.8 \pm 0.3	10.5 \pm 6.7	-22.4 \pm 1.2
B (mouth of estuary)	28.8 \pm 1.1	2.77 \pm 1.33	390 \pm 116	67 \pm 21	137 \pm 38	6.9 \pm 0.1	8.6 \pm 4.2	-22.3 \pm 0.5
C (bay channel)	32.0 \pm 2.4	1.93 \pm 0.44	418 \pm 45	64 \pm 6	225 \pm 73	7.8 \pm 0.1	4.1 \pm 3.2	-19.8 \pm 1.3

bay channel station during the study period (Table 2). The concentration of suspended particulate matter (SPM) was consistently higher at the estuarine sites (8.6 \pm 4.2 mg l⁻¹ to 10.5 \pm 6.7 mg l⁻¹) than those at the upper stream (1.6 \pm 0.5 mg l⁻¹) and at the bay channel (4.1 \pm 3.2 mg l⁻¹). Such a tendency was also observed for the distribution of POC and PON. Chlorophyll *a* concentration was also higher at the estuarine sites (2.77 \pm 1.33 $\mu\text{g l}^{-1}$ to 5.06 \pm 1.95 $\mu\text{g l}^{-1}$) than that at the upper stream station (0.74 \pm 0.16 $\mu\text{g l}^{-1}$), indicating a high phytoplankton production at the estuary. POC:Chlorophyll *a* is used as an indicator of the relative detrital content of POM. Zeitzschel (1970) suggested that values of 100 or less are typical of living phytoplankton, while Cifuentes *et al.* (1988) regarded POM with ratios >200 as detrital. The typical POC:

Chlorophyll *a* of live phytoplankton was observed only at the estuarine stations. Terrestrial organic matter generally has a C:N ratio >12 (Pocklington and Leonard, 1979), while riverine phytoplankton has values typically around 6 (Kilham, 1986). Along with the high POC:Chlorophyll *a* ratios, the high molar C:N ratios of 12.6 (\pm 0.4) in Seomjin River clearly reflected a high proportion of terrestrial detritus of the river POM. At the estuary and the bay channel, the C:N ratios of 6.9 to 7.8 corresponded to that of typically marine particulate matter (Redfield, 1958).

Stable carbon isotope ratios of POM from each station were relatively constant during the study period (Table 2). Apparent variation in $\delta^{13}\text{C}$ values was observed among sampling stations, showing a gradient from the river to the bay channel. POM from

the riverine station had a mean $\delta^{13}\text{C}$ value of $-26.0 (\pm 0.8)\text{‰}$, while the bay channel POM exhibited much heavier $\delta^{13}\text{C}$ value in a mean of $-19.8 (\pm 1.3)\text{‰}$. POM of the estuarine stations displayed intermediate $\delta^{13}\text{C}$ values with a mean of $-22.4 (\pm 0.9)\text{‰}$. The $\delta^{13}\text{C}$ value of the riverine POM was close to those of the marsh plants (-27.8 to -26.8‰) and the typical values of upland C_3 plants (Sternberg *et al.* 1984; Riera & Richard 1996). It was difficult to estimate the contribution of riverine autochthonous phytoplankton to the riverine POM because we had no isotopic data for freshwater phytoplankton. High C:N (>12) and POC:Chlorophyll *a* (mean 319 ± 71) ratios indicated the low contribution of live algae to the riverine POM. Therefore, the $\delta^{13}\text{C}$ value for riverine POM was likely to reflect a dominant contribution of organic matter from terrestrial origin and marsh plant detritus rather than riverine autochthonous planktonic production.

The carbon isotope composition of the estuarine and bay channel POM reflected a complex mixture of various sources such as terrestrial POM ($-26.0 \pm 0.8\text{‰}$), macroalgae ($-14.4 \pm 0.6\text{‰}$) and microphytobenthos ($-14.2 \pm 0.6\text{‰}$) along with estuarine ($-20.7 \pm 0.8\text{‰}$) and oceanic phytoplankton (-19.7 to -18.6‰). More negative $\delta^{13}\text{C}$ value of the estuarine POM than that of phytoplankton is likely to reflect an increased contribution of terrestrial POM to the estuarine POM pool. While benthic macroalgae are not an important component of the Kwangyang Bay ecosystem, benthic microalgae of a high standing crop in the Galsa delta can be an important source of organic matter. Resuspended microphytobenthic biomass can exceed that of phytoplankton in the mud-dominated tidal flat environments (References in Introduction). *Zostera* detritus may be also available to the POM pool of the bay. However, although measured $\delta^{13}\text{C}$ value ($-19.8 \pm 1.3\text{‰}$) of the bay channel POM was slightly less negative than that of phytoplankton, the heavy isotopic composition of benthic vegetation was not significantly reflected in $\delta^{13}\text{C}$ of the bay channel POM. Recent data set of National Fisheries Research & Development Institute (unpubl. data) showed a mean $\delta^{13}\text{C}$ value of $-19.2 \pm 1.1\text{‰}$ for the sedimentary organic carbon (SOC) at 15 stations in Kwangyang Bay, suggesting that inputs of terrestrial organic matter are of little importance. $\delta^{13}\text{C}$ of the bay channel POC is rather close to that of SOC. The results may imply that isotopically heavier sources such as microphytobenthos and eelgrass detritus were resuspended simultaneously with a large amount of fine sediments, as

speculated by Riera and Richard (1996) in Marennes-Oléron Bay (France).

