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Contribution of Pelagic and Benthic Grazing and Detritus Food Chains to the Coastal Ecosystem of the Western Seto Inland Sea: A Stable Isotope and Bayesian Mixing Model Analysis Approach

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Abstract—Food webs are a critical attribute in the material flow of ecosystems. Coastal ecosystem food webs are constructed by three major food chains, which include pelagic and benthic grazing and detritus-based food chains, the structure of which can vary depending on regional environments. The Seto Inland Sea (SIS) of Japan, which is consists of subsystem basins with high environmental heterogeneity, is one of the most vulnerable coastal ecosystems because it is relatively enclosed by islands restricted flow to the ocean. In this study, we elucidate the proportional contribution of three food chains in food web structure in the western SIS regions by using stable isotope analysis and Bayesian estimation. Contribution of the pelagic food chain was largest in the Bungo channel, which is the deepest region, with the benthic food chain contributing more in the shallow regions of Suo-nada and the Aki-nada, suggesting an effect of water depth on the food web structure. Furthermore, our result reveals a consistent large contribution by the detritus food chain to the entire coastal community member at all regions. This suggests that the detritus chain is a critical material-providing process for ecosystem maintenance or for pollutant accumulation to animals at the western SIS.

Keywords: detritus food chain, benthic grazing food chain, pelagic grazing food chain, Bayesian stable isotope mixing model, Seto Inland Sea

INTRODUCTION

Food webs consist of networks of feeding relationships between species by which

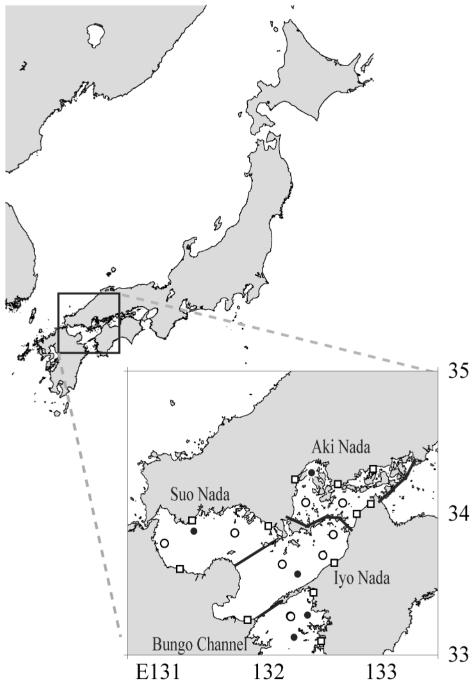

Fig. 1. Map of the western Seto Inland Sea, Japan. Sampling locations are shown as circles (black: collected both POM and detritus, white: collected only POM) and squares (collected littoral benthic microalgae).

energy and nutrients are passed through the system. Therefore, it is a necessary to elucidate food webs for understanding material and energy flow within the ecosystem (Begon *et al.*, 1999) or accumulation processes of pollutants in wild animals (Kelly *et al.*, 2007). Coastal ecosystem may have particularly complicated food web structures, because animals living in the coastal ecosystem mainly rely on three organic sources of production of pelagic phytoplankton, benthic algae, and detrital material. Aquatic food webs are fueled by primary producers, either pelagic phytoplankton or benthic algae, and also detritus which is mainly accumulated dead organic matter. To fully understand how the focal animal community is maintained by provisions of organic sources or how pollutants are accumulated in each specimen, it is important to elucidate contributions of each material source to coastal community members.

The Seto Inland Sea is a semi-enclosed coastal sea surrounded by Honshu, Shikoku and Kyushu Islands, and is a representative coastal sea of Japan (Takeoka, 2002). The sea is divided by islands and peninsulas into wide basins (“nada”) and these basins are connected by narrow channels called “seto”. This complicated geometry results in wide variations in the marine environment that may uniquely shape food web structure in each region. From some regions of the

Table 1. Geographical characteristics of each region of the western Seto Inland Sea.

