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Spatial dietary variations in *Laternula marilina* (Bivalva) and *Hediste* spp. (Polychaeta) along environmental gradients in two brackish lagoons

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ABSTRACT: Spatial dietary variations in deposit feeding polychaetes *Hediste* spp. and the suspension-feeding bivalve *Laternula marilina* were investigated at 6 stations along environmental gradients in 2 brackish lagoons (Gamo and Idoura, Japan) using stable isotopic analyses. In the productive and marine-dominated Gamo lagoon, *Hediste* spp. ($\delta^{13}C$: –19.1 to –15.0‰) assimilated mainly benthic diatoms (–16.4‰) and autochthonous phytoplankton (–23.6‰). Dietary contribution of phytoplankton clearly increased in the central lagoon with increasing phytoplanktonic biomass (chlorophyll *a*: up to 110 µg l^{-1}). In Gamo, *L. marilina* ($\delta^{13}C$: –18.7 to –17.8‰) mainly assimilated both marine particulate organic matter (POM) and resuspended benthic diatoms, while their low $\delta^{15}N$ values suggested a contribution of ^{15}N-depleted diets (e.g. N_2-fixing cyanobacteria). Conversely, in the less productive and river-dominated Idoura lagoon, benthic diatoms and marine POM were only minor diets. Low $\delta^{13}C$ values for *Hediste* spp. (–26.1 to –23.2‰) and *L. marilina* (–27.6 to –25.0‰) indicated that terrestrial and riverine materials provided the primary sources of carbon. In each lagoon, the stable isotopic signatures of *L. marilina* differed distinctly from those of the sympatric suspension-feeding bivalves *Ruditapes philippinarum* and *Crassostrea gigas*. This suggests that *L. marilina* has physiological characteristics that allow utilization of refractory organic substances (e.g. digestive enzymes). The low $\delta^{13}C$ values of *Hediste* spp. in Idoura also imply direct assimilation of plant detritus using cellulase. Dietary plasticity of the consumers may allow them to gain energy in brackish waters where indigestible terrestrial detritus is the major source of carbon.

KEY WORDS: Macrozoobenthos · Stable isotope ratios · Feeding habits · C/N ratio · Terrestrial plant detritus · Autochthonous microalgae · Cellulase

INTRODUCTION

Estuaries receive large amounts of organic matter from a variety of sources. For example, autochthonous materials including phytoplankton, microphytobenthos, macroalgae, and marsh plants are the important sources of organic particles in estuarine ecosystems (Heip et al. 1995). Marine and river waters also supply a certain amount of allochthonous materials (i.e. marine POM and riverine terrestrial materials) to the system (Heip et al. 1995).

Although estuarine soft bottom habitats are rich with river-derived terrestrial plant detritus (e.g. Wada et al. 1987, Thornton & McManus 1994, Chanton & Lewis 2002), these sources are rich in refractory cellulose and lignin and are hardly utilized by aquatic invertebrates (Hargrave 1970, Kristensen 1972, Tenore 1983). Hence, detritivores in general use only the digestible fractions in the detrital pool, such as bacteria, settling phytoplankton, and microphytobenthos including their extracellular polymeric substances (EPS) (e.g. Tsuchiya & Kurihara 1979, Smith & Underwood 1998, Kurata et al. 2001, Kanaya et al. 2005, 2007). Because most ingested detritus is ejected as feces, it is difficult to determine the assimilated diet of benthic detritivores using traditional methods such as stomach con-

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tent analysis. Consequently, many ecologists have used carbon and nitrogen stable isotope analyses because the ratios provide time-integrated measures of the assimilated diet (Fry & Sherr 1984).

A number of early studies had pointed out the dietary importance of vascular plant detritus for estuarine invertebrates after degradation by bacteria and/or transformation into bacterial biomass (e.g. Tsuchiya & Kurihara 1979, Tenore 1983, see review Lopez & Levinton 1987). However, recent stable isotopic studies have emphasized the trophic importance of locally produced microalgae for benthic detritivores in estuarine and coastal habitats (Sullivan & Moncreiff 1990, Page & Lastra 2003, Yokoyama et al. 2005, Kang et al. 2006, 2007). Only a few studies have shown a significant dietary contribution from terrestrial plant detritus (e.g. Riera & Richard 1996, Chanton & Lewis 2002) since the material is less nutritive than microalgal sources (Kristensen 1972). However, recent studies have shown that some benthic animals have a cellulase (Brock & Kennedy 1992, Sakamoto et al. 2007) that allows the organisms to use terrestrial plant material as a major carbon source (Kasai & Nakata 2005, Kasai et al. 2006). These findings imply a direct linkage between the terrestrial and marine food webs (i.e. a trophic pathway from terrestrial primary production to estuarine secondary production).

The polychaetes of the *Hediste* spp. complex (*H. atoka*, *H. diadroma*, and *H. japonica*) and the bivalve *Laternula marilina* are commonly found in Asian brackish waters (Wada et al. 1996, Sato & Nakashima 2003, Kanaya 2005, Kang et al. 2006, 2007). *Hediste* spp. are surface-deposit feeders that ingest sediment organic matter (SOM) at the sediment surface, with little selectivity (Tsuchiya & Kurihara 1980, Kikuchi & Wada 1996). *L. marilina* is an infaunal suspension feeder that ingests particulate organic matter (POM) in the water column using a siphon (Tsuchiya & Kurihara 1980, Kang et al. 2006). These species often dominate the estuarine macrozoobenthic community (Kurihara et al. 2000, Kanaya 2005, Kang et al. 2007) and thus may play significant roles in the local food webs. Previous studies have reported that *Hediste* spp. (*H. atoka* and *H. diadroma*) assimilate bulk SOM that is primarily comprised of riverine terrestrial material in river-dominated estuarine habitats (Kikuchi & Wada 1996, Doi et al. 2005). In contrast, Kang et al. (2007) noted the trophic importance of benthic microalgae (i.e. autochthonous microalgae) for *H. japonica* in a seaward intertidal salt marsh. Kang et al. (2006, 2007) also reported that the major dietary component of *L. marilina* differed between 2 Korean estuaries (resuspended benthic microalgae and coastal phytoplankton, respectively). These results strongly suggest that the major dietary components of *Hediste*