Consumers

A total of 89 consumer species representative of all the feeding modes were sampled and analyzed in both November 1999 and May 2000 to estimate seasonal variability in $\delta^{13}\text{C}$ of the consumers and to include different species, which are collected in different seasons. For most the consumers that were collected in both sampling periods, the seasonal differences were very small, as shown from the distribution of standard deviation (SD) for the mean values in Table 3. The exceptions were found only for two fish species of *Setipinna taty* and *Konosirus punctatus* at the upper estuarine station. Relatively large differences between the values from high standard deviations in two different seasons presumably indicated dietary changes during their migration (Table 3). Overall, the $\delta^{13}\text{C}$ values of consumers were spanned in a narrower range (-20.2 to -11.3‰) relative to those of potential food resources (Table 3; Fig. 2). The same species showed a great resemblance in $\delta^{13}\text{C}$ values between stations.

These consumer isotopic ratios strongly suggested the assimilation of the relatively positive carbon sources (phytoplankton and intertidally produced benthic vegetation) by consumers of the whole bay food webs with the slight isotopic fractionation depending on trophic positions in the food webs. Many studies have reported that consumers had on average 0.7 to 1.4‰ more positive $\delta^{13}\text{C}$ values than their diets due to metabolic fractionation along food chains (DeNiro and Epstein, 1978; Rau *et al.*, 1983; see also Fry and Sherr, 1984). In this study, the relatively positive $\delta^{13}\text{C}$ values of predators and scavengers compared with consumers of other trophic groups clearly indicated the isotopic fractionation with increasing trophic level in the bay consumers. However, consumer $\delta^{13}\text{C}$ values were more positive than those predicted from the metabolic fractionation. For example, suspension-feeding bivalves of primary consumers had a mean $\delta^{13}\text{C}$ of $-16.7 (\pm 1.3)\text{‰}$ ($n=21$ for 14 species), which was much more positive than values of POC (-22.4 to 19.8‰) and phytoplankton (-20.7‰). 3 to 6‰ difference between consumers and their potential food resources is too large to be explained by the metabolic fractionation alone. The difference was more evident in benthic deposit-feeders, another primary consumer group, being about 5‰ differences between the deposit-

Table 3. $\delta^{13}\text{C}$ values (‰) of various consumers collected in Kwangyang Bay in November 1999 and May 2000. Values represent a single analysis of a pooled sample into 10 to 20 animals. PG, pelagic grazer; BG, benthic grazer; S, suspension-feeder; D, deposit-feeder; O, omnivore; P, predator; Sc, scavenger; Pl, plankton-feeder; B, benthic feeder. ^a, animals collected in November 1999; individuals collected in both two sampling dates are indicated with \pm SD in parenthesis; the others, collected in May 2000

Consumer		$\delta^{13}\text{C}$			
		Station A	Station B	Station C	Station S
Crustaceans					
Mixed pelagic copepods	PG	-19.7	-20.2	-18.9	
Mixed benthic copepods	BG				-11.6
<i>Corophium</i> sp. (amphipod)	D				-12.5
<i>Cyathura carinata</i> (isopod)	D			-17.8 ^a	
<i>Oniscus asellus</i> (European pill bug)	D			-13.1 ^a	
<i>Pagurus</i> sp. (hermit crab)	D			-14.9	-13.6
<i>Uca</i> spp. (fiddler crab)	D		-16.0 (0.2)		
<i>Upogebia major</i> (mud shrimp)	S				-16.0
<i>Alpheus brevicristatus</i> (Teppo snapping shrimp)	O			-13.1	
<i>Alpheus japonicus</i> (Japanese snapping shrimp)	O			-13.8	
<i>Crangon affinis</i> (Japanese sand shrimp)	O	-15.8	-14.9	-13.3	
<i>Metapenaeopsis dalei</i> (Kishi velvet shrimp)	O			-15.5	
<i>Pandalus prensor</i> (Pacific shrimp)	O	-14.9			
<i>Parapenaeopsis tenellus</i> (smooth shell shrimp)	O			-14.4	
<i>Trachypenaeus curvirostris</i> (southern rough shrimp)	O			-15.4	
<i>Charybdis bimaculata</i> (charbdid crab)	P			-14.2	
<i>Eucrate crenata</i> (goneplacid crab)	P			-14.9	
<i>Oratosquilla oratoria</i> (Japanese mantis shrimp)	P			-16.0	
<i>Portunus trituberculatus</i> (blue crab)	P	-16.4	-15.9		
Bivalves					
<i>Artrina pectinata</i> (pen shell)	S			-15.2	
<i>Crassostrea gigas</i> (Pacific oyster)	S				-18.2 (0.8)
<i>Cyclina sinensis</i> (Chinese cyclina)	S			-17.8	-17.1 ^a
<i>Dosinorbis japonicus</i> (Japanese dosinia)	S			-15.9 ^a	-16.5
<i>Laternula flexuosa</i> (laternulid clam)	S				-16.9 ^a
<i>Meretrix lusoria</i> (hard clam)	S		-14.9		
<i>Musculus senhausia</i> (Asian mussel)	S	-20.0	-16.6 ^a		
<i>Mya arenaria</i> (soft shell clam)	S	-18.7	-16.9 ^a	-16.7	-16.5
<i>Mytilus edulis</i> (blue mussel)	S		-17.0		
<i>Phaxas attenuatus</i> (attenuated phaxas)	S			-15.3 ^a	
<i>Potamocorbula amurensis</i> (Asian clam)	S			-14.7 ^a	
<i>Saxidomus purpuratus</i> (purple Washington clam)	S			-16.0 (0.0)	
<i>Solecurtus divaricatus</i> (sunset shell)	S			-16.6 (0.6)	
<i>Solen strictus</i> (razor clam)	S				-17.3
<i>Macoma</i> sp. (tellinid clam)	D				-12.3
Gastropods					
<i>Umbonium costatum</i> (sand snail)	D				-14.5
Polychaetes					
<i>Arenicola brasiliensis</i> (lugworm)	D				-14.7
<i>Cirratulus cirratus</i> (cirratulid worm)	D				-12.3
<i>Notomastus latericeus</i> (capitellid worm)	D				-12.5
<i>Ceratonereis erythraensis</i> (nereid worm)	O				-12.4
<i>Lumbrinereis nipponica</i> (nereid worm)	O				-11.3

