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Sand banks contribute to the production of coastal waters by making a habitat for benthic microalgae in the sublittoral zone: food web analyses in Aki-Nada using stable isotopes

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Abstract: There are many sand banks in Seto Inland Sea, making patchy shallow zones less than 10 m deep. Due to the shallow environment, the surface sediment on the sand banks in the Hojo area, in the southern part of Aki Nada, Shikoku Island, Japan, often has a larger amount of benthic microalgae than other areas. We hypothesized that benthic microalgae contributed to the secondary production of coastal waters around sand bank areas, and investigated the food-web structure of the Hojo area using stable isotopes in early summer, mid summer and fall. Mean carbon isotopic signatures of several consumers in early summer (−16.9 to −15.1‰ for polychaeta; −17.3 to 13.9‰ for brachyuran crabs; −17.2 to −15.3 for fish) and fall (−16.2 to −14.3‰ for shrimps; −14.0 to −11.2‰ for brachyuran crabs) were more enriched than that of the particulate organic materials of the surface water around sand banks (mainly phytoplankton) (−20.5±0.0‰ in early summer and −18.3±0.1‰ in fall). Organic materials attached to cobbles, representative of benthic microalgae, showed similar or more enriched signatures than consumers (−14.7±0.0‰ in early summer and −10.3±0.0‰ in fall). These results suggest that benthic microalgae on the sand bank contribute greatly to the secondary or higher production of coastal waters in Hojo area.

Key words: benthic microalgae, food web, sand bank, stable isotope

Introduction

Topographic structures in oceans can affect various aspects of marine organisms. For example, primary production via nutrient supply (Ragueneau et al. 1996; Solorzano and Grantham 1975), foraging efficiency in benthic suspension feeder (McFadden 1986), and community structure (Guichard & Bourget 1998). Topographic alteration due to human activity therefore may have a great impact on marine ecosystems.

In Seto Inland Sea, Japan, sand and gravel used to be mined intensively from bottom sand banks. The effect of sand mining on bottom topography is clearly significant (e.g. Takahashi et al. 2002), and 14% of the areas shallower than 40 m deep have been lost as a result. Many benthic organisms on and/or around the sand banks are presumably important for transporting energy fluxes from primary producers to higher trophic organisms of coastal waters. Hence, it is desirable to evaluate the ecological role of sand banks at the ecosystem level to predict future coastal ecosystem dynamics.

In Hojo area, a southern part of Aki-Nada in Seto Inland Sea, there are intact sand banks. In the surface sediment of the sand banks, there exists a great amount of benthic microalgae such as *Navicula* spp., *Diploneis* spp. and *Melosira* spp. (Fukumoto 2002). The photosynthetic rate of benthic microalgae is higher than their respiration rate even at 0.1% of the surface light intensity (Burkholder & Mandelli 1965). Thus microalgae attached on sand banks (~10 m deep) are capable of positive net production (Fukumoto 2002). If the benthic microalgae in sand banks contribute to secondary or higher production such as fish inhabiting coastal waters through grazing or detrital path, this may constitute an incentive to protect sand banks as a structure