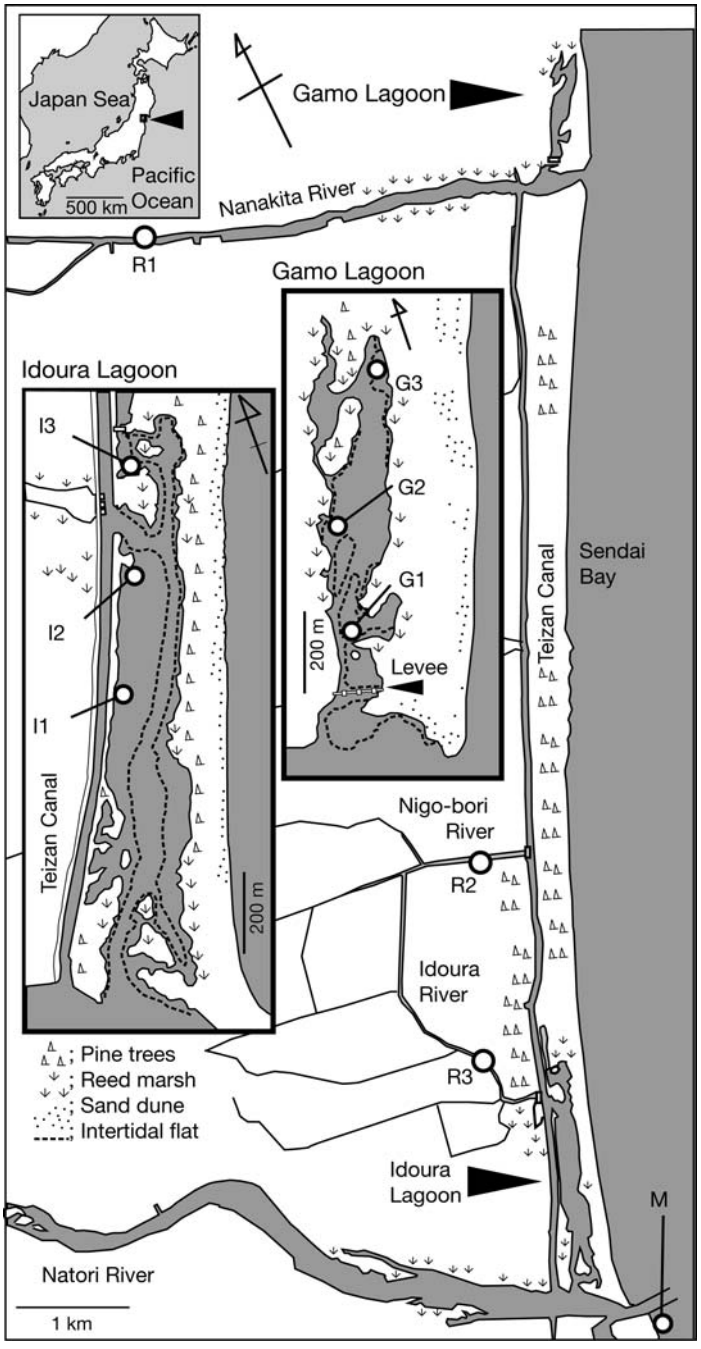

Fig. 1. Sampling stations in the Nanakita River and Natori River estuaries. Food sources and benthic consumers were sampled at 6 stations in the lagoons (Gamo: G1, G2, and G3; Idoura: I1, I2, and I3). Riverine particulate organic matter (POM) was sampled at R1, R2, and R3 and marine POM was sampled at M

spp. and *L. marilina* vary among habitats in relation to environmental differences.

In the present study, spatial dietary changes in the polychaetes *Hediste atoka* and *H. diadroma* and the bivalve *Laternula marilina* were examined using stable carbon and nitrogen ratios ($\delta^{13}C$ and $\delta^{15}N$) along an estuarine environmental gradient. Series of field surveys were conducted in 2 brackish lagoons, Gamo and Idoura, located in 2 neighboring estuaries (the Nanakita and Natori Rivers, respectively) facing Sendai Bay, Japan. Both lagoons have a similar shape and location, but differ in hydrological properties and sediment characteristics (Kanaya & Kikuchi 2004, Kanaya 2005). The aims of the present study were to (1) reveal spatial environmental changes including the biomass of microphytobenthos and phytoplankton and the origin of POM and SOM, (2) assess spatial dietary variations in *Hediste* spp. and *L. marilina* in the 2 lagoons, and (3) surmise the environmental factors responsible for any dietary variations.

MATERIALS AND METHODS

Study site. Field surveys were conducted in the Gamo (area: 0.11 km^2; mean water depth: 0.8 m) and Idoura (0.40 km^2; 1.3 m) lagoons, located on the north side of the Nanakita and Natori River mouths, respectively (Fig. 1). In the marine-dominated and highly productive Gamo lagoon, a stone levee with 3 water gates (opening: 1.8 × 1.35 m) restricted tidal water exchange. The salinity rarely falls below 10 psu and the diurnal average ranges from 21 to 25 psu (Kurihara et al. 2000). High autochthonous phytoplankton biomass, which is the major source of SOM in the inner lagoon, is maintained by water stagnation (chlorophyll *a* [chl *a*]: up to 200 µg l^{-1}; Kikuchi et al. 1992, Kanaya & Kikuchi 2004). In contrast, Idoura lacks distinct autochthonous phytoplankton biomass because of a high rate of water exchange (Kanaya & Kikuchi 2004). In spring tides, up to 94% of the lagoon water (in volume) is exchanged during one tidal cycle (Kanaya & Kikuchi 2004). The lagoon receives freshwater directly from the Idoura River during low tides (salinity: near 0 psu at low tide to over 30 psu at high tide) (Miyagi Prefecture 1988, G. Kanaya unpubl. data). As a result, Idoura receives a large amount of riverine terrestrial material, providing a major source of SOM (Kanaya & Kikuchi 2004, Kanaya 2005). The edges of the 2 estuaries are vegetated with the reed *Phragmites australis* and partly with pine *Pinus densiflora* and *P. thunbergii*. Macroalgal patches of *Gracilaria vermiculophylla* were found in the inner portion of each lagoon. Seagrass is never present in the estuaries.

Sampling stations in the lagoons. Three stations were located in the unvegetated intertidal flats of each lagoon (Gamo: G1, G2, and G3; Idoura: I1, I2, and I3; Fig. 1). Sediments at the stations were muddy-sand in Gamo (silt-clay: <30%) and mud in Idoura (silt-clay: 57 to 92%) (Kanaya 2005, G. Kanaya unpubl. data). Macroalgal patches (*Gracilaria vermiculophylla*) were found around G2 and G3. Macrozoobenthos and their potential food sources were sampled in July and August 2005 at each station. Samples were kept at 4°C and brought to the laboratory.

Collection and sample preparation of animals. The nereidid polychaetes *Hediste* spp. are one of the most dominant and permanent inhabitants of the study estuaries (Kurihara et al. 2000, Kanaya 2005). At our study sites, the *Hediste* complex consists of 2 species, *H. atoka* and *H. diadroma* (Sato & Nakashima 2003). In this study, the 2 species were not distinguished. The bivalve *Laternula marilina* is also commonly found at our study sites (Kurihara et al. 2000, Kanaya 2005). *Hediste* spp. (total length [TL]: 30 to 50 mm) were sampled using a 1 mm mesh sieve at the 6 stations. After the gut contents were removed under a dissecting microscope, the whole body was analyzed. *L. marilina* (shell length [SL]: 18 to 35 mm) was collected by hand at G1, G2, I1, and I2. The sympatric suspension-feeding bivalves, *Ruditapes philippinarum* (G1, G2, and G3, SL: 29 to 41 mm) and *Crassostrea gigas* (I1 and I2, SL: 45 to 120 mm), were also collected for comparison. Bivalve muscle tissue was picked out and used for analyses. After washing with deionized water, animal samples were freeze-dried (24 h), ground into a powder, and treated with a chloroform–methanol solution (2:1 by volume, 24 h) to remove lipids.

Collection and sample preparation of potential food sources. To obtain POM, lagoon water was sampled at the 6 stations at both low and high tides on the same day (n = 3 for each) in July and August 2005. During low tides, when the stations were emerged, POM samples were collected at the water channel nearest each station. Riverine POM was collected at R1, R2, and R3, and marine POM was collected at M (see Fig. 1). Riverine and marine POM were sampled on the same day (n = 3 for each) in July and August 2005. Sampling dates for the POM samples are listed in Table 1. After being prefiltered through a 250 µm screen, particles in the filtrate were concentrated onto a precombusted GF/F filter (500°C, 2 h) for stable isotope analyses. Salinity of the water was determined *in situ* using a hand-held water quality meter (U-22, HORIBA).