Table 3. Continued.

Consumer		$\delta^{13}\text{C}$			
		Station A	Station B	Station C	Station S
<i>Nereis</i> sp. (rag worm)	O				-12.9 ^a
<i>Diopatra bilobata</i> (onuphid worm)	P				-12.2
<i>Glycera chirori</i> (bloodworm)	P			-13.2	-12.9 (1.1)
<i>Glycera denticulata</i> (bloodworm)	P			-14.8 ^a	-12.7
<i>Nephtys</i> sp. (cat-worm)	P			-13.4	-14.4 ^a
<i>Owenia</i> sp. (polychaete worm)	P			-15.5 ^a	
Fish					
<i>Coilia nasus</i> (estuary tapertail anchovy)	PI	-18.8 ^a			
<i>Engraulis japonica</i> (Japanese anchovy)	PI			-16.3	
<i>Leiognathus nuchalis</i> (spotnape ponyfish)	PI	-19.4 (0.4)	-18.5 (1.0)	-18.1 (1.1)	
<i>Pampus echinogastor</i> (Korean pomfret)	PI			-18.3	
<i>Pholis nebulosa</i> (tidepool gunnel)	PI			-17.5	
<i>Sardinella zunasi</i> (scaled sardin)	PI	-19.0 ^a			
<i>Setipinna taty</i> (half-fin anchovy)	PI	-17.2 (1.6)	-18.6 (0.4)	-18.6 (0.5)	
<i>Acanthogobius flavimanus</i> (yellowfin goby)	B		-16.5		
<i>Acanthogobius lactipes</i> (white limbed goby)	B	-16.5	-17.3	-14.9	
<i>Cryptocetrus filifer</i> (gobiid fish)	B			-14.5	
<i>Cynoglossus joyneri</i> (red tongue sole)	B			-15.5	
<i>Cynoglossus robustus</i> (robust tonguefish)	B			-14.7 ^a	
<i>Hapalogenys mucronatus</i> (belted beard grunt)	B	-17.4	-15.2		
<i>Kareius bicoloratus</i> (stone flounder)	B	-15.9	-16.4		
<i>Limanda yokohamae</i> (marbled sole)	B			-15.0	
<i>Repomucenus lunatus</i> (dragonet)	B		-15.9	-15.6	
<i>Sillago japonica</i> (Japanese whiting)	B	-16.0	-15.6	-16.8	
<i>Sillago sihama</i> (silver whiting)	B	-16.1	-17.1		
<i>Hexagrammos otakii</i> (greenling)	O			-15.0	
<i>Konosirus punctatus</i> (gizzard shad)	O	-15.5 (1.3)	-17.1	-14.2	
<i>Acropoma japonicum</i> (Acropomatid fish)	P			-16.9	
<i>Argrosomus argentatus</i> (white croaker)	P			-12.8 ^a	
<i>Conger myriaster</i> (conger eel)	P			-15.8	
<i>Eopsetta grigorjewi</i> (shotted halibut)	P	-16.1 ^a			
<i>Harpadon nehereus</i> (bornbay duck)	P			-14.7 ^a	
<i>Hemitripterus americanus</i> (sea raven)	P			-14.9 ^a	
<i>Johnius belengerii</i> (Belengers jewfish)	P		-16.6 ^a	-16.3 (0.8)	
<i>Lateolabrax japonicus</i> (sea bass)	P	-15.9 (0.3)	-15.3	-15.4	
<i>Muraenesox cinereus</i> (daggertooth pike-conger)	P	-15.6 ^a			
<i>Pseudosciaena crocea</i> (yellow croaker)	P			-15.7	
<i>Saurida undosquamis</i> (lizard fish)	P		-16.5		
<i>Sphyrna pinnatus</i> (brown barracuda)	P	-14.2 ^a	-15.1 ^a		
<i>Takifugu niphobles</i> (grass puffer)	P		-13.2	-12.7	
<i>Trachurus japonicus</i> (horse mackerel)	P		-16.9		
<i>Trichiurus lepturus</i> (cutlass fish)	P			-13.7 ^a	