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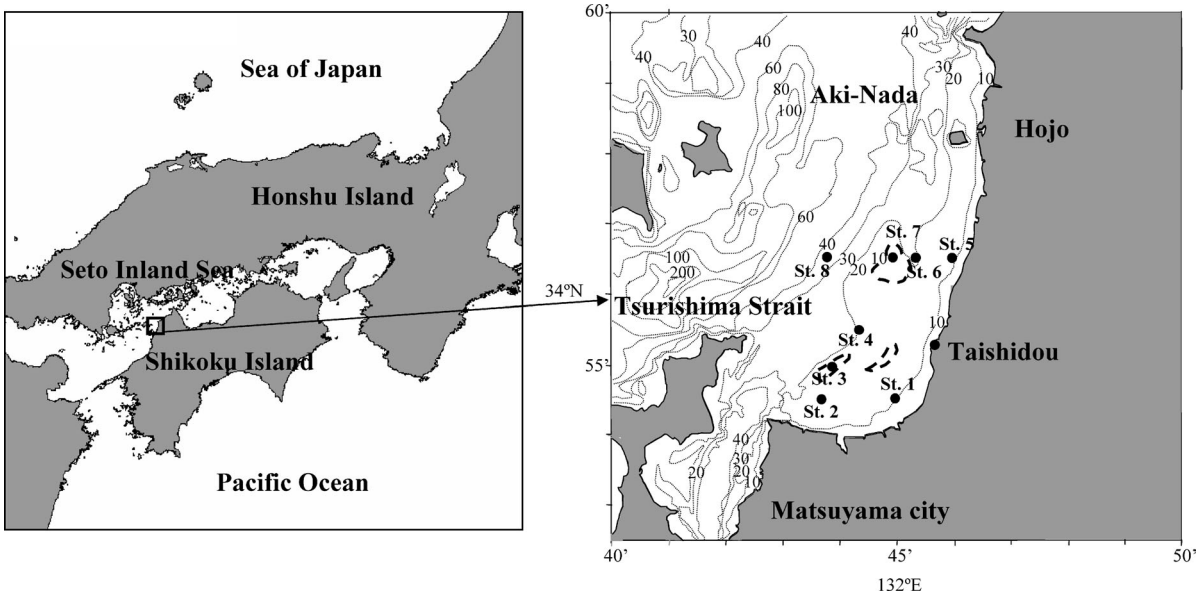

Fig. 1. The location of study area and the sampling stations in Hojo area. Dotted lines indicate water depth. Sand banks are indicated by the dashed lines (10 m deep).

sustaining production of the coastal waters in Seto Inland Sea.

In this study, we investigated the food web structure of Hojo area in Aki-Nada using carbon and nitrogen stable isotopes. The carbon isotopic signature is suitable for analyzing the derivation of energy sources in food webs, and the nitrogen isotopic signature is suitable for analyzing the trophic levels of organisms (Post 2002). Our goal is to clarify through food web analyses that the energy (carbon) source from benthic microalgae contribute to higher production around sand bank areas, and to discuss the significance of sand banks to the productivity of coastal waters.

Materials and Methods

Study site

Hojo area, Ehime Prefecture, is located in the southern part of Aki Nada, and 10 to 20 m deep shallow coastal zone and 40 m deep Tsurishima Strait in the west (Fig. 1). There are one large sand bank and two small sand banks at the point of ca 33°55′N, 132°44′E, 33°57′N, 132°44′E and 33°57′N, 132°45′E, respectively, and they make ~10 m deep patchy shallow zone (Fig. 1), which enables photosynthesis by benthic microalgae (Fukumoto 2002). The median particle diameters (Mdϕ) of sediments in Hojo area are variable and range from granules to silts (Ohira et al. 2001). Benthic communities also appear to be reflected in sediment to some extent: the lancelet *Branchiostoma belcheri* is dominant at sand banks, while there is an abundance of polychaetes, which dominated in the overall benthic community (Fukumoto 2000). We set 8 stations including two sand bank sites (Sts. 3 and 7) off Hojo (Fig. 1, Table 1) so as to collect as many benthic taxa as possible taking the particle size compositions of sediments into account. From Ohira et al. (2001), median particle diameters (Mdϕ) in the present stations are about $-2\sim0\phi$ (granules and coarse sands) for St. 7, $0\sim1\phi$ (coarse sands) for St. 3 and 6, $1\sim2\phi$ (medium sands) for Sts. 2, 4 and 5, and $2\sim4\phi$ (fine and micro sands) for St. 1, respectively.

Table 1. The location of the benthic sampling stations.