SOM (0 to 1 cm deep, n = 3) was sampled at each station using a core (2.8 cm internal diameter [id]) and freeze-dried (24 h) for stable isotope analyses. Surface sediments (0 to 3 mm deep, n = 3) were also sampled at each station to collect benthic diatoms by exploiting

Table 1. Salinity (July/August), chl *a*, and the TOC/chl *a* ratio for water samples collected in the 2 estuaries. Data are means ± 1 SD (n). J: 22 July 2005; A: 22 August 2005; h: high tide; l: low tide. Data for Stns G1 and G2 (except for the POM data during high tides), Nanakita River, and adjacent sea are reported in Kanaya et al. (2007)

Stn	Date/tide	Salinity (psu)	Chl *a* (µg l^{-1})	TOC/chl *a*
ADJACENT SEA (marine POM)				
M	J, A	24.6/31.0	6.2 ± 3.9 (6)	229 ± 97 (6)
GAMO LAGOON				
G1	J/l, A/l	17.4/30	5.8 ± 0.7 (6)	120 ± 42 (6)
	J/h	18	3.4 ± 0.2 (3)	126 ± 10 (3)
	A/h	32.9	7.5 ± 0.3 (3)	44 ± 2 (3)
G2	J/l, A/l[a]	8.3/15.6	111 ± 6.6 (6)	48 ± 14 (6)
	J/h	16	10.4 ± 4.3 (3)	127 ± 57 (3)
	A/h	32.3	5.6 ± 0.4 (3)	138 ± 11 (3)
G3	J/l, A/l	17.1/27.6	7.3 ± 2.6 (6)	167 ± 130 (6)
	J/h	17.5	3.6 ± 0.3 (3)	135 ± 16 (3)
	A/h	27.9	19.0 ± 0.4 (3)	28 ± 7 (3)
Mean		**21.7 ± 8.0 (12)**	**24.8 ± 39.4 (36)**	**105 ± 76 (36)**
NANAKITA RIVER (riverine POM/phytoplankton)				
R1	J	1.4	7.9 ± 0.2 (3)	118 ± 11 (3)
	A[b]	3.7	17.9 ± 0.8 (3)	50 ± 2 (3)
IDOURA LAGOON				
I1	J/l, A/l	2.9/4.6	11.2 ± 7.6 (6)	183 ± 66 (6)
	J/h, A/h	18.7/17.0	3.5 ± 0.2 (6)	164 ± 20 (6)
I2	J/l, A/l	1.4/1.3	10.4 ± 1.5 (6)	126 ± 57 (6)
	J/h, A/h	7.4/13.0	2.3 ± 1.0 (6)	279 ± 233 (6)
I3	J/l, A/l	10.2/7.9	13.3 ± 5.9 (6)	127 ± 23 (6)
	J/h, A/h	3.9/8.8	6.7 ± 2.1 (6)	140 ± 7 (6)
Mean		**8.1 ± 5.6 (12)**	**7.9 ± 5.6 (36)**	**173 ± 113 (36)**
NIGO-BORI (R2) & IDOURA (R3) RIVERS (riverine POM/phytoplankton)				
R2	J	0.1	4.1 ± 0.7 (3)	251 ± 44 (3)
R3	J	0.1	12.2 ± 0.1 (3)	90 ± 9 (3)
Mean		**0.1**	**8.2 ± 4.5 (6)**	**171 ± 93 (6)**
R2	A	0.1	31.4 ± 2.9 (3)	35 ± 6 (3)
R3	A	0.3	64.2 ± 3.7 (3)	31 ± 0 (3)
Mean[b]		**0.2**	**47.8 ± 18.2 (6)**	**33 ± 4 (6)**

[a]Regarded as autochthonous phytoplankton
[b]Riverine phytoplankton

their phototactic movement (Couch 1989, Riera & Richard 1996). After being extracted from the sediment, diatoms were concentrated onto a precombusted GF/F filter (500°C, 2 h). Because the diatom samples from Idoura were rich with detrital matter (G. Kanaya pers. obs.), possibly due to low biomass, reported isotopic data for benthic diatoms in the Natori River Estuary (Ito 2002) were used for food source analyses. The data (Ito 2002) were obtained from benthic diatoms *Entomoneis alata* and *Cylindrotheca closterium* cultured *in situ* for several days in dialysis membrane tubes. We also used isotopic data for benthic diatoms collected in other seasons (G1 and G2, Kanaya et al. 2007) to calculate overall means in Gamo because their $\delta^{13}C$ value generally exhibited distinct seasonal fluctuations (4 to 7‰ in range; Ito 2002, Kang et al. 2006). The macroalga *Gracilaria vermiculophylla* and the marsh plant *Phragmites australis* were sampled around the stations. Needles of *Pinus* spp. were collected from the pine forests adjacent to the lagoons. Plant materials were washed in deionized water to remove any attached material, freeze-dried (24 h), and ground into a powder.

Collection and analyses of POM and sediment samples. After the POM collections, a known volume of the residual water was filtered through a GF/C filter to determine chl *a* concentrations (n = 3 from each station). After extraction by N, N-dimethylformamaide, chl *a* concentrations were determined by fluorometry (10-AU, Turner Designs). A known volume of the residual water was filtered through a precombusted (500°C, 2 h) and weighed GF/F filter to obtain total organic carbon content (TOC, n = 3). The filters were oven-dried (60°C, 48 h), weighed and acidified with 1 M HCl to remove carbonates. TOC content was determined using an elemental analyzer (NC-2500, ThermoQuest).

Sediment cores (0 to 1 cm deep, 2.8 cm i.d., n = 3) were taken at each station for chl *a* and pheophytin *a* (pheo *a*) content analyses. The contents were determined by spectrophotometry (Model 101, Hitachi) using 90% acetone as an extractant (see Kanaya & Kikuchi 2004). For stable isotope analyses, a portion of dried sediment was treated with 1 M HCl and freeze-dried (24 h). The TOC and total nitrogen (TN) contents of the sediment were determined using an elemental analyzer (NC-2500, ThermoQuest).

Stable isotope analyses. POM, SOM, and diatom samples were freeze-dried for 24 h after treatment with 1 M HCl to remove carbonates. This treatment has no significant effect on the $\delta^{15}N$ value (Kanaya et al. 2007). Carbon and nitrogen stable isotope ratios were determined using a mass spectrometer (DELTA plus, Finnigan Mat). Isotope ratios are expressed in delta notation:

$$\delta^{13}C \text{ or } \delta^{15}N\ (‰) = (R \text{ sample}/R \text{ standard} - 1) \times 1000$$

where R is the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio for $\delta^{13}C$ or $\delta^{15}N$, respectively. Pee Dee Belemnite (PDB) and atmospheric N_2 were used as references for $\delta^{13}C$ and $\delta^{15}N$, respectively. Analysis errors were within ± 0.2‰ (1 SD) for both $\delta^{13}C$ and $\delta^{15}N$, which were based on repeated

measurements of *L*-histidine (standard substance). An animal's isotopic ratios reflect those of their assimilated diet over time with trophic enrichments (e.g. $\delta^{13}C$: 0 to +1‰; $\delta^{15}N$: +3 to +5‰ per trophic level) (Fry & Sherr 1984, Minagawa & Wada 1984, Peterson & Fry 1987).

Statistics. Data are presented as means with standard deviations. Spatial differences in stable isotopic signatures of animals and sediment characteristics (see Tables 3 & 4) were tested using 1-way ANOVA and the Tukey-Kramer test. Homogeneity of the data was tested in advance using the Bartlett test and, if needed, data were log- or square-root-transformed. Spatial changes in $\delta^{13}C$ and $\delta^{15}N$ values of *Crassostrea gigas* were tested using a *t*-test.