feeders ($-14.1 \pm 1.7\%$, $n=11$ for 10 species) and SOM ($-19.2 \pm 1.1\%$). Moreover, our data set tended to be more positive for most the consumers than values reported for the phytoplankton-based offshore food

webs (Table 7 in Gearing *et al.*, 1984). For example, $\delta^{13}\text{C}$ of shrimp, bivalves, polychaetes, gastropods and fish in the phytoplankton-based offshore food webs were -17.1% , -17.9% , -18.3 to -17.1% , -16.1% and

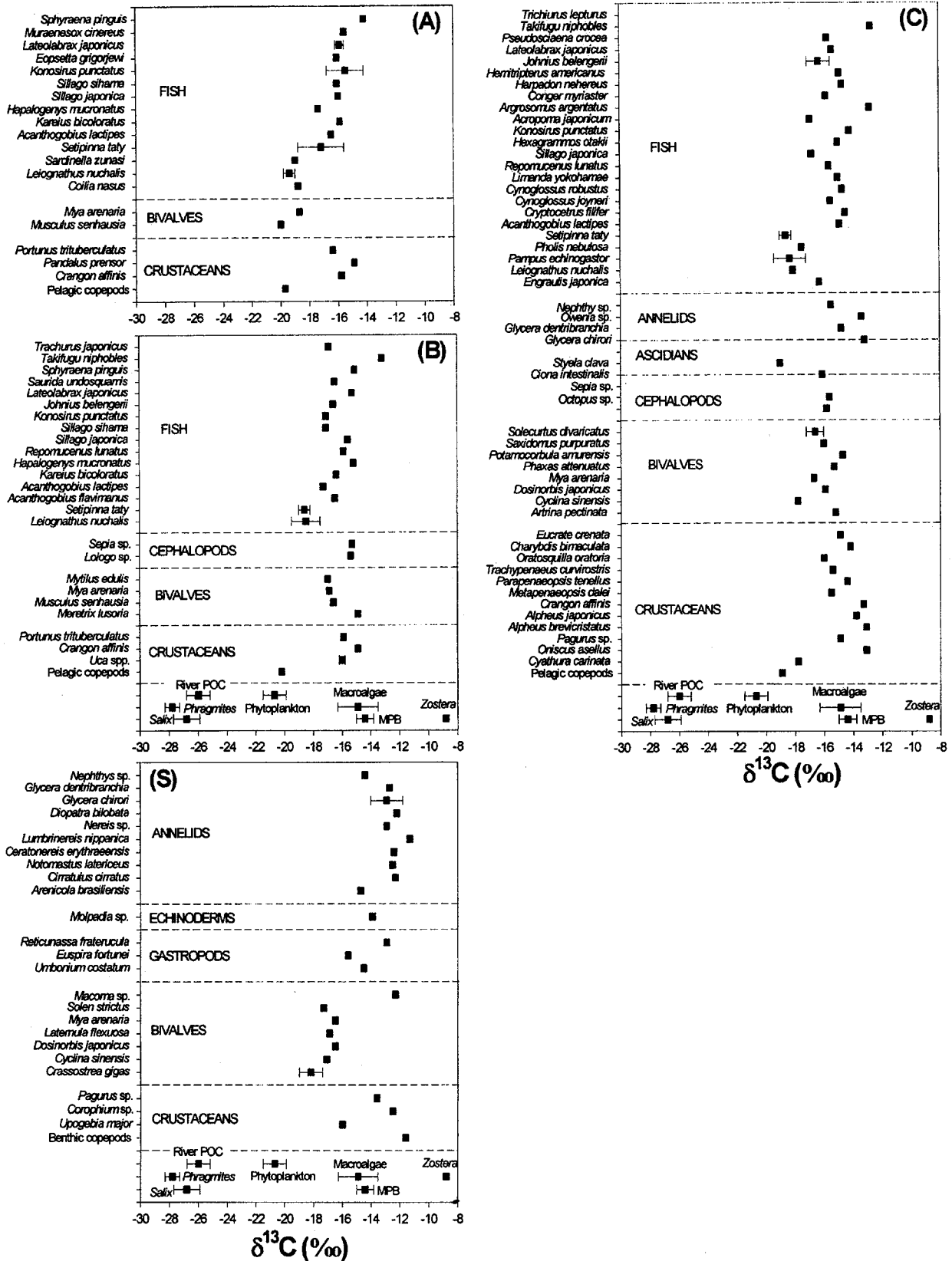


Fig. 2. Mean $\delta^{13}\text{C}$ (‰, \pm SD) of organic matter sources and consumers at the upper estuary (A), the mouth of estuary (B), the bay channel (C) and the intertidal sandflat of Galsa delta (S) in the Kwangyang Bay system. MPB represents micro-phytobenthos.