Station	Latitude (N)	Longitude (E)
1	33°54′50″	132°45′
2	33°54′50″	132°43′50″
3	33°55′00″	132°43′70″
4	33°55′50″	132°44′25″
5	33°56′50″	132°45′95″
6	33°56′50″	132°45′20″
7	33°56′50″	132°44′80″
8	33°56′50″	132°43′63″

Sample collection

Benthic invertebrates were collected using the Smith McIntyre grab (sampling scale: 22×22 cm^2) at each station in June 23, August 10 and October 21 in 2004, respectively. The sampled sediment was sieved on a 1 mm mesh, and the retained materials were brought to the laboratory, sorted and identified under a stereoscopic microscope to the species or family depending on taxa. Fish samples were collected by fishing around the sand bank area (Sts. 3 and 7) on the same day or adjacent day of the benthos collection. A 5 mm^3 cube of muscle tissue was cut off from each fish. We also sampled pelagic particulate organic materials

(POM) on the same day as fish collection by towing surface water around the sand bank using a 100 μm net for five minutes. We repeated this trial until sufficient samples were collected. The collected POM was filtered through a 250 μm mesh to remove macrozooplankton such as copepods, arrow worms and mysids. Materials passing through the mesh were further collected on precombusted (450°C for 2 h) Whatman GF/C glass-fiber filters after zooplankton visible to the naked eye were further eliminated by tweezers. To remove sea salt, we filtered the samples in 200 mL distilled water. As it is difficult to collect sufficient benthic microalgae for analyses from the sublittoral sand bank area, instead we collected organic materials (mainly microalgae) attached to pebbles or cobbles (hereafter attached organic materials, AOM) at the shore of Hojo area, Taishidou (Fig. 1) once in July 30, September 13 and November 26 in 2004. To reduce contamination by other organic materials than microalgae, we selected pebbles or cobbles with a large amount of microalgae attached and washed the surface of the algae before scraping it off with a plastic brush. Small animals visible to the naked eye (e.g. amphipods) were further eliminated with tweezers. We repeated this trial until sufficient samples were collected. On the same day macroalga *Ulva pertusa*, which was often stranded on the shore, was collected by hand. AOM samples were brought to the laboratory and collected on GF/C filters in the same way as POM. In November, we could not find stranded *U. pertusa*. All samples were preserved frozen at −30°C until analysis.

Sample preparation and analyses

For benthic invertebrates, 1 to 3 individuals were combined into one sample depending on their size. All samples were dried at 60°C in an oven for 24 h and then ground to powder. POM and AOM samples were removed from the glass filter and ground to powder. Powdered POM, AOM, and *U. pertusa* were acidified by 12 N-HCl fume in a desiccator for 24 h to remove carbonates. All animal samples were immersed in a mixed solution of methanol and chloroform (2 : 1) to remove their lipid component. In addition, brittle stars were immersed in 1 N-HCl for 24 h to remove carbonates. All samples were placed into tin capsules, and the carbon and nitrogen isotope ratios of the samples were analyzed with a mass spectrometer (ANCA-SL, PDZ Europa Inc.). Stable isotope values were denoted as δ, a measure of the amount of a heavier isotope in a sample relative to known standards, which is calculated as follows:

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

where R indicates $^{13}C/^{12}C$ or $^{15}N/^{14}N$, respectively. Standards for C and N are PeeDee belemnite and atmospheric nitrogen, respectively. Analyses for benthos were repeated 1 to 5 times per combined sample, and once per individual for fishes. POM, AOM, and *U. pertusa* were analyzed three times.

Statistical analyses

Because of isotopic fractionation, consumers of high trophic level show more enriched $\delta^{13}C$ than consumers of low trophic level, even if they assimilate the same carbon source. Assuming that the fractionation of carbon and nitrogen isotopes by assimilation is 1‰ and 3‰, respectively, we estimated the predicted $\delta^{13}C$ when the consumers depended on the POM, based on consumers' trophic levels (i.e. $\delta^{15}N$). First, we formed equation of fractionation, $\delta^{15}N = 3 \times \delta^{13}C + \text{intercept}$, from mean $\delta^{13}C$ and $\delta^{15}N$ of POM for each season. Writing the calculated intercept as I, then the predicted $\delta^{13}C$ for a consumer of a given trophic level, $*\delta^{13}C$, is

$$*\delta^{13}C = (\text{mean } \delta^{15}N \text{ of a combined sample} - I)/3$$

We evaluated the difference between $\delta^{13}C$s and their $*\delta^{13}C$s within taxa using paired t-test. The significance level was set at 1% in consideration of the variation in fractionation equation.