RESULTS

Chemical properties of the water samples

Salinity in the water column was higher in Gamo (range, mean: 8.3 to 32.9 psu, 21.7 psu) than in Idoura (1.3 to 18.7 psu, 8.1 psu) (Table 1). In Idoura, salinity declined sharply during low tides at I1 and I2. In Gamo, salinity declined sharply during low tides at G2, whereas no changes were noted at G1 or G3 (Δ salinity = 0.3 to 2.9 psu). In Gamo lagoon and the adjacent waters (i.e. G1, G2, G3, R1, and M), the chl *a* concentration was highest at G2 (low tides, 111 µg l^{-1}) and much lower at G1, G3, R1, and M (3.4 to 19.0 µg l^{-1}). In Idoura lagoon and the adjacent waters (i.e. I1, I2, I3, R2, R3, and M), the concentration was highest at the Idoura River (R3; up to 64.2 µg l^{-1}). In Idoura, the chl *a* concentration increased during low tides (10.4 to 13.3 µg l^{-1}) and declined sharply (2.3 to 6.7 µg l^{-1}) during high tides with the seawater influx. In the lagoons, the TOC/chl *a* ratio was higher than 100 at most of the stations, but was below 50 at G2 (low tide), G1 (August, high tide), and G3 (August, high tide). At the riverine stations (R1, R2, and R3), the ratio sharply declined in August (<51) with increasing chl *a* concentrations.

Stable isotopic signatures of POM

In Gamo, $\delta^{13}C$ and $\delta^{15}N$ values of POM ranged from –23.6 to –20.0‰ and from 5.0 to 9.1‰, respectively (data from 22 August at high tide were excluded; see the following paragraph). The lagoonal mean POM-$\delta^{13}C$ value (–21.9‰) was nearly identical to that of marine POM (M, –19.9‰). In Idoura, $\delta^{13}C$ and $\delta^{15}N$ values of POM ranged from –30.4 to –23.0‰ (mean: –27.2‰) and from 2.5 to 5.7‰ (4.7‰), respectively. The lagoonal mean $\delta^{13}C$ value was close to riverine materials at R2 and R3 (–29.1‰). At I1 and I2, POM-$\delta^{13}C$ values (mean of the 2 sampling occasions) sharply increased during high tides (–25.6 to –23.0‰) as the salinity increased, and declined sharply (<–28.0‰) during low tides. POM-$\delta^{15}N$ values at the riverine stations (R1, R2, and R3) increased in August with decreasing $\delta^{13}C$ values.

POM-$\delta^{15}N$ values in Gamo were extraordinary low on 22 August at high tide (mean: –0.1‰, salinity: 27.9 to 32.9 psu) (Tables 1 & 2) compared to those on the other sampling occasions ($\delta^{15}N$: 5.0 to 9.1‰) and to previous measurements (5.0 to 10.4‰; Kanaya et al. 2005, T. Toya unpubl. data) in the lagoon. On the other hand, POM-$\delta^{13}C$ values on 22 August (high tide, mean: –20.0‰) were similar to those on the other sampling occasions (–23.6 to –20.0‰). Microscopic observation determined that the samples were dominated by marine dinoflagellates (G. Kanaya pers. obs.) that are rarely found in the lagoon (E. Nobata pers. comm.). The low POM-$\delta^{15}N$ values should be due to N_2-fixing marine microorganisms (e.g. cyanobacteria) that have similar $\delta^{15}N$ values to atmospheric N_2 (0‰) (Peterson & Fry 1987). In this study, these data were excluded from the calculation of the lagoonal mean.

Isotopic signatures of benthic diatoms, plants, and macroalgae

Isotopic signatures in the 2 lagoons clearly differed among the primary producers (Table 2). Benthic diatoms were the most ^{13}C-enriched potential food source (Gamo: –16.4‰; Idoura: –14.8‰), whereas C_3 plants were much more depleted in ^{13}C (*Phragmites australis* and *Pinus* spp.: –30 to–25.5‰). The $\delta^{13}C$ value for the macroalga *Gracilaria vermiculophylla* (Gamo: –21.7‰; Idoura: –24.6‰) was intermediate between them. The $\delta^{15}N$ values for benthic diatoms ranged from 7.4 to 9.9‰ (mean in Gamo: 8.7‰; Idoura: 7.7‰), whereas those of *G. vermiculophylla* (Gamo: 9.6‰; Idoura: 11.0‰) and *P. australis* (Gamo: 9.3‰; Idoura: 9.7‰) were higher. The terrestrial plant, *Pinus* spp., exhibited the lowest $\delta^{15}N$ values (Gamo: –1.6‰; Idoura: –3.7‰) among the potential food sources.

Difference in SOM quality among the stations

The C/N ratio and the stable isotopic signatures of SOM exhibited significant spatial variation (1-way ANOVA; Table 3). The C/N ratio of SOM was significantly higher in Idoura (11.1 to 11.5) than in Gamo (6.1 to 7.4; Tukey-Kramer test: $p < 0.05$; Fig. 2a). In Gamo, the C/N ratio was lower in the innermost lagoon (G3: 6.1) than at G1 and G2 (7.3 and 7.4, respectively)

(Tukey-Kramer test: $p < 0.05$). The $\delta^{13}C$ value of SOM was much lower in Idoura (–25.7 to –25.3‰) than in Gamo (G1, G2, and G3: –22.0, –23.7, and –20.0‰, respectively) (Tukey-Kramer test: $p < 0.05$, Fig. 2b). In Gamo, the value also differed significantly among the stations (Tukey-Kramer test: $p < 0.05$). The $\delta^{15}N$ value of SOM was lower at I2 (4.4‰) and higher at G1 and G3 (7.3 and 8.4‰, respectively) than at I1, I3, and G2 (4.8, 5.3, and 6.0‰, respectively) (Tukey-Kramer test: $p < 0.05$).

Table 2. Carbon and nitrogen stable isotope ratios of potential food sources in the 2 lagoons. Data are means ±1 SD (n). M: March 2004; J: July 2005; A: August 2005; h: high tide; l: low tide. Data for Stns G1 and G2 (except for the POM data during high tides), Nanakita River, and adjacent sea are reported in Kanaya et al. (2007)