Region	Area (km^2)	Mean depth (m)	Volume ($\times 10^8$ m^3)
Bungo Channel	2575	72.5	1865
Suo Nada	3100	23.7	736
Iyo Nada	3974	46.1	2136
Aki Nada	1909	26.8	522

Seto Inland Sea, the food web structure was examined by using stable isotope analyses, and it has been suggested that benthic production provides a large amount of organic matter to higher consumers such as fishes (e.g., Takai and Mishima, 2002; Okuda *et al.*, 2004; Nakashima *et al.*, 2007). However, because these studies mainly noted the contribution of benthic production to demersal fishes, we have a little knowledge about the relative contribution of each benthic or pelagic grazing and detritus food chains in each region of the SIS. The detritus food chain may have a very important role in the environmental science of marine ecosystem, particularly by exposure pathways to animals by pollutants accumulated on the sea bottom by sinking detritus, which may account for large fluxes of pollutants in marine ecosystem (Dachs *et al.*, 2002). However, there currently is little knowledge on what ecological traits of animals are affected by materials provided through detritus food chains and how sinking flux of pollutants can be re-incorporated to marine organisms.

For investigation of food web structure, stable isotope analysis is very useful, because carbon and nitrogen stable isotope ratios of consumers reflect that of their food sources, with a constant increase in isotope ratios with trophic level (Deniro and Epstein, 1978; Minagawa and Wada, 1984). Traditional stable isotope analysis using carbon and nitrogen stable isotope ratios and a mixing model approach can estimate contribution of only two sources to a focal organism when we simultaneously estimate trophic level of the focal organisms in order to consider an effect of trophic enrichment for both stable isotope ratios. However, recent analytical improvements using Bayesian techniques allows us to estimate contributions by more than two sources (Moore and Semmens, 2008). In this study, we aimed to examine the contributions of three major food chains to whole coastal ecosystems from four regions of the western SIS using the carbon and nitrogen stable isotope analysis and a Bayesian mixing model approach.

MATERIALS AND METHODS

Sample collection

We collected higher consumers which were various ecological types of pelagic to benthic animals and primary consumers to top predators and major organic sources of three food chains consisting of pelagic and benthic primary producers, and detritus from four western SIS regions of Bungo channel, Suo nada, Iyo nada and Aki nada, which vary in their geographical characteristics (Fig. 1 and Table 1). We selected two top predators of sea bass, *Lateolabrax japonicus*, and hairtail, *Trichiurus japonicus*, demersal fishes which included red seabream, *Pagrus major*, and lizard fish, *Saurida* spp., pelagic fishes which included jack mackerel, *Trachurus japonicus* or *Decapterus maruadsi*, and anchovy, *Engraulis japonicus*, and major intermediate food animals of cuttlefishes, *Sepiida* spp. and shrimps, *Penaeidae* spp. as higher consumers. These higher consumers were collected by buying specimens caught in each region from fishermen in June to July 2008, May to October 2009 and June to September 2010. We also collected representative samples of pelagic and benthic primary producers, which consisted of particulate organic matter (POM, predominantly phytoplankton) and littoral benthic microalgae, respectively, and benthic detritus at four regions of the Seto Inland Sea (Fig. 1) in June 2008, May and July 2009 and October 2010. To collect POM sample, we collected surface water (depth 1 to 3 m) offshore and filtered the water through 100 μm mesh to eliminate macro- and meso-plankton. POM samples were collected by filtering the pre-filtered surface water using Whatman GF/F grass-fiber filters (pre-combusted at 550°C for 3 h). To collect littoral benthic microalgae, we took some stones at shore and then brushed off epilithic microalgae. Detritus were obtained by taking the upper 3 cm surface of offshore sediment collected by using Smith-McIntyre grab sampler. All of the samples for stable isotope analysis were stored at –20°C until stable isotope analysis.