Results

Fig. 2 indicates the relationship between carbon and nitrogen isotopic signatures of energy sources and consumers in the three seasons (i.e. early summer, mid summer and fall), the details of which $\delta^{13}C$ and $\delta^{15}N$ were listed in Tables 2, 3 and 4, respectively. The nitrogen isotopic signatures of POM were 8 to 10‰, and those of AOM were a little higher at 10 to 12‰. The signatures of lancelets were about 10‰ in any season, and they were similar to those of POM in early (9.9‰) and mid summer (9.6‰). The mean signatures of overall polychaetes were 13 to 14‰, and glycerid and goniadid polychaetes showed high signatures (14 to 16‰) in any season. The mean signatures of overall shrimps and brachyuran crabs in each season were 12 to 13‰ and 11 to 13‰, respectively, though pinnotherid species often showed high signatures (about 16‰).

Although carbon isotopic signatures of autotrophs varied with season (POM: −22 to −19‰, ANOVA, $p<0.001$; attached algae −15 to −10‰, ANOVA, $p<0.001$), the signatures of benthic consumers were relatively constant. In early summer, the mean carbon isotopic signatures of overall polychaetes (−16.3‰) were much more enriched than the predicted signatures of POM, −19.6‰ ($t_{11}=18.99$, $p<0.0001$), while their signatures in mid-summer (−16.0‰) were close to that of POM, −16.6‰ ($t_8=3.04$, $p=0.016$). The signatures in the fall (−15.8‰) were statistically more enriched than the predicted value, −16.3‰ ($t_9=4.91$, $p<0.001$), but the signatures were close to the signatures of POM. The shrimps were fueled by POM in mid-summer (predicted: −17.0‰; actual: −16.8‰, $t_3=0.288$, $p=0.79$), but in fall by more enriched sources as well (predicted; −17.6‰, actual −14.9‰, $t_7=4.22$, $p=0.004$). Fish consumers depended on POM in mid-summer (predicted: −16.4‰; actual: −16.4‰, $t_4=0.18$, $p=0.86$),

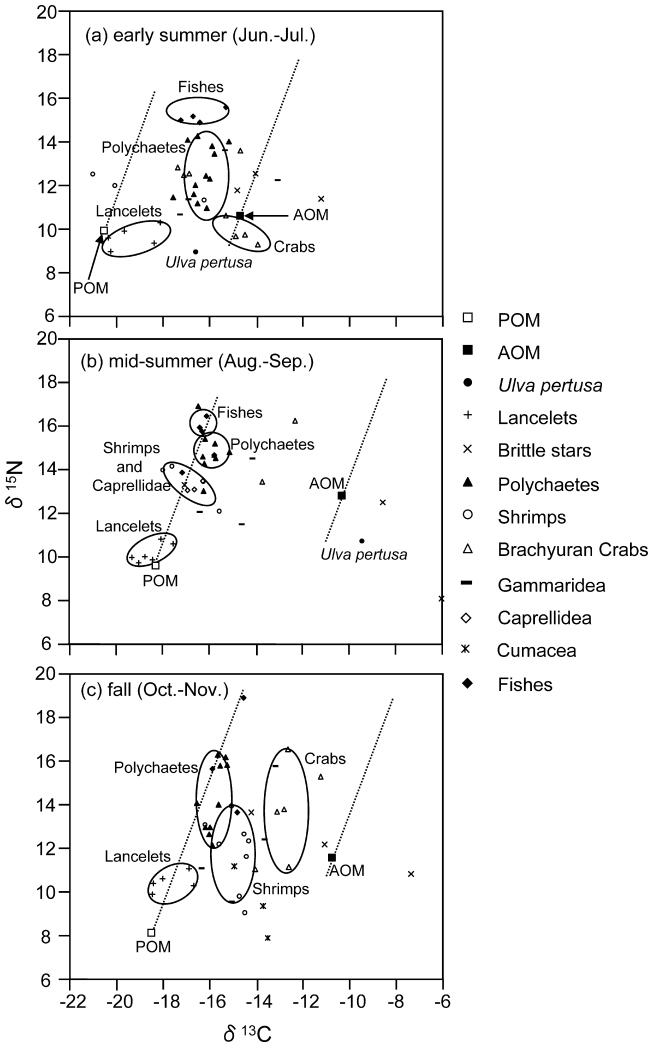

Fig. 2. $\delta^{13}C$ vs $\delta^{15}N$ plots of all samples collected in early summer (a), mid-summer (b) and fall (c) in 2003. The dashed lines indicate the rules of thumb on the carbon and nitrogen fractionation by assimilation.