-17.1 to -16.1‰, respectively, while those in the present study site were -14.8‰, -16.7‰, -13.2‰, -14.3‰ and -15.9‰.

Instead, $\delta^{13}\text{C}$ values of most the invertebrate consumers in Kwangyang Bay were consistent with values reported for the tidal flat and channel systems of the California salt marsh that are mainly supported by algal sources (both benthic microalgae and phytoplankton) (Page, 1997). In coastal area where macroalgae or seagrass are abundant, significant incorporation by consumers of the carbon derived from these benthic vegetation detritus has been reported (Fry and Parker, 1979; Nichols *et al.*, 1985; Simenstad and Wissmar, 1985; Jennings *et al.*, 1997). Since most of the *Zostera* beds disappeared from the bay and macroalgae distributed in limited area in the Kwangyang Bay system, benthic microalgae can explain much of the positive $\delta^{13}\text{C}$ values of the consumers. Many studies have reported the resuspension mechanism of benthic microalgae and its importance as food for both benthic and pelagic consumers in the tidal flat and channel habitats (Haines and Montague, 1979; Currin *et al.*, 1995; Riera and Richard, 1996; Deegan and Garritt, 1997; Page, 1997). Since part of the lower intertidal flat is still covered by *Zostera* bed, it is difficult to exclude completely its role as carbon source for the bay channel consumers from the present results. In this study, consumers within the *Zostera* beds were not sampled.

Seasonal variation in phytoplankton $\delta^{13}\text{C}$ values may also influence isotopic composition of consumers (Goering *et al.*, 1990). However, in the present study, this factor did not seem to explain the positive consumer $\delta^{13}\text{C}$ values. The $\delta^{13}\text{C}$ of phytoplankton is positively correlated to temperature, increasing with an increase in temperature (Sackett *et al.*, 1965; Degens *et al.*, 1968). To rule out such seasonality, field samplings of this study were conducted during early spring and late fall. Accordingly, an increase in phytoplankton $\delta^{13}\text{C}$ value by temperature prior to the sampling periods was not expected. Extensive phytoplankton bloom can also result in a high $\delta^{13}\text{C}$ value because of the use of increased ^{13}C of dissolved inorganic carbon (DIC) during bloom due to preferential ^{12}C fixation of phytoplankton in a marine environment of which the waters are stagnant (see Goering, 1990). Kim *et al.* (1994) found very high ratios of -15.4 to -9.2‰ during the spring and summer phytoplankton blooms in the inner part of Masan Bay. The Kwangyang Bay system is an estuarine macrotidal bay. Phytoplankton blooms comparable to

that of Masan Bay has not been observed in this bay.

Since lipids are much more negative in $\delta^{13}\text{C}$ than protein and carbohydrates, the increase of lipid content in different tissues or chemical fractions of the same organism can shift animal $\delta^{13}\text{C}$ value more negatively than its diet (DeNiro and Epstein, 1977; Focken and Becker, 1998). The $\delta^{13}\text{C}$ of lipid-rich tissue of invertebrates is lower than the $\delta^{13}\text{C}$ of muscle tissue (Hughes and Sherr, 1983). However, this effect is unlikely to be important for $\delta^{13}\text{C}$ values of whole tissue of invertebrate species because percent lipid content of invertebrate tissue is relatively low (e.g. Kang *et al.*, 1999). The influence of lipid content on the $\delta^{13}\text{C}$ values of fish is apparent because of a great variability in the proximate composition of fish bodies (Focken and Becker, 1998). Our isotope data contains the results that were analyzed using total dry matter of animal muscle without any lipid elimination treatment. Accordingly, the negative correlation between $\delta^{13}\text{C}$ values and lipid content of animals taken into account, the general trend in the bay ecosystems toward more positive ratios in consumers than phytoplankton and/or benthic microalgae suggests that the present isotope data may underestimate the contribution of the relatively positive sources (benthic microalgae or *Zostera* detritus) as food components for the whole bay consumers.

Although the bay is directly influenced by the inputs of Seomjin River, the results preclude the contribution of carbon from riverine terrestrially derived POM and riverine and estuarine marsh plants to consumers. In this study, only two suspension-feeding bivalves (*Musculus senhousia* and *Mya arenaria*) and a fish species (*Hapalogenys mucronatus*) had a tendency that the upper estuarine individuals (-20.0, -18.7 and -17.4‰, respectively) are slightly more negative than those from the other stations (-16.9 to -15.2‰). Even though taking the metabolic fractionation of 0.7 to 1.4‰ in consumers over their food into consideration, the $\delta^{13}\text{C}$ values of the two bivalves rather reflected a high contribution of phytoplankton (-20.7‰) to their diet. Another result obtained from a brackish water clam *Corbicula* sp., which was collected in the estuarine gradient, also confirms this conclusion (Fig. 3). While *Corbicula* individuals from the upstream station showed a mean $\delta^{13}\text{C}$ of $-25.2 \pm 0.9\text{‰}$ (n=3), the upper estuarine ones had a mean of $-19.9 \pm 0.1\text{‰}$ (n=3). This result strongly indicated that the role of riverine POC for higher trophic levels was limited to the riverine portion of the estuary and was of little importance even for the upper estuarine