Stable isotope analysis

POM, littoral benthic microalgae and detritus samples were dried at 60°C and removed inorganic carbon by exposing conc. HCl vapor for POM or 0.5 N HCl for benthic microalgae and sediment for 24 h to prior to isotope measurement. Higher consumers were dissected for muscle tissue. The muscle samples were dried at 60°C then ground into fine powder and treated with 2:1 chloroform:methanol solution for 24 h to remove lipids (Bligh and Dyer, 1959). Carbon and nitrogen stable isotope ratios were measured with a continuous flow isotope ratio mass spectrometer (ANCA-SL; PDZ Europe Ltd.). Isotopic notations of carbon (δ^{13}C) and nitrogen (δ^{15}N) were expressed as per mil deviation from the standards (atmospheric N_2 gas for nitrogen and PeeDee belemnite carbonate for carbon) as defined by the following equation:

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

where R denotes ^{15}N/^{14}N or ^{13}C/^{12}C, respectively. Analytical errors of reproducibility (±1 SD) were usually ±0.3‰ for both δ^{15}N and δ^{13}C, but were ±0.6~0.8‰ for δ^{15}N of some POM or sediment samples with low nitrogen content. Some samples of POM and sediment did not have enough material to analyze stable isotope ratios and were therefore excluded from analysis.

Contributions of POM, benthic microalgae and detritus to each consumer species was estimated using Bayesian estimation for following isotope mixing

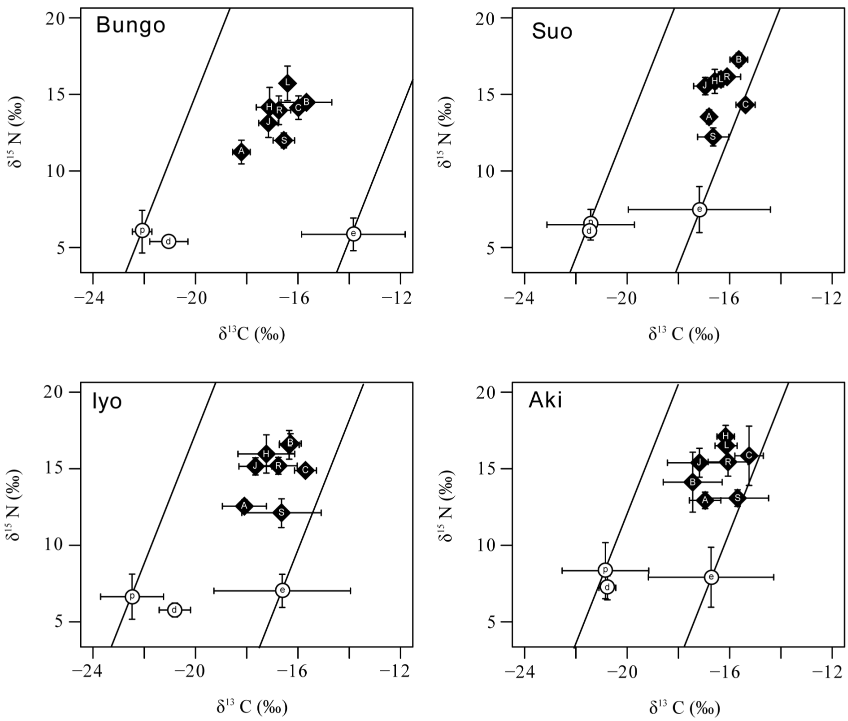

Fig. 2. Mean (±SD) of carbon and nitrogen stable isotope ratios from each sub-region in the western Seto Inland Sea. Open circles denote organic sources of food web; p: POM, d: Detritus and e: littoral benthic microalgae. Closed circles denote consumers of; A: anchovy, B: sea bass, C: cuttlefish, H: hairtail, J: jack mackerel, L: lizardfish, R: red sea bream and S: shrimp.

models (Moore and Semmens, 2008; Ward *et al.*, 2011).