but more enriched sources as well in early-summer (predicted; −18.7‰, actual −16.4‰, t_3=6.33, p=0.008). In contrast, lancelets depended on POM in any season (predicted: −20.6 to −17.7‰; actual: −19.3 to −17.7‰, all t<2.92, p>0.043) and crabs depended on more enriched sources (predicted: −20.0 to −16.6‰; actual: −15.5 to −12.7‰, all t>7.17, p<0.001; but August data were not analyzed due to small sample size). C/N ratios of autotrophs are presented in Table 4.

Discussion

The carbon signatures of POM samples showed −22 to −19‰. Takai et al. (2002) also showed that the $\delta^{13}C$s of POM from offshore surface water (0.7∼125 μm) in Hiroshima Bay, western Seto Inland Sea, range from −23 to −19‰. Although the particle size of POM samples in our data (100∼250 μm) differed from those of Takai et al. (2002), the $\delta^{13}C$s showed quite similar values. As the $\delta^{13}C$ of marine phytoplankton in middle latitude ranges from -24 to −18‰ (Fry & Sherr 1984), the signatures of our POM samples would represent mainly phytoplankton-derived organic materials.

The carbon isotopic signatures of consumers showed that several consumers changed their dependence on food sources seasonally. Most consumers depended on the POM in the surface water in mid-summer (Fig. 2b). In July and August, high concentration of phytoplankton occurs in the stratified surface water at sand bank sites (Fukumoto 2002). The high contribution of POM in mid summer would reflect benthic-pelagic coupling (reviewed in Herman et al. 1999). In early summer, on the other hand, the carbon isotopic signatures of several consumers showed the middle between POM and AOM or between POM and *U. pertusa* (Fig. 2a). A similar pattern was found in fall, though *U. pertusa* could not be collected (Fig. 2c). These results suggest that benthic microalgae and *U. pertusa* may contribute to the production of higher trophic levels in this area.

According to Atkinson & Smith (1983), C/N ratio of unicellular algae is 6 to 8, and 15 to 100 in macroalgae. In fact, the C/N ratio of POM, which was considered to consist of mainly phytoplankton, was similar to unicellular algae. The C/N ratio of *U. pertusa* in early summer showed a high value, 34.4±0.4 (Table 4). However, the C/N ratio of AOM was close to that of macroalgae rather than unicellular algae except for in the fall (Table 4). Also, as the literature suggests that carbon isotopic signatures in benthic microalgae range between −14 and −16‰ on average (Riera & Richard 1996, Herman et al. 2000, Kurata et al. 2001, Takai et al. 2002, Yokoyama & Ishihi 2003), −14 to −10‰ of AOM in this study may represent a mainly macroalgal component. However, the isotopic signatures of benthos and fishes in June, and brachyuran crabs and shrimps in the fall clearly showed that they depended on other sources than POM. In Hiroshima Bay, Takai et al. (2002) suggested that benthic micro- and macroalgae are a considerable carbon source to benthic organisms inhabiting a depth of 10~30 m. Although *U. pertusa* dominates in rocky intertidal substrates to a depth of ∼2 m from the low tide line (Chihara 1990, Arasaki & Tokuda 2002), the detrital fraction from *U. pertusa* may be assimilated by organisms of higher trophic levels through benthos in Hojo. Similarly it is highly likely that the products from benthic microalgae on the sand banks contribute to the secondary to tertiary productions, because a great amount of benthic microalgae inhabit the surface of the sand bank sediment. In fact, benthic microalgae are observed in the gut contents of many polycheate species in the Hojo area (Fukumoto 2000). Sand banks have the potential to enhance the production of coastal waters by making euphotic habitats in the subtidal zone for benthic microalgae.