Producers/organic matter	Stn	(Date/tide)	Stable isotope ratio (‰) $\delta^{13}C$		$\delta^{15}N$	
ADJACENT SEA (marine POM)						
Marine POM	M	(J, A)	–19.9 ± 1.6	(6)	6.0 ± 0.8	(5)
GAMO LAGOON						
POM	G1	(J/l, A/l)	–22.4 ± 0.9	(6)	5.0 ± 0.5	(5)
		(J/h)	–21.8 ± 0.5	(3)	7.0 ± 1.4	(3)
	G2	(J/l, A/l)[a]	–23.6 ± 0.2	(6)	7.9 ± 0.8	(6)
		(J/h)	–22.6 ± 0.3	(3)	6.2 ± 0.6	(3)
	G3	(J/l, A/l)	–20.0 ± 1.1	(6)	9.1 ± 2.5	(6)
		(J/h)	–21.1 ± 0.4	(3)	6.4 ± 0.5	(3)
Mean of lagoon POM			**–21.9 ± 1.5**	**(27)**	**7.1 ± 1.9**	**(26)**
POM (N_2-fixing marine microorganisms)	G1, 2, 3	(A/h)	–20.0 ± 1.5	(8)	–0.1 ± 1.3	(8)
Phragmites australis (common reed, leaf)	G1, 2, 3	(A)	–25.5 ± 0.7	(9)	9.3 ± 1.5	(9)
Pinus spp.[b] (pine tree, leaf)		(A)	–28.1 ± 1.3	(6)	–1.6 ± 2.2	(6)
G. vermiculophylla (macro red alga)	G2, 3	(A)	–21.7 ± 1.0	(6)	9.6 ± 2.1	(6)
Benthic diatoms	G1, 2	(M)	–14.5 ± 3.3	(6)	7.4 ± 0.2	(6)
	G1	(J)	–17.7	(2)	9.9 ± 0.2	(3)
	G2	(J)	–19.8 ± 0.5	(3)	8.8 ± 0.3	(3)
	G3	(J)	–16.0 ± 1.0	(3)	9.8 ± 0.3	(3)
Mean of benthic diatoms			**–16.4 ± 3.0**	**(14)**	**8.7 ± 1.1**	**(15)**
NANAKITA RIVER						
Riverine POM	R1	(J)	–26.0 ± 0.1	(3)	4.7 ± 0.8	(3)
Riverine phytoplankton	R1	(A)	–28.9	(2)	7.8 ± 0.4	(3)
Mean of riverine materials			**–27.2 ± 1.4**	**(5)**	**6.2 ± 1.0**	**(6)**
IDOURA LAGOON						
POM	I1	(J/l, A/l)	–28.0 ± 1.3	(6)	4.6 ± 1.4	(6)
		(J/h, A/h)	–23.0 ± 0.9	(6)	5.7 ± 1.4	(6)
	I2	(J/l, A/l)	–29.0 ± 1.6	(6)	5.4 ± 3.0	(6)
		(J/h, A/h)	–25.6 ± 0.5	(6)	2.5 ± 1.9	(6)
	I3	(J/l, A/l)	–30.4 ± 0.4	(6)	5.3 ± 1.1	(6)
		(J/h, A/h)	–27.4 ± 0.5	(6)	4.8 ± 1.8	(6)
Mean of lagoon POM			**–27.2 ± 2.6**	**(36)**	**4.7 ± 2.1**	**(36)**
Phragmites australis	I2, 3	(A)	–28.4 ± 1.9	(6)	9.7 ± 0.6	(6)
Pinus spp.[b]		(A)	–30.0 ± 0.7	(6)	?3.7 ± 0.9	(6)
G. vermiculophylla	I1, 3	(A)	–24.6 ± 1.3	(6)	11.0 ± 1.2	(6)
Benthic diatoms cultured *in situ*[c]			–14.8 ± 2.7	(6)	7.7 ± 0.8	(6)
NIGO-BORI & IDOURA RIVERS						
Riverine POM	R2, 3	(J)	–27.2 ± 0.9	(6)	1.4 ± 1.2	(6)
Riverine phytoplankton	R2, 3	(A)	–30.9 ± 0.3	(6)	6.6 ± 1.0	(6)
Mean of riverine materials			**–29.1 ± 2.0**	**(12)**	**4.0 ± 2.9**	**(12)**

[a]Autochthonous phytoplankton
[b]Sampled in the pine forest adjacent to the lagoon
[c]Data from Ito (2002)

Table 3. One-way ANOVA for the mean chemical parameters of the surface sediment (0 to 5 mm) at the 6 sampling stations

Variables	df	*F*	p
C/N ratio	5,30	83.2	<0.001
$\delta^{13}C$ value	5,30	120	<0.001
$\delta^{15}N$ value	5,29	56.8	<0.001
Chl *a* content			
July 2005	5,12	58.7	<0.001
August 2005	5,12	6.58	<0.01
Pheo *a*/chl *a* ratio	5,30	42.6	<0.001

Sediment content and the pheo *a*/chl *a* ratio also differed significantly among sampling locations (1-way ANOVA; Table 3). In July, chl *a* content was 5.2 to 44 times higher in Gamo (12.4, 20.2, and 46.3 µg cm^{-2}) than in Idoura (1.0 to 2.4 µg cm^{-2}) (Tukey-Kramer test: $p < 0.05$) (Fig. 2c). In August, chl *a* content was highest at G3 (11.0 µg cm^{-2}) (Tukey-Kramer test: $p < 0.05$) and did not differ significantly among the other stations (2.2 to 4.4 µg cm^{-2}; Tukey-Kramer test: $p > 0.05$). The pheo *a*/chl *a* ratio at the sediment surface was lower than 1.0 in Gamo (G1, G2, and G3: 0.6, 0.5, and 0.08, respectively, Fig. 2d) and much higher in Idoura (1.4 to 2.5) (Tukey-Kramer test: $p < 0.05$).

Isotopic signatures of the consumers

The $\delta^{13}C$ and $\delta^{15}N$ values of *Hediste* spp. showed significant spatial variation (1-way ANOVA; Table 4). The $\delta^{13}C$ values were much lower in Idoura (–26.1 to –23.2‰) than in Gamo (–19.1 to –15.0‰) (Tukey-Kramer test: $p < 0.05$). In each lagoon, the lowest $\delta^{13}C$ values were found at the central or innermost areas (G2, I2, and I3) (Tukey-Kramer test: $p < 0.05$). The $\delta^{15}N$ value was highest at the innermost area (G3 and I3) in each lagoon (Tukey-Kramer test: $p < 0.05$).

Laternula marilina exhibited a significant spatial difference in $\delta^{13}C$ value, but not in $\delta^{15}N$ (1-way ANOVA; Table 4). The $\delta^{13}C$ value was significantly lower in Idoura (< –25.0‰) than in Gamo (> –18.7‰) (Tukey-Kramer test: $p < 0.05$). A lower $\delta^{13}C$ value was found at I2 than at I1 (Tukey-Kramer test: $p < 0.05$). No spatial differences were found in Gamo ($p > 0.05$). The $\delta^{15}N$ value (6.8 to 7.8‰) was much lower than in sympatric *Hediste* spp. (8.7 to 14.0‰).

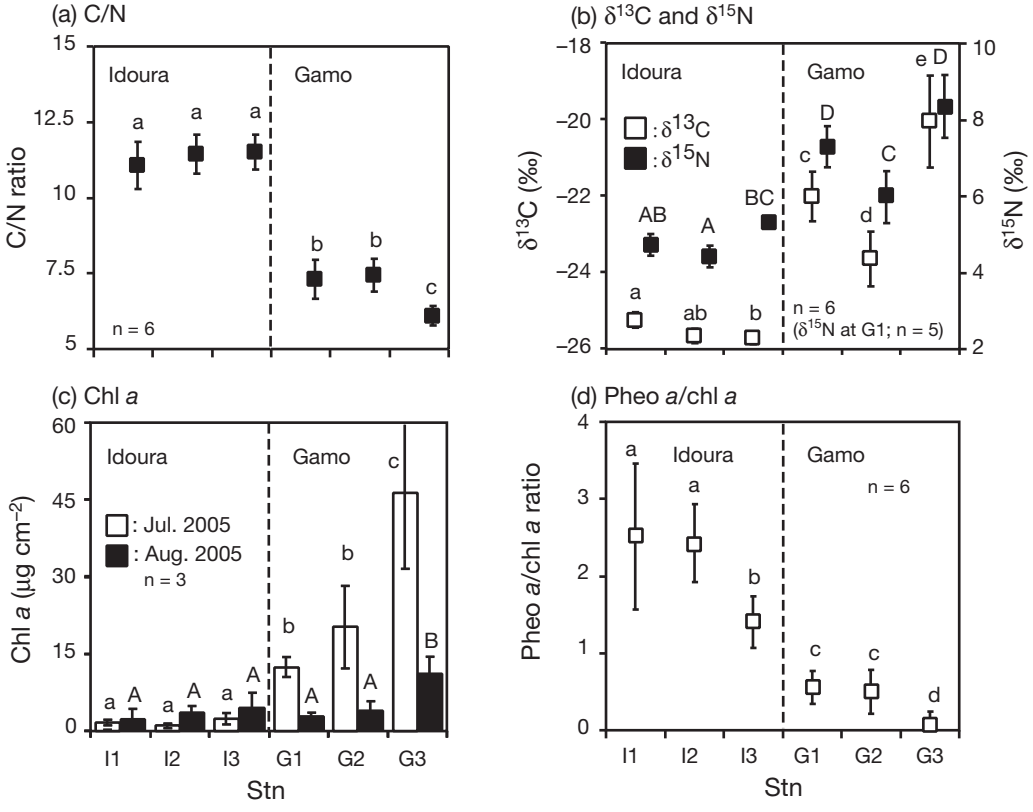

Fig. 2. Spatial differences in sediment characteristics at the Gamo and Idoura lagoons. (a) C/N ratio, (b) $\delta^{13}C$ and $\delta^{15}N$ values, (c) chl *a* content, and (d) the pheo *a*/chl *a* ratio at the sediment surface. Bars represent means ± 1 SD. Different letters indicate significant differences between means (Tukey-Kramer test: $p < 0.05$)