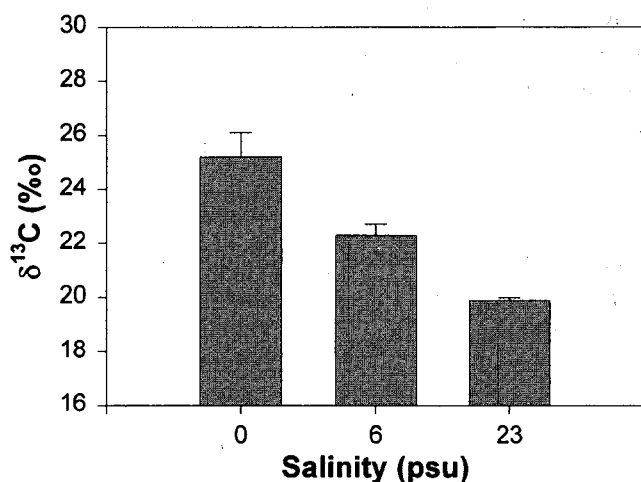


Fig. 3. Stable carbon isotope ratios (‰) of the brackish water clam *Corbicula* sp. collected along the salinity gradient.

consumers. This seems to be attributed to the lack of availability due to low SPM concentration in the Seomjin River waters (Table 2) and/or the poor quality of riverine POM as food for estuarine consumers due to high C:N ratio. Several studies found that despite the large export of terrestrial POM by river, terrestrial carbon did not play an important role to the estuarine food webs (Simenstad and Wissmar, 1985; Bunn *et al.*, 1989; Deegan and Garritt, 1997). Additionally, the lack of its availability in the subtidal zones due to the sedimentation of dead *Phragmites* within the supralittoral zone is also likely to result in a lower contribution of marsh plant (*Phragmites*) detritus to consumer diet.

Another interesting result in this study was a difference in $\delta^{13}\text{C}$ values between pelagic and benthic consumers. Pelagic consumers such as pelagic grazer, suspension-feeder and planktivorous fishes (-20.2 to -14.7‰ , mean = $-17.4 \pm 1.5\text{‰}$, $n=37$) had more negative $\delta^{13}\text{C}$ values (two sided t-test, $p < 0.001$) than benthic consumers such as benthic grazer, deposit-feeder and benthic feeder (-17.2 to -11.6‰ , mean = $-15.2 \pm 1.6\text{‰}$, $n=31$). The results perhaps reflected a relative difference in the dependence of the pelagic and benthic consumers on phytoplankton and benthic vegetation. Differences in $\delta^{13}\text{C}$ values between pelagic and benthic consumers have been reported in other studies in marine systems (Fry and Parker, 1979; Simenstad and Wissmar, 1985; Deegan and Garritt, 1997; Riera *et al.*, 1999).

Invertebrates: Isotope values of pelagic copepods were nearly identical (-20.2 to -18.9‰) among sta-

tions but differed greatly from those of intertidal benthic copepods (-11.6‰). The $\delta^{13}\text{C}$ values suggested that the pelagic ones used primarily phytoplankton with the trophic fractionation of about 1‰ and the benthic groups assimilated mostly benthic microalgal carbon. $\delta^{13}\text{C}$ values of benthic copepods in the present study were more positive than values reported from phytoplankton-based ecosystem (-21.0 to -17.2‰ , Gearing *et al.*, 1984) and values for benthic copepods that fed on a mixture of detrital *Spartina* (predominant) and benthic microalgae (some proportion) (-14.5 to -14.2‰ , Couch, 1989). The $\delta^{13}\text{C}$ value of benthic copepods was 7.6‰ more positive than that of SOC ($-19.2 \pm 1.1\text{‰}$). This difference cannot be explained by the coefficient of average trophic enrichment of about 1‰ , suggesting that the benthic copepods do not assimilate all the components of the SOC pool. As a result, the enrichment of benthic copepods in ^{13}C relative to SOC might indicate an incorporation of the carbon derived from ^{13}C -enriched benthic vegetation (e.g. Riera *et al.*, 1996).