Nitrogen isotopes enrich 3 to 4‰ by assimilation in general and are often used for analyzing the trophic levels of

Table 2. Details of isotope signatures of the materials collected in early summer (23-Jun and 30-Jul, 2004) in Fig. 2a (Mean±SE.).

	$\delta^{13}C$	$\delta^{15}N$	Station	Replication
Source				
POM	−20.5±0.1	9.9±0.2	–	3
AOM	−14.7±0.0	10.6±0.5	–	3
Ulva pertusa	−16.5±0.0	8.9±0.2	–	3
Zostera marina	−8.8±0.0	9.3±0.2	–	3
Lancelets				
Branchiostoma belcheri	−19.6±0.1	9.9±0.1	1	3
	−20.2±0.1	8.9±0.1	2	3
	−18.3±0.1	9.3±0.0	5	3
	−20.3±0.0	9.6±0.0	6	3
	−18.1±0.1	10.3±0.0	7	3
Brittle stars				
Ophiocoma dentata	−11.2±1.3	11.4±0.8	4	3
	−14.8±1.9	11.7±0.1	5	2
	−14.0±1.8	12.5±0.1	7	2
Polychaetes				
Glyceridae gen. spp.	−15.1±0.2	14.0±0.0	1	3
	−16.5±0.2	14.2±0.2	2	3
	−16.9±0.1	14.0±0.5	7	2
Lumbrineridae gen. spp.	−16.6±0.1	12.0±0.6	1	5
	−15.7±0.1	13.4±0.0	3	3
	−15.8±0.2	13.8±0.1	6	3
	−16.1	12.4	7	1
Scalibregmidae gen. spp.	−15.9±0.1	12.3±0.2	6	3
	−17.5±0.2	11.4±0.0	7	3
Maldanidae gen. spp.	−16.6±0.1	11.6±0.0	1	3
	−16.1±0.0	10.9±0.1	6	2
	−16.5±0.1	11.1±0.1	7	3
Shrimps				
Leptochela gracilis	−16.2±0.1	11.3±0.0	1	2
	−20.9±0.0	12.5±0.3	2	2
	−23.2±0.3	12.6±0.0	4	3
	−20.0±0.1	12.0±0.1	7	3
Brachyuran crabs				
Pinnotheridae gen. sp.	−14.6±0.1	13.6±0.0	2	2
Heteroplax nitida	−17.1±0.0	12.4±0.1	3	3
	−16.8±0.1	12.5±0.1	4	5
	−17.3	12.8	5	1
Typhlocarcinus villosus	−14.8±0.1	9.7±0.2	2	3
	−14.4±0.5	9.7±0.2	3	3
	−13.9±0.1	9.3±0.2	4	2
	−15.3±0.1	10.6±0.1	7	3
Amphipods (Gammaridea)				
Ampeliscidae gen. spp.	−17.2±0.2	10.6±0.1	6	3
Lysianassidae gen. spp.	−13.0±0.1	12.2±0.2	3	3
	−16.9	11.3	5	1
	−15.3±0.4	13.6±0.0	6	2
Fishes				
Halichoeres poecilo	−16.4±0.2	14.9±0.6	–	4
Sillago japonica	−17.2±0.5	15.0±0.8	–	2
Pseudorhombus pentophthalmus	−15.3±0.0	15.5±1.0	–	2
Parapercis sexfasciata	−16.7±0.2	15.1±0.6	–	7

Table 3. Details of isotope signaturs of the materials collected in mid summer (10-Aug and 13-Sep, 2004) in Fig. 2b (Mean±SE).