$$X_j \sim N\left(\mu_j, \sigma_j\right)$$

$$\mu_j = \sum_{i=1}^{3} p_i \left(\mathrm{m}_{\mathrm{source}ij} + \mathrm{TL} \times \mathrm{m}_{\mathrm{frac}j}\right)$$

$$\sigma_j = \sqrt{\sum_{i=1}^{3} p_i^2 \left(\mathrm{s}_{\mathrm{source}ij}^2 + \mathrm{s}_{\mathrm{frac}j}^2\right)}$$

$$p_i \sim Dirichlet(\alpha_i)$$

$$\mathrm{TL} \sim U(1, 10)$$

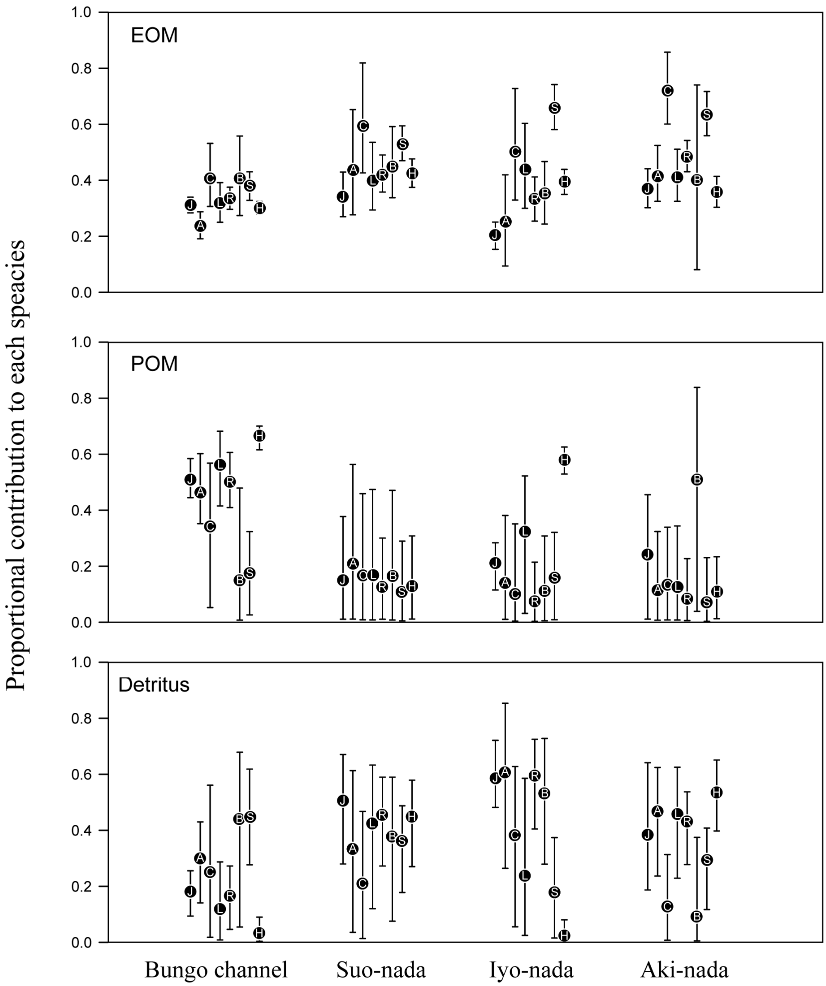

Fig. 3. Proportional contributions of benthic microalgae, POM and detritus are shown in median and 95% confidence interval of the post-probability distribution of Bayesian estimation results. Representations are same as Fig. 2.

where $m_{sourceij}$ is the mean of the jth isotope ($j = 1$ is carbon and $j = 2$ is nitrogen) of the ith source ($i = 1$ is POM, $i = 2$ is littoral benthic microalgae and $i = 3$ is detritus), m_{fracj} the mean trophic fractionation factor of the jth isotope, $s^2_{sourceij}$ the variance of the jth isotope of the ith source, s^2_{fracj} the variance of trophic fractionation factor of the jth isotope, and p_i proportional contribution of ith source to the focal animal. We adopted past reported mean and standard deviation of trophic fractionation factors of 0.91 ± 1.04‰ for carbon and 3.24 ± 0.41‰ for nitrogen stable isotope ratio (Vander Zanden and Rasmussen, 2001) in this study.

Table 2. Results of analysis of variance and post-hoc test for median of the proportional contribution of three food chains of common 8 consumers among 4 regions in the western Seto Inland Sea. In the analyses the proportional contributions were transformed by arcsin transformation.