Fourteen suspension-feeding bivalves had a homogeneous isotopic ratio of -18.2 to -14.9‰ , except for two values from the upper estuarine station. These values were intermediate between those of phytoplankton and benthic microalgae, reflecting the use of a mixed carbon from both these two sources. The homogeneity of isotope values of suspension-feeding bivalves is not surprising because the bay is a macrotidal system and it is well known that tide- and/or wind-induced resuspended benthic diatoms may be an important food resource in estuarine tidal flats and channels (see Introduction). Two suspension-feeding ascidians, *Ciona intestinalis* and *Styela* sp., had also $\delta^{13}\text{C}$ values of -19.0 and -16.1‰ , respectively. $\delta^{13}\text{C}$ value of the surface deposit-feeding bivalve *Macoma* sp. (-12.3‰) was more positive than those reported for populations from phytoplankton-based ecosystem (-18.3‰ , Gearing *et al.*, 1984; $-16.9 \pm 1.0\text{‰}$, Goering *et al.*, 1990). This value was also 6.9‰ more positive than that of SOC, indicating that this bivalve assimilated predominantly benthic microalgae. Several authors reported isotopically positive carbon values of *Macoma* spp. relative to suspension-feeding bivalves, suggesting that *Macoma* assimilated selectively carbon from ^{13}C -enriched benthic microalgae (Incze *et al.*, 1982; Page, 1997; Riera *et al.*, 1999; Herman *et al.*, 2000).

Seven species of omnivorous shrimps were collected in this study. Their $\delta^{13}\text{C}$ values ($-14.6 \pm 1.0\text{‰}$)

were closely related to benthic microalgae. Fry and Parker (1979) and Rodelli *et al.* (1984) reported an identical isotope value of -16.5‰ for the shrimps that assimilated mostly phytoplankton carbon and a 4.5‰ increase relative to phytoplankton along the food web. Gearing *et al.* (1984) showed 2.4‰ increase for omnivorous shrimp (-17.9‰), which selectively assimilated carbon mostly from pelagic diatoms. The present data for omnivorous shrimps were 6.1‰ more positive compared to the phytoplankton $\delta^{13}\text{C}$ (-20.7‰), exceeding value previously reported for their trophic fractionation. This result implies that isotopically positive carbon sources compared to phytoplankton may account for some portion of the carbon assimilated by the shrimps. $\delta^{13}\text{C}$ values for five deposit-feeding crustaceans, *Corophium* sp., *Cyathura carinata*, *Oniscus asellus*, *Pagurus* sp. and *Uca* spp., (mean $-14.7 \pm 2.0\text{‰}$; -17.8 to 12.5‰) were much more positive than that of bulk sedimentary organic carbon (-19.2‰), suggesting the significant use of carbon derived from ^{13}C -enriched sources such as benthic microalgae and *Zostera*. Four predatory crustaceans (*Charybdis bimaculata*, *Eucrate crenata*, *Oratosquilla oratoria* and *Portunus trituberculatus*) had $\delta^{13}\text{C}$ values (-16.4 to -14.2‰) similar to the other groups of crustaceans.

More positive $\delta^{13}\text{C}$ values compared to phytoplankton were also found in deposit-feeding gastropod (*Umbonium costatum*, -14.5‰) and predatory gastropod (*Euspira fortunei*, -15.6‰). Selective feeding of deposit-feeding gastropod on benthic diatoms has been reported (Créach *et al.*, 1997). A scavenger gastropod, *Reticunassa fratercula*, had more positive $\delta^{13}\text{C}$ value (-12.9‰) than the two other gastropods, *Umbonium costatum* and *Euspira fortunei*. Overall, the isotope ratios of gastropods suggest the significant incorporation of the ^{13}C -enriched carbon derived from benthic microalgae. $\delta^{13}\text{C}$ values of three predatory cephalopods (*Loligo* sp., *Octopus* sp. and *Sepia* sp.) (-15.8 to -15.3‰) were similar to those of omnivorous and predatory fish (see later discussion).

^{13}C -enrichment of macro-consumer groups is most striking in benthic annelid worms. Most the worms exhibited much more positive $\delta^{13}\text{C}$ values (-15.5 to -11.3‰) than bulk sedimentary organic carbon (-19.2‰) but slightly ^{13}C -enriched compared to benthic microalgae, indicating a predominant assimilation of ^{13}C -enriched benthic microalgal carbon with the gradual trophic shift in $\delta^{13}\text{C}$ along food chains. Kang *et al.* (2000) reported a $\delta^{13}\text{C}$ range of -18.6 to -16.9‰ for benthic polychaetes in the Youngil

Bay (Korea), which is a phytoplankton-based system. This bay is free from intertidal flats and thereby benthic algae are not expected to contribute to the carbon pool. $\delta^{13}\text{C}$ values for polychaetes in the present study were doubtless distinct from those (-18.3 to -17.1‰) in other phytoplankton-base ecosystems (Gearing *et al.*, 1984). Fry and Parker (1979) showed that benthic polychaetes (-14.2 to -10.6‰) fed on benthic vegetation were significantly enriched in ^{13}C relative to polychaetes (-19.4 to -17.7‰) collected in the phytoplankton-based offshore environments. McLusky (1989) documented that various deposit-feeding polychaetes ingest large quantities of mud, digest off some organic material and reject the bulk of the mud in the worm cast. When benthic microalgae are available, the worms may feed directly on benthic microalgae in the estuarine environment. For example, the nereid worm *Nereis*, known as an omnivorous species, can ingest directly benthic microalgae as a deposit feeder (Créach *et al.*, 1997). Recently, Herman *et al.* (2000) found that both deposit-feeding and predatory polychaetes were more ^{13}C -enriched than suspension-feeders, confirming a strong benthic microalgal $\delta^{13}\text{C}$ signature as a food source for deposit feeders from a tidal flat in the Westerschelde estuary in the Netherlands.