	$\delta^{13}C$	$\delta^{15}N$	Station	Replication
Source				
POM	−18.3±0.0	9.6±0.1	–	3
AOM	−10.3±0.0	12.8±0.2	–	3
Ulva pertusa	−9.4±0.0	10.7±0.1	–	3
Lancelets				
Branchiostoma belcheri	−19.3±0.0	10.0±0.4	2	3
	−18.8±0.1	10.0±0.4	3	3
	−17.6±0.0	10.6±0.2	4	3
	−18.4±0.0	9.9±0.0	5	3
	−19.0±0.0	9.8±0.2	7	3
	−18.1±0.0	10.8±0.3	8	3
Brittle stars				
Ophiocoma dentata	−6.0±0.4	8.1±1.1	4	3
	−8.5±1.5	12.5±1.4	5	3
	−17.1±0.0	13.3±0.2	7	2
Polychaetes				
Glyceridae gen. spp.	−16.5±0.1	16.9±0.4	1	2
	−16.2	14.3	2	1
Lumbrineridae gen. spp.	−15.7±0.0	14.5±0.1	1	3
Scalibregmidae gen. spp.	−16.2±0.1	13.0±0.4	7	3
Eunicidae gen. spp.	−15.1±0.1	14.8±0.3	2	3
	−16.3±0.0	14.6±0.0	6	3
Goniadidae gen. spp.	−15.8±0.1	14.7±0.3	1	3
	−15.8±0.1	15.2±0.5	4	2
	−16.2±0.1	15.4±0.3	8	3
Shrimps				
Leptochela gracilis	−17.6±0.1	14.1±0.5	5	3
	−18.0±0.0	14.0±0.3	6	3
Metapenaeopsis sp.	−16.2±0.1	13.5±0.4	2	3
Alpheidae gen. sp.	−15.6±0.0	12.1±0.1	1	3
Brachyuran crabs				
Pinnotheridae gen. sp.	−13.7±0.2	13.5±0.7	2	3
	−12.3±0.4	16.3±0.4	8	3
Amphipods				
Ampeliscidae gen. spp.	−16.4±0.0	12.0±0.1	8	3
Pontogeneiidae gen. spp.	−14.6±0.0	11.5±0.1	2	2
Lysianassidae gen. spp.	−14.1±0.0	14.5±0.0	5	2
Caprellidae gen. spp.	−16.6±0.1	13.1±0.7	2	3
	−16.9±0.0	13.1±0.2	4	3
	−16.3±0.0	13.5±0.3	6	2
Fishes				
Halichoeres poecilo	−16.1±0.2	16.5±0.3	–	6
Sillago japonica	−16.4	16.0	–	1
Pseudorhombus pentophthalmus	−15.8±0.4	14.7±2.2	–	2
Evynnis japonica	−17.2	13.9	–	1
Parapercis sexfasciata	−16.3±0.2	15.8±0.2	–	8

Table 4. Details of isotope signatures of materials collected in fall (21-Oct and 26-Nov, 2004) in Fig. 2c (Mean±SE).

	$\delta^{13}C$	$\delta^{15}N$	Station	Replication
Source				
POM	−18.4±0.1	8.1±0.1	–	3
AOM	−10.6±0.0	11.6±0.2	–	3
Lancelets				
Branchiostoma belcheri	−18.0±0.0	10.6±0.3	2	3
	−16.8±0.0	11.1±0.1	4	3
	−16.6±0.0	10.3±0.3	6	3
	−18.4±0.0	9.9±0.1	7	3
	−18.4±0.0	10.4±0.3	8	3
Brittle stars				
Ophiocoma dentata	−11.0±0.3	12.2±0.5	4	2
	−7.3±0.6	10.8±1.0	5	3
	−14.2±1.7	13.6±0.3	6	3
Polychaete				
Glyceridae gen. spp.	−15.5±0.0	15.8±0.3	2	3
	−15.3±0.0	16.1±0.2	4	3
	−15.9±0.7	13.0±1.2	6	3
	−16.5±0.0	14.1±0.2	7	3
Lumbrineridae gen. spp.	−15.6±0.0	14.0±0.1	1	3
Eunicidae gen. spp.	−16.2±0.1	13.0±0.2	5	3
Goniadidae gen. spp.	−15.6	16.3	4	1
	−15.2±0.0	15.8±0.2	8	2
Tereberidae gen. spp.	−15.8±0.1	12.1±0.1	2	3
	−16.0±0.2	12.6±0.2	8	4
Shrimps				
Leptochela gracilis	−14.7±0.0	9.8±0.1	1	3
	−16.2±0.0	13.1±0.3	2	3
	−15.5±0.0	12.2±0.1	4	3
	−15.0±0.1	13.9±0.2	5	3
	−14.4±0.1	9.1±0.9	6	3
Alpheidae gen. sp.	−14.5±0.0	12.7±0.2	4	3
	−14.3±0.2	12.3±0.2	5	3
	−14.4±0.1	11.6±0.1	6	3
Brachyuran crabs				
Pinnotheridae gen. sp.	−12.6±0.1	16.5±0.9	8	3
Heteroplax nitida	−12.5±0.1	11.2±0.1	2	3
	−12.8±0.2	13.8±0.3	3	2
	−11.2±0.1	15.3±1.6	8	2
Typhlocarcinus villosus	−14.0±0.0	11.0±0.1	1	3
	−13.1±0.1	13.7±0.9	5	3
Amphipods				
Ampeliscidae gen. spp.	−16.3±0.1	11.1±0.1	6	3
	−15.0±0.1	9.5±0.7	7	3
Lysianassidae gen. spp.	−13.6±	12.4±	5	1
	−13.1±0.1	15.7±0.0	7	2
Cumacea				
Heterocuma sarsi	−13.5±0.0	7.9±0.1	5	2
	−13.7	9.4		71
	−14.9±0.1	11.2±0.0	8	3
Fishes				
Sillago japonica	−14.8	13.6	–	1
Parapercis sexfasciata	−15.8±0.2	15.6±0.2	–	3
Pagrus major	−14.5	18.9	–	1