Table 4. Carbon and nitrogen stable isotope ratios of the macrozoobenthos at the stations. Values are means ± 1 SD (n = 3). ns: not significant (p > 0.05). Different letters indicate significant differences in stable isotope ratios among the sites (Tukey-Kramer test: p < 0.05)

Species	Stn	Stable isotope ratio (‰) $\delta^{13}C$		$\delta^{15}N$	
Surface-deposit feeder					
Hediste spp.	G1	–16.5 ± 0.8	a	11.9 ± 0.3	a
	G2	–19.1 ± 0.5	b	10.4 ± 0.2	b
	G3	–15.0 ± 0.5	c	14.0 ± 0.2	c
	I1	–23.2 ± 0.5	d	9.3 ± 0.2	d
	I2	–26.1 ± 0.4	e	8.7 ± 0.2	d
	I3	–25.0 ± 0.5	e	9.9 ± 0.2	b
1-way ANOVA (df = 5,12)		F = 230 p < 0.001		F = 212 p < 0.001	
Obligatory suspension feeders					
Laternula marilina	G1	–17.8 ± 0.7	a	7.8 ± 0.2	
	G2	–18.7 ± 0.3	a	7.2 ± 0.5	
	I1	–25.0 ± 0.9	b	7.3 ± 0.4	
	I2	–27.6 ± 0.7	c	6.8 ± 0.4	
1-way ANOVA (df = 3,8)		F = 139 p < 0.001		F = 3.46 ns	
Ruditapes philippinarum	G1[a]	–17.0 ± 0.7	a	9.0 ± 0.1	
	G2[a]	–20.7 ± 0.5	b	9.4 ± 0.3	
	G3	–19.8 ± 0.3	b	9.6 ± 0.4	
1-way ANOVA (df = 2,6)		F = 39.6 p < 0.001		F = 2.66 ns	
Crassostrea gigas	I1	–19.1 ± 0.7		10.2 ± 0.5	
	I2	–20.4 ± 0.7		10.6 ± 0.4	
t-test (df = 4)		t = 2.28 ns		t = –1.2 ns	

[a]Data from Kanaya et al. (2007)

The isotopic signatures of *Laternula marilina* differed from those of sympatric suspension-feeding bivalves *Ruditapes phillipinarum* and *Crassostrea gigas*, despite similar feeding habits. In Gamo, the $\delta^{15}N$ value of *L. marilina* (<7.8‰) was lower than that of *R. phillipinarum* (>9.0‰). In Idoura, the $\delta^{13}C$ and $\delta^{15}N$ values of *L. marilina* were 5.9 to 7.2‰ and 2.9 to 3.8‰ lower, respectively, than those of *C. gigas*. *R. phillipinarum* showed a significant spatial difference in $\delta^{13}C$ value, similar to that of *Hediste* spp. (1-way ANOVA; Table 4), whereas *C. gigas* did not (t-test: p > 0.05).

DISCUSSION

Isotopic signatures of food sources in the 2 estuaries

The TOC/chl *a* ratio provides information about the nature of POM: values < 100 indicate the dominance of microalgae, whereas values > 100 indicate the dominance of detrital matter (Berg & Newell 1986). At our study sites, riverine POM in July (R1, R2, and R3) exhibited high TOC/chl *a* ratios (118 to 251, Table 1), indicating the dominance of riverine terrestrial plant detritus (i.e. riverine POM). In contrast, the ratios declined sharply in August (< 50), suggesting the dominance of microalgae (i.e. riverine phytoplankton). The isotopic signatures of marine POM (M, $\delta^{13}C$: –19.9‰; $\delta^{15}N$: 6.0‰) were similar to those of temperate marine phytoplankton ($\delta^{13}C$: –20‰; $\delta^{15}N$: 4 to 9‰) (Fry & Sherr 1984, Wada et al. 1987, Yokoyama et al. 2005) and therefore regarded as pure marine POM. In Gamo, there was a significant autochthonous phytoplanktonic biomass in the central region (G2; chl *a*: 110 to 113 µg l^{-1}; Table 2) and the isotopic signatures ($\delta^{13}C$: –23.6‰; $\delta^{15}N$: 7.9‰) were common to those of estuarine phytoplankton (Chanton & Lewis 1999). In contrast, no apparent phytoplankton-rich water bodies were observed in Idoura (Table 2).

In the 2 lagoons, benthic diatoms were the most ^{13}C-enriched potential food source (Table 2). The $\delta^{13}C$ and $\delta^{15}N$ values (–16.4 to –14.8‰ and 7.7 to 8.7‰, respectively) were similar to values previously reported from estuarine and coastal waters (–18.8 to –12.1‰ and 3.8 to 11‰, respectively) (Couch 1989, Doi et al. 2005, Kang et al. 2006, 2007). In contrast, $\delta^{13}C$ values of *Phragmites australis* and *Pinus* spp. were much lower (–30.9 to –25.5‰), which were common to terrestrial C_3-plants (–30 to 27‰) (Riera & Richard 1996, Chanton & Lewis 2002). The macroalgae *Gracilaria vermiculophylla* showed intermediate $\delta^{13}C$ values (Gamo: –21.7‰; Idoura: –24.6‰) between the C_3-plants and benthic diatoms, while exhibited distinctively high $\delta^{15}N$ values (Gamo: 9.6‰; Idoura: 11.0‰). High $\delta^{15}N$ values for macroalgae have been reported from the other estuaries (e.g. Yokoyama et al. 2005, Kang et al. 2007). In Gamo lagoon, the green macroalgae *Enteromorpha prolifera* is occasionally found during summer (G. Kanaya pers. obs.). Although the stable isotope ratio of *E. prolifera* was not measured in this study, it would hardly contribute to the consumers' diet since it exhibited distinctively high $\delta^{13}C$ and $\delta^{15}N$ values (–13.1 and 10.5‰, respectively) (Kanaya et al. 2007).

In the present study, diet of the consumer species was surmised from the stable isotope ratios of consumers and organic matter (see Tables 2 & 4). As mentioned previously, a certain amount of organic matter would be assimilated by deposit feeders after being

transferred into microbial biomass (Tsuchiya & Kurihara 1979, Tenore 1983, Lopez & Levinton 1987). In general, heterotrophic bacteria exhibit a similar $\delta^{13}C$ value to their carbon source (Boschker & Middelburg 2002). Therefore, we could not strictly distinguish the 2 trophic pathways (i.e. direct assimilation and through a microbial trophic mediation) from the isotopic signatures (see also the following sections).

POM and SOM qualities at each station

Generally, riverine terrestrial material with low $\delta^{13}C$ values (<–25‰) was distinctive from marine POM (nearly –20‰) (Wada et al. 1987, Thornton & McManus 1994). In Gamo, lagoonal POM (mean $\delta^{13}C$: –21.9‰) should be primarily derived from 2 sources, marine POM and autochthonous phytoplankton (–19.9 and –23.6‰, respectively), with smaller contributions from riverine materials (R1, –27.2‰). In contrast, lagoonal POM in Idoura should mainly consist of allochthonous sources, because the lagoon lacks significant autochthonous phytoplanktonic biomass (Table 1). In fact, lagoonal POM-$\delta^{13}C$ values sharply declined (<–28.0‰) as the salinity decreased, while increased sharply during high tides (Tables 1 & 2). This supports the idea that the lagoonal POM was primarily a mixture of marine POM (–19.9‰) and riverine materials (R2 & R3, –29.1‰). The low POM-$\delta^{13}C$ values in Idoura lagoon (–27.2‰) indicate a high fractional contribution of the river-derived materials to the POM pool.

Spatial differences in POM quality should be responsible for the SOM composition at each habitat (Table 3, Fig. 2). The low SOM-$\delta^{13}C$ values in Idoura (–25.7 to –25.3‰) imply a dominance of riverine terrestrial material in the SOM pool. Higher SOM-C/N ratios (>11.1) in Idoura also indicate the dominance of terrestrial plant detritus (>20) (Meyers 1994). The high $\delta^{13}C$ values (> –23.7‰) and low C/N ratios (<7.4) of SOM in Gamo, in contrast, indicate the greater importance of estuarine or marine microalgae (C/N: 6 to 10; Meyers 1994) in the SOM pool. High microphytobenthic biomass (chl *a*: >12.4 µg cm^{-2} in July) and low pheo *a*/chl *a* ratios (<0.6) in Gamo also imply a high fractional contribution of benthic microalgae to the SOM pool.

Major diets of consumers in the productive and marine-dominated Gamo lagoon

Spatial variations in the POM and SOM qualities should alter the dietary components of the consumers in each habitat. Figs. 3 & 4 show the isotopic signatures of consumers and available food sources in the Gamo lagoon. We estimated isotopic ranges of a consumer assimilating a diet (indicated in each plot) assuming reported trophic enrichments (0 to +1‰ for $\delta^{13}C$; +3 to +5‰ for $\delta^{15}N$) (Fry & Sherr 1984, Minagawa & Wada 1984, Peterson & Fry 1987). The high $\delta^{13}C$ values of *Hediste* spp. and *Laternula marilina* (–20.7 to –15.0‰) (Table 4) indicated that the dietary contribution of river-derived materials was negligible.

At G1 and G3, *Hediste* spp. exhibited 4.6 to 5.5‰ higher $\delta^{13}C$ values (–16.5 to –15.0‰) than those of SOM (–22.0 to –20.0‰), suggesting the selective assimilation of benthic diatoms (–16.4‰). Recent studies have mentioned that a certain amount of diatom-derived carbon is deposited into the sediment as EPS (e.g. Smith & Underwood 1998). EPS would contribute to the rapid transformation of diatom-derived carbon to bacteria in the sediment (Middelburg et al. 2000). Thus EPS produced by benthic diatoms and its associating bacteria may also contribute to the diet of *Hediste* spp.

At G2, *Hediste* spp. exhibited a lower $\delta^{13}C$ value (–19.1‰) than at the other 2 stations, indicating an increasing contribution of ^{13}C-depleted foods in the diet. In the central lagoon, settling autochthonous phytoplankton is the major source of SOM (Kanaya & Kikuchi 2004, Kanaya 2005). Present data also showed that the SOM-$\delta^{13}C$ value at G2 (–23.7‰) was nearly identical to that of autochthonous phytoplankton (–23.6‰). Therefore, settling phytoplankton was the most probable carbon sources for *Hediste* spp. at this site.

Based on $\delta^{13}C$ values (–18.7 to –17.8‰), marine POM was the primary dietary component of the suspension feeder *Laternula marilina* in Gamo. Slightly higher $\delta^{13}C$ values at G1 imply dietary intake of benthic diatoms as well as marine POM. These $\delta^{15}N$ values, however, were different from that of marine POM, assuming the reported trophic enrichments (see Fig. 3). $\delta^{15}N$ values of *L. marilina* also differed from those of the sympatric suspension feeder *Ruditapes philippinarum.* To explain the data, we propose a hypothesis that *L. marilina* assimilates the ^{15}N-depleted fraction(s) in its diet; this fraction may consist of N_2-fixing marine cyanobacteria ($\delta^{13}C$: –20.0‰; $\delta^{15}N$: –0.1‰) (Table 2). In general, cyanobacteria cell walls are rich with mucopolysaccharides and indigestible to aquatic animals (Hargrave 1970). However, some aquatic organisms have specific enzymes (Kristensen 1972, Brock & Kennedy 1992) that account for the dietary separation of sympatric bivalve species in estuarine habitats (Kasai & Nakata 2005). *L. marilina* may have some physiological characteristics (e.g. digestive enzymes) that allow the digestion and assimilation of typically indigestible cyanobacteria. Further studies should be conducted on the physiological characteristics of *L. marilina*.

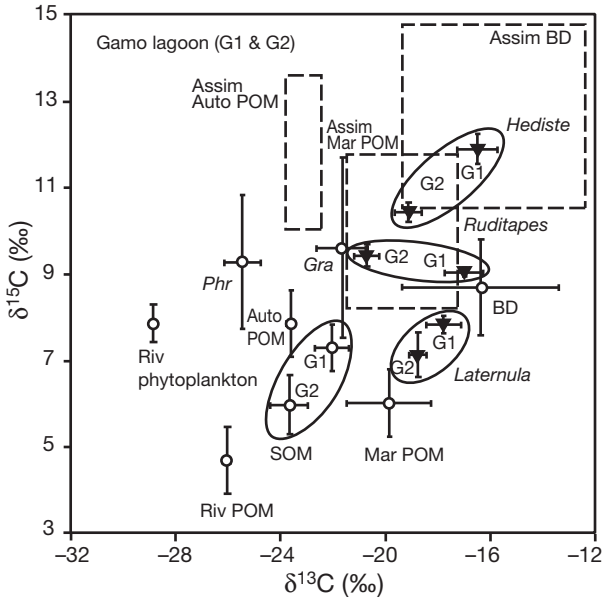

Fig. 3. *Hediste* spp., *Laternula marilina* and *Ruditapes philippinarum*. $\delta^{13}C$ and $\delta^{15}N$ values for consumers (▼) and potential food sources (○) in Gamo (G1 and G2). Generic names for consumers, macroalgae, and plants are abbreviated and denoted in italics. See Tables 2 & 3 for full names and sample sizes (n). Bars indicate 1 SD. Assim: assimilating; Mar: marine; Riv: riverine; Auto: autochthonous; POM: particulate organic matter; SOM: sediment organic matter; BD: benthic diatoms. (---): expected isotope ranges of a consumer assimilating the diet that were estimated from the isotope range of each food source (mean ± 1 SD). Trophic enrichments were assumed as 0 to +1‰ for carbon and +3 to +5‰ for nitrogen (Peterson & Fry 1987)

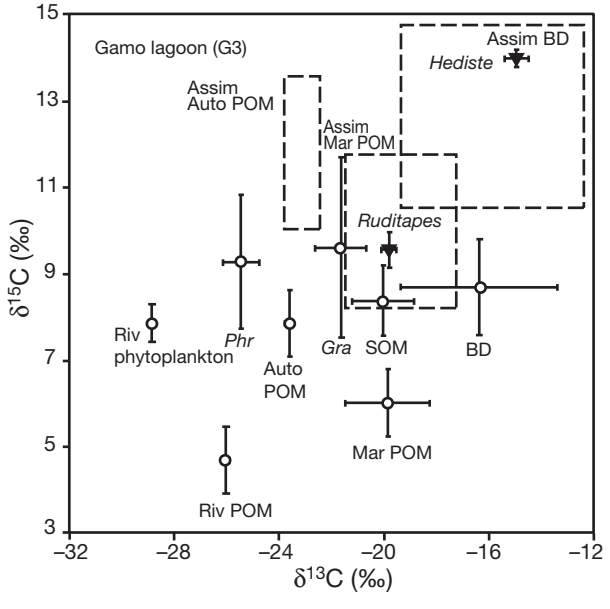

Fig. 4. *Hediste* spp. and *Ruditapes philippinarum*. $\delta^{13}C$ and $\delta^{15}N$ values for consumers (▼) and potential food sources (○) in Gamo (G3). See Tables 2 & 3 for full names and sample sizes (n). Bars indicate 1 SD. Abbreviations and (---) are as defined in Fig. 3

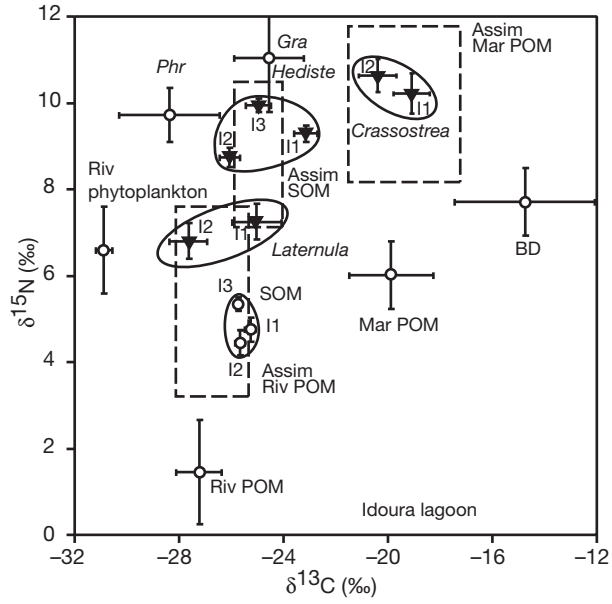

Fig. 5. *Hediste* spp., *Laternula marilina*, and *Crassostrea gigas*. $\delta^{13}C$ and $\delta^{15}N$ values for consumers (▼) and potential food sources (○) in Idoura (I1, I2, and I3). Data for benthic diatoms are from Ito (2002). See Tables 2 & 3 for full names and sample sizes (n). Bars indicate 1 SD. Abbreviations and (---) are as defined in Fig. 3

Major diets of consumers in the river-dominated lagoon (Idoura)

In Idoura, *Laternula marilina* exhibited low $\delta^{13}C$ values (–27.6 to –25.0‰) that were 5.9 to 7.2‰ lower than those for the sympatric *Crassostrea gigas* (–20.4 to –19.1‰) (Table 4). The discrepancy indicates a dietary separation between the 2 suspension feeders. $\delta^{13}C$ values showed that *C. gigas* assimilated little river-derived material, selectively assimilating marine POM (Table 2, Fig. 5). In contrast, *L. marilina* assimilated terrestrial plant materials that are rich in indigestible cellulose and lignin (Hargrave 1970, Kristensen 1972, Tenore 1983). Some bivalves have recently been reported to have a cellulase and can directly assimilate plant detritus (Brock & Kennedy 1992, Kasai & Nakata 2005, Sakamoto et al. 2007). Sakamoto et al. (2007) showed that *Corbicula japonica*, a common brackish bivalve species in Japan, has an endogenous cellulase. Kasai et al. (2006) also showed that *C. japonica* assimilated mainly terrigenous plant detritus in freshwater-dominated brackish habitats. These findings accord with the present results; therefore, it is strongly suggested that *L. marilina*, like *C. japonica*, utilizes a cellulase to assimilate plant material.

In general, deposit feeders assimilate only nutritive fractions in their diet, ejecting the indigestible frac-

tions as feces (e.g. Tsuchiya & Kurihara 1979, Tenore 1983, Kurata et al. 2001). However, the present results showed that the majority of SOM ($\delta^{13}C$: –25.7 to –25.3‰), derived mainly from indigestible terrestrial plant material, contributed significantly to the diets of *Hediste* spp. in Idoura (–26.1 to –23.2‰) (Fig. 5). Distinctively low $\delta^{13}C$ values in *Hediste* spp. (< –25‰) in upper estuarine habitats were reported by Kikuchi & Wada (1996). These $\delta^{13}C$ values were comparable to those of *Corbicula japonica* measured in other brackish habitats (Kasai & Nakata 2005, Kasai et al. 2006). Doi et al. (2005) also found that the $\delta^{13}C$ value of *Hediste* spp. collected in the Kitakami River Estuary (around –25‰) was significantly lower than values for the sympatric nereidid polychaete *Tyllorhynchus heterochaetes* (–22‰), being closer to those of the sympatric *C. japonica*. These results further support the hypothesis that *Hediste* spp. have a cellulase.

Hediste spp. exhibited higher $\delta^{15}N$ values than the sympatric *Laternula marilina*. One possible explanation is that a portion of the diet of *Hediste* spp. is derived from microbial trophic mediation in the SOM pool. Refractory plant detritus is known to become more nutritious after degradation by microbes or conversion into microbial biomass (e.g. Tsuchiya & Kurihara 1979, Tenore 1983). During decomposition, detrital organic matter is gradually enriched in ^{15}N due to microbial nitrogen transformation in the sediment (Wada et al. 1987, Thornton & McManus 1994). In fact, SOM-$\delta^{15}N$ values in Idoura were much higher than riverine POM (i.e. major source of SOM). The microbially ^{15}N-enriched fractions in the POM and SOM pools may partly contribute to the diet of *Hediste* spp. (and possibly to *L. marilina* diet) in Idoura lagoon.

Although our data could not clearly distinguish the 2 possible trophic pathways (i.e. direct assimilation/microbial trophic mediation), we conclude that terrestrial primary production in the catchment area supports secondary production by *Hediste* spp. and *Laternula marilina* in Idoura lagoon.

Dietary plasticity in the brackish detritivores: ecological implications

The among site variation in dietary components for *Hediste* spp. and *Laternula marilina* demonstrated by the present and previous studies (e.g. Kikuchi & Wada 1996, Doi et al. 2005, Kang et al. 2006, 2007) could be specific to animals inhabiting brackish environments. Many isotopic studies have emphasized the trophic importance of phytoplankton and benthic microalgae for benthic consumers in estuarine and coastal ecosystems (e.g. Sullivan & Moncreiff 1990, Page & Lastra 2003, Yokoyama et al. 2005, Kang et al. 2006, 2007). This is mainly because microalgae are more nutritive than terrestrial plant materials, which are rich in cellulose and lignin (e.g. Kristensen 1972, Tenore 1983).

The present results show, however, that terrestrial plant detritus supported the secondary production of *Hediste* spp. and *L. marilina* in Idoura lagoon, suggesting the presence of a cellulase in all of these species. Assimilation of cyanobacteria by *L. marilina* in Gamo may also be due to its specific physiological characteristics. Although further physiological and genetic research is needed, high plasticity in food source utilization may allow the 2 consumer species to gain energy in brackish waters where indigestible terrestrial detritus is the major source of carbon.

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