	POM	Littoral benthic microalgae	Detritus
One-way ANOVA among regions			
	$F_{3,28} = 5.79$ $P = 0.033$	$F_{3,28} = 2.54$ $P = 0.077$	$F_{3,28} = 1.30$ $P = 0.294$
P value in Fisher's PLSD post-hoc test			
Bungo vs. Suo	0.001	0.049	0.084
Bungo vs. Iyo	0.008	0.339	0.121
Bungo vs. Aki	0.002	0.018	0.220
Suo vs. Iyo	0.453	0.287	0.847
Suo vs. Aki	0.882	0.655	0.595
Iyo vs. Aki	0.546	0.135	0.734

In this Bayesian estimation, we gave non-informative prior to p_i (i.e., $\alpha_1 = \alpha_2 = \alpha_3 = 1$ for Dirichlet distribution). To estimate the post probability distribution of each proportional source contribution, Gibbs sampling MCMC simulation was performed for each calculation using 3 parallel chains in JAGS (Plummer, 2003) with *R* (R Development Core Team, 2009). Following a burn-in phase of 10000 iterations, we sampled a million remaining iterations (retaining every 10th sample). We present the median and 95% confidence intervals of the proportional source contributions p_i from the estimated post probability distribution.

RESULTS AND DISCUSSION

The carbon and nitrogen stable isotope ratios of organic matter sources and higher consumers varied among regions and species (Fig. 2), suggesting establishment of regionally-specific unique food web structure. Based on these carbon and nitrogen stable isotope ratios, we estimated proportional source contributions of POM, littoral benthic microalgae and detritus to each consumers collected from the four western SIS regions (Fig. 3). Regional mean of the POM contribution to common 8 consumers in the Bungo channel was 0.42 (SD = 0.18) and was significantly higher than other regions (0.15 ± 0.03 at Suo-nada, 0.21 ± 0.17 at Iyo-nada and 0.17 ± 0.15 at Aki-nada; Table 2). Although there was no only a marginal non-significant difference in the regional means of contribution of benthic algae among regions (one-way ANOVA, $P = 0.077$), we can find a significant lower contribution of the benthic algae in the Bungo channel ecosystem (0.34 ± 0.06) than the Suo-nada (0.45 ± 0.08) and Aki-nada (0.47 ± 0.13; Table 2). These results indicate that the Bungo channel ecosystem at the deepest region (Table 1) in the western SIS was fueled more by contributions of the pelagic grazing food chain relative to other regional ecosystems which expressed values indicative of contributions by the benthic grazing food chain in relatively shallow regions of the Suo-nada and Aki-nada (Table 1). At least, results about food web structure in Aki-nada are consistent with the food web characteristic reported by Takai and Mishima (2002) that also revealed from stable isotopes that benthic production largely affected higher consumers in Hiroshima Bay in the Aki-nada. Furthermore, the relationship between food web structure and water depth characteristic found in our study is very reasonable because benthic organic production likely increases in more shallow regions and this material can be easily integrated into the benthic-demersal food web. Therefore, variation in food web structure appeared in our study and likely reflects the constant regional-specific traits over years.

The detritus contribution did not significantly differ among regions (Table 2). The average detritus contribution of all four regions was 0.34 ± 0.17 (Fig. 3). Furthermore, our result show that the large effect of the detritus food chain as a material source was found in not only demersal species but also in pelagic species and top predators. Although the contribution of the detritus food chain has been mainly noticed with respect to the effect for demersal and lower trophic level invertebrates (Mann, 1988), results of this study reveal that the detritus food chain played an important role in maintenance of almost of all types of consumers, which include pelagic species and top predators, in the western SIS coastal ecosystems through food web linkage. This large contribution of detritus food chain to animals living in coastal areas may have a critical meaning in the context of environmental science. The detritus component has been considered one of the large sinks of discharged pollutants (Dachs *et al.*, 2002). Thus, evidence of large and long-term or past detritus contribution to coastal animals suggests that pollutants accumulated within the detritus can largely affect present-living animals, which include not only demersal but also pelagic species, again through the detritus food chain in the coastal region. In future studies we should pay more attention to ecological and toxicological functioning of the detritus food chain for whole coastal communities.

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