Table 5. C/N ratios of source organic materials in each season.

Season		Autotroph	C/N ratio (mean±SE)
Early summer	23-Jun, 2004	POM	7.8±0.2
	30-Jul, 2004	AOM	17.3±1.0
	30-Jul, 2004	*Ulva pertusa*	34.4±0.4
Mid summer	10-Aug, 2004	POM	8.3±0.0
	13-Sep, 2004	AOM	14.8±0.4
	13-Sep, 2004	*Ulva pertusa*	18.2±0.0
Fall	21-Oct, 2004	POM	7.8±0.1
	26-Nov, 2004	AOM	9.9±0.1

organisms (Post 2002). The nitrogen signatures of benthic consumers varied from 8.9 to 16.9‰, and the variation of the signatures probably reflects the difference of trophic level between benthos. In fact, Glyceridae and Goniadidae are carnivorous polychaetes (Fauchald & Jumars 1979), and their signatures (ca 14 to16‰) indicate that they are at least one trophic level higher than lancelets (about 10‰).

In this study, however, the nitrogen isotopic signatures of several benthos were often the same as or lower than those of POM and/or AOM. Lancelets and crabs in early summer (Fig. 2a) strongly showed this pattern. As bacterial decomposition decreases overall nitrogen isotopic signatures (Currin et al. 1995), these benthic organisms may selectively assimilate bacterially decomposed detritus, or bacterial protein as suggested by Little (2000). The rules of thumb may not be applicable to the consumers of low trophic levels in coastal waters where various sources of organic materials aggregate as well as estuarine ecosystems (Kurata et al. 2001).

It has been considered that the productivity of coastal waters is sustained by phytoplankton production (Mann 2001), and that benthic production is correlated with phytoplankton biomass (reviewed in Herman et al. 1999). Recent studies have shown that benthic microalgae contribute to the food sources for macrobenthos in the mangrove habitat (e.g. Bouillon et al. 2002, Guest & Connolly 2003), saltmarsh (e.g. Moncrieff & Sullivan 2001, Kurata et al. 2001) and estuarine intertidal flat (e.g. Herman et al. 2000). However, the contribution of subtidal benthic microalgae has until now remained unclear. Our study suggests that subtidal benthic microalgae sustained the fish production through food webs. In other words, considerable contribution to the production of high trophic levels can be made by the autotrophs on sand banks with unique topographic characteristics such that irradiance at the bottom is sufficient for photosynthesis by benthic microalgae. Thus, loss of sand banks can decrease the production of coastal waters, and we must draw more attention to the conservation and future rehabilitation of the unique topographic characteristics.

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