Fish: No isotopic differences among stations were found in the same fish species. However, fish previously identified as planktivorous ($-18.2 \pm 0.9\text{‰}$, $n=11$ for 7 species) were readily distinguishable (two sided t-test, $p < 0.001$) from fish belonging to benthic feeders ($-15.9 \pm 0.9\text{‰}$, $n=19$ for 11 species). The $\delta^{13}\text{C}$ values of planktivorous fish were close to those of plankton. On the other hand, the $\delta^{13}\text{C}$ values of benthic feeders of fish species were shifted to the benthic vegetation and deposit-feeding and omnivorous invertebrates. The ^{13}C enrichment in benthic feeder fish suggest that the carbon derived from intertidal benthic vegetation might be incorporated to fish food webs mostly through benthic food chains. This result is consistent with the conclusion of Pinnegar and Polunin (2000) who identified from gut content and isotope data that ^{13}C enrichment tended to be associated with benthic food chains and ^{13}C depletion with planktonic chains for food webs of rocky littoral ecosystems in the Mediterranean. Two omnivorous and fifteen predatory fishes ($-15.4 \pm 1.3\text{‰}$, $n=29$ for 17 species) tended to have $\delta^{13}\text{C}$ values similar to benthic feeders. Based on the trophic enrichment in ^{13}C , these results probably indicated their

dependence on both benthic and plankton-derived carbon.

In addition to the resuspension mechanism of benthic microalgae, another possible explanation for the export of intertidal benthic vegetation to the subtidal food webs is here likely to be associated with the tidal migration of fish. Recently, Hong and Seo (unpublished data, Inha University) observed in a Korean intertidal flat that a large variety of consumers such as fish, crustaceans and cephalopods immigrated to intertidal flats due to their tidal migration despite a difference in species composition in night and day shifts. Reise (1985) documented that tidal flats provide the nurplings with favorable growth condition, ample small-sized prey, and with a refuge from large predatory fish. He also reviewed from the results of numerous experiments that predation of the consumers on the tidal flats has strong effects on their benthic prey population. Accepting this hypothesis, our isotope data indicate that after feeding of the immigrants on the tidal flats during the flood tide, they emigrated to the subtidal channels when the tide flew out.

Our results suggested that although phytoplankton-derived carbon was probably important for the production of some fishes, benthic plant sources in the intertidal zone seemed to also be incorporated into the subtidal fish food webs. However, since many fishes may undergo ontogenetic changes in diet and lipid content amongst the fishes differ each other, detailed $\delta^{13}\text{C}$ studies for lipid-free tissues depending on fish size may enable us to detect more effectively sources of diet and changes of food item for fishes and the general carbon flow for entire food webs.

CONCLUSIONS

1) Dominant benthic vegetations were isotopically divided into two distinct groups within the Kwangyang Bay system: vascular marsh plants had a mean of $-27.4 \pm 0.8\text{‰}$, while microbenthic algae ($-14.5 \pm 0.9\text{‰}$) and seagrass (-8.8‰) were more positive. Phytoplankton were intermediate ($-20.7 \pm 0.8\text{‰}$) between these two sources.

2) Riverine POM had a mean $\delta^{13}\text{C}$ value of $-26.0 (\pm 0.8)\text{‰}$, while the bay channel POM exhibited much heavier $\delta^{13}\text{C}$ value in a mean of $-19.8 (\pm 1.3)\text{‰}$. Estuarine POM displayed intermediate $\delta^{13}\text{C}$ values with a mean of $-22.4 (\pm 0.9)\text{‰}$.

3) The $\delta^{13}\text{C}$ values of eighty-nine consumer species were spanned in a narrower range (-20.2 to -11.3‰) relative to those of potential food resources, showing

a great resemblance for the same species within the whole bay systems. These consumer isotopic ratios strongly suggested the assimilation of the relatively positive carbon sources (phytoplankton and benthic vegetation including algae and seagrass).

4) The $\delta^{13}\text{C}$ values of pelagic consumers (e.g. pelagic copepods, suspension-feeders and planktivorous fishes: mean $-17.4 \pm 1.5\text{‰}$) reflected a greater dependence on phytoplankton than those of benthic consumers (e.g. benthic copepods, deposit-feeders and benthic feeders of fishes: mean $-15.2 \pm 1.6\text{‰}$), which were closer to benthic vegetation. The isotopic difference between pelagic and benthic consumers indicated that the carbon derived from intertidal benthic vegetation might be incorporated to food webs mostly through benthic food chains.

5) The present results are quite different from published values for the phytoplankton-based ecosystem, particularly in the ^{13}C enrichment of benthic grazers, deposit-feeders and benthic feeders of fishes. This tendency of the ^{13}C enrichment was also found in suspension-feeding bivalves. Taking the biomasses of benthic vegetation into consideration, benthic microalgae was likely to account for the consumer ^{13}C enrichment.

6) Role of riverine terrestrially derived POM was limited to the riverine system and was not evident from the estuary to the bay channel systems.

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