Seasonal fluctuation in food sources of herbivorous gastropods in a subtropical seagrass bed estimated by stable isotope analysis

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Abstract

Various herbivorous invertebrates in seagrass beds are considered to be generalists in food use and their diets may temporally fluctuate according to the availability of food sources. We assessed whether food sources of herbivorous gastropods vary in a subtropical seagrass bed in Nagura Bay, Ishigaki Island, where coexisting seaweeds grow densely in spring but minimally in summer. Abundant gastropods and their possible food sources were collected in spring and summer of 2013 and 2015, and their stable carbon and nitrogen isotope ratios were measured. Between the two seasons, each possible food source had similar isotopic values, but all the herbivorous gastropod species in summer were more enriched in ^{13}C than the gastropod samples in spring. The mixing models in SIAR (Stable Isotope Analysis in R) showed that the total contribution rates of seaweeds, i.e. rhodophytes, phaeophytes and chlorophytes, for all herbivorous gastropod species decreased from spring to summer; in contrast, the contribution rate of seagrasses increased. Linear Mixed Models showed that the seasonal variation in $\delta^{13}C$ of the herbivorous gastropods was larger than that of the possible food sources, adding further evidence to the seasonal change in food sources of the herbivorous gastropods. This seasonal change in food use appears to correspond to the change in seaweed biomass, suggesting that herbivorous gastropods flexibly change their diets depending on food availability.

Introduction

Seagrasses are widely distributed from tropical to arctic regions (Short *et al.*, 2007) and form extensive meadows termed seagrass beds. Seagrass beds are one of the most productive systems in coastal areas (Duarte & Chiscano, 1999) and provide habitats for a wide variety of animals from small invertebrates to large vertebrates including commercially important fishes (Horinouchi & Sano, 2000; Nakamura *et al.*, 2003). In particular, small herbivorous invertebrates such as gastropods and amphipods inhabit seagrass beds in high densities. They are major prey items for crabs and fishes thus providing a trophic link between plants and carnivorous animals in seagrass beds (Duffy, 2006; Douglass *et al.*, 2008; Fukuoka & Yamada, 2015; Yamada *et al.*, 2016a).

In seagrass beds, food value for herbivorous invertebrates differs among macrophyte types. For example, seagrasses are considered to have a lower food value than seaweeds for many herbivorous invertebrates because seagrasses have tough, cellulose and lignin-defended cells (Zapata & McMillan, 1979; Unabia, 2011). Therefore, seagrasses have been considered to be rarely consumed by herbivorous invertebrates (Nienhuis & Van Ierland, 1978; Van Montfrans *et al.*, 1982; Jernakoff *et al.*, 1996). However, various invertebrates have been reported recently to feed on and assimilate seagrasses (Valentine & Heck, 1999; Kharlamenko *et al.*, 2001; Nakaoka, 2005), while there are a few invertebrates which specialize in seagrasses (Brearley & Walker, 1995; Unabia, 2011). Whether herbivorous invertebrates feed on seagrasses may relate not only to the feeding organs or digestive ability of each invertebrate species but also to the availability of each food source.

In tropical and subtropical areas, seagrass beds are formed on sandy bottoms in back reef moats as well as in reef lagoons. Seaweeds can grow inside tropical and subtropical seagrass beds (Heijs, 1985; Lewis, 1987; Davis & Fourqurean, 2001) because hard substrata such as coral rocks and coral gravel are patchily concentrated on sandy bottoms in back reef moats. Abundance of seaweeds fluctuates seasonally, usually increasing toward spring and decreasing to summer (Tsai *et al.*, 2004; Tytlyanov *et al.*, 2014). By contrast, abundances of tropical and subtropical seagrass species such as *Thalassia hemprichii* and *Cymodocea rotundata* are relatively constant throughout the year (Agawin *et al.*, 2001; Paula *et al.*, 2001). Consequently, food sources for herbivorous invertebrates are expected to vary temporally in those seagrass beds in response to seasonal fluctuations of seaweeds, which are likely to be one of the
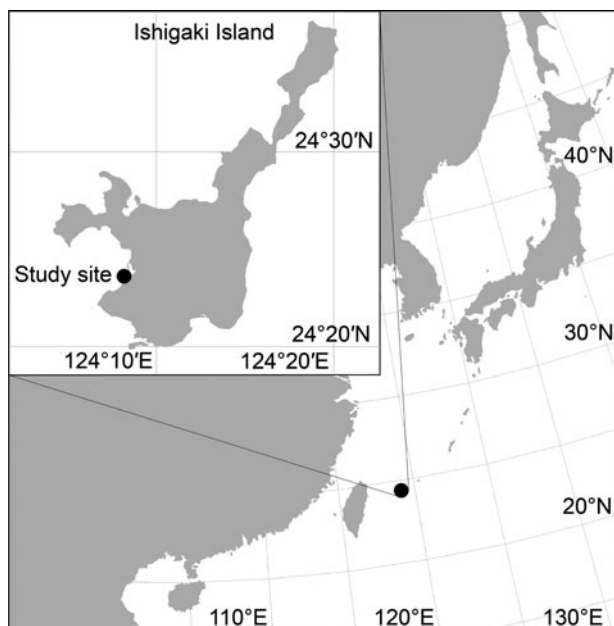
Fig. 1. The study site in Nagura Bay, Ishigaki Island, Okinawa, Japan.

main food sources for inhabiting herbivorous invertebrates (Jaschinski *et al.*, 2008; Douglass *et al.*, 2011). However, few studies have addressed temporal variations in the food sources for herbivorous invertebrates in seagrass beds.

Stable isotopes have often been used to identify the food sources of herbivorous invertebrates in seagrass beds (Jaschinski *et al.*, 2008; Douglass *et al.*, 2011; Michel *et al.*, 2015). While gut content analysis reflects the composition of ingested diets just before sampling and many gut contents in herbivorous invertebrates cannot be identified (Douglass *et al.*, 2011), stable isotopes record the composition of digested and assimilated diets into animal tissue. $\delta^{13}C$ is widely used for estimating the origin of food items used in the diet because $\delta^{13}C$ values vary among primary producers (Won *et al.*, 2007; Jaschinski *et al.*, 2008). $\delta^{15}N$ is used to estimate the trophic level of organisms because $\delta^{15}N$ values are relatively constant among primary producers and because $\delta^{15}N$ is enriched from prey to consumers (Minagawa & Wada, 1984). Using these two stable isotopes together, the relative contribution of each food source can be estimated (Jeong *et al.*, 2012; Lebreton *et al.*, 2012; Michel *et al.*, 2015).

In the present study, we examined the seasonal changes in carbon and nitrogen stable isotope ratios of dominant invertebrates and their possible food sources in Nagura Bay, Ishigaki Island, Japan in order to assess the temporal variability in food sources of the marine herbivorous invertebrates.

Materials and methods

Study site

Samplings of benthic organisms were conducted in back reef moats in Nagura Bay, Ishigaki Island, Okinawa, Japan (24° 23′18″N 124°08′17″E; Figure 1). The depth of the study site is ~0.1 m at the spring ebb tide. On sandy bottoms of the back reef moats, seagrasses, mainly *Cymodocea rotundata* and *Thalassia hemprichii*, grow all year round, and from winter to spring, small seaweeds such as *Tolypiocladia glomerulata* and *Hydroclathrus tenuis* grow on coral rocks and gravel fragments that occur on the sandy bottom. These hard substrata were abundant even inside the seagrass bed, so that seagrass-seaweed mixed beds were formed from winter to spring.

Sample collection and preparation

The samples were collected in spring (April in 2013 and 2015) and summer (July in 2013 and June in 2015). The biomass of seagrasses in April and July 2013 was 15.3 ± 7.8 gDW m^{-2} (mean ± SD) and 45.7 ± 7.2 gDW m^{-2}, respectively. The biomass of seaweeds in April and July 2013 was 17.1 ± 15.6 gDW m^{-2} and 0 gDW m^{-2}, respectively. Although water temperature in 2013 and 2015 was not measured, that in April 2014 varied from 21.5 to 27.3°C and from the second half of June to the first half of July 2014 varied from 28.7 to 33.6°C. Among invertebrates, gastropods were abundant throughout the study period so that dominant gastropods as well as dominant seagrasses and seaweeds were collected in 2013. Seagrasses and seaweeds were cut with a pair of scissors at the sheath or stem, respectively, and then collected in a net with coexistent gastropods. In addition, epibenthic gastropods were collected with sand using a scoop. No seaweeds were collected in summer of 2013 as few seaweeds were found at the study site. In addition to gastropods and macrophytes, periphyton on the seagrass *Cy. rotundata*, bottom surface sediment and surface water were collected in 2015. Bottom surface sediment was collected using a core sampler to ~1 cm depth. In summer 2015, the seaweed *To. glomerulata* was collected in small patches attached to hard substrate in the seagrass bed. All samples were immediately put into a cool box filled with seawater and seawater ice, and then transported to the Research Center for Subtropical Fisheries, Seikai National Fisheries Research Institute.

In the laboratory, attached materials on *Cy. rotundata* blades were scraped with a brush and then sieved with a 200 μm net. The filtrates were filtered again on GF/F filters, which were combusted at 450°C for at least 6 h prior to filtration, and used as the periphyton sample. Surface water through a 200 μm net were filtered on pre-combusted GF/F filters and used as the POM sample. Foot muscles of gastropods were rinsed with ultrapure water (Milli-Q; Millipore) and used as samples. Several individuals of some gastropod species, that is, *Cantharidus urbanus*, *Cerithium* sp. and *Clithon parvulum* in both years and *Euplica scripta* in spring 2013, were pooled for the measurement because individuals were too small to obtain sufficient material for the stable isotope analysis. In order to reduce any biases of $\delta^{13}C$ caused by the lipids in the samples, lipid extraction was conducted for the gastropod samples collected in 2013 according to Folch *et al.* (1957). However, lipid extraction was not conducted for the samples collected in 2015 considering the possible influence on $\delta^{15}N$ by the lipid extraction (Mateo *et al.*, 2008). Instead, the $\delta^{13}C$ values of gastropods collected in 2015 were normalized using the regression equation between the C:N ratio and $\delta^{13}C$ (Post *et al.*, 2007). This mathematical normalization for $\delta^{13}C$ has an equivalent effect to the direct lipid extraction (Post *et al.*, 2007). As lipid extraction may affect $\delta^{15}N$ values, only samples collected in 2015 were used in evaluating the trophic levels and estimating the contribution rates of food sources. POM and periphyton samples were dried and fumigated with 12 M HCl for 2 h to remove carbonate. Sieved sediment was rinsed with 1 M HCl until bubbles could not be seen. All samples were dried (60°C), homogenized and stored in a desiccator.

Stable isotope analysis

Approximately 1.5 mg of homogenized plants and about 0.5 mg of homogenized gastropods were packed into tin capsules and then combusted using a flash elemental analyser (Flash 2000, Thermo). Generated gases were sent to an isotope ratio mass spectrometer (DELTA V, Thermo) through a continuous flow interface (Conflo IV, Thermo). $\delta^{13}C$ and $\delta^{15}N$ was calculated as:

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

Table 1. Size, $\delta^{13}C$ and $\delta^{15}N$ values (mean ± SD) of possible food sources and gastropods in spring and summer 2013 and 2015

2013				Spring (10 April)				Summer (24 July)		
Taxa	Species	Size (mm)	N	$\delta^{13}C$ (‰)	$\delta^{15}N$(‰)	Size (mm)	N	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Seagrasses	Cymodocea rotundata		6	−10.4 ± 0.3	3.2 ± 1.2		6	−8.8 ± 0.7	3.0 ± 0.7
	Thalassia hemprichii		6	−8.4 ± 0.4	3.3 ± 0.9		6	−8.0 ± 0.5	2.8 ± 0.7
Rhodophytes	Tolypiocladia glomerulata		6	−16.4 ± 0.9	3.1 ± 0.3				
Phaeophytes	Cladosiphon okamuranus		6	−12.8 ± 0.4	4.0 ± 0.3				
	Hydroclathrus tenuis		6	−10.7 ± 1.3	4.4 ± 0.7				
Gastropods	Cantharidus urbanus	3.3 ± 0.7	3	−12.5 ± 0.7	5.3 ± 0.2				
	Cerithium sp.	4.2 ± 0.5	3	−12.0 ± 0.6	4.5 ± 0.1	4.5 ± 0.6	1	−8.7	5.5
	Clithon parvulum	2.7 ± 0.4	2	−12.2	5.0	3.9 ± 0.6	2	−8.5	5.6
	Euplica scripta	6.8 ± 1.9	1	−14.2	5.9	12.6 ± 0.9	6	−9.3 ± 0.5	5.9 ± 0.4
2015				Spring (8 April)				Summer (30 June)		
Taxa	Species	Size (mm)	n	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Size (mm)	n	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Seagrasses	Cymodocea rotundata		3	−9.1 ± 0.8	2.1 ± 0.9		3	−8.6 ± 0.2	3.2 ± 0.3
	Thalassia hemprichii		3	−8.2 ± 0.6	4.3 ± 0.9		3	−7.9 ± 0.2	4.5 ± 1.1
Rhodophytes	Hypnea charoides		3	−18.8 ± 0.8	3.4 ± 0.7				
	Tolypiocladia glomerulata		3	−15.3 ± 0.9	3.3 ± 0.2		3	−17.9 ± 1.5	3.7 ± 0.0
Phaeophytes	Cladosiphon okamuranus		3	−12.9 ± 0.5	3.9 ± 0.5				
	Hydroclathrus tenuis		3	−10.2 ± 1.5	3.6 ± 0.2				
Chlorophyte	Acetabularia ryukyuensis		3	−9.6 ± 0.2	3.0 ± 0.6				
Other food sources	Periphyton		6	−14.4 ± 1.1	2.0 ± 1.0		6	−14.2 ± 1.3	2.9 ± 1.1
	POM		3	−17.5 ± 0.2	2.2 ± 0.5		3	−17.8 ± 0.3	3.4 ± 0.3
	Sediment		3	−17.5 ± 4.1	3.0 ± 0.2		3	−18.2 ± 0.7	2.5 ± 0.2
Gastropods	Canarium mutabile	28.7 ± 2.4	3	−14.3 ± 0.2	4.3 ± 0.2	38.0	1	−12.7	4.2
	Cantharidus urbanus	3.2 ± 0.5	3	−13.2 ± 0.1	3.9 ± 0.1	3.6 ± 0.9	3	−9.8 ± 0.6	5.1 ± 0.3
	Cerithium sp.	4.7 ± 0.4	3	−13.6 ± 0.1	4.5 ± 0.1	5.0 ± 0.4	3	−12.3 ± 0.4	4.4 ± 0.1
	Cerithium zonatum	15.4 ± 1.1	6	−13.4 ± 0.3	4.4 ± 0.3	14.5	2	−11.8	5
	Clithon parvulum					3.4 ± 0.5	2	−10.5	3.7
	Euplica scripta	12.1 ± 1.0	6	−12.6 ± 0.5	5.0 ± 0.3	13.3 ± 0.3	3	−11.0 ± 0.6	5.1 ± 0.3
	Petalifera punctulata					21.2	2	−12.9	4.7

Size represented by shell height in gastropods except for Clithon parvulum and as shell width in Clithon parvulum. The number of analysed samples are represented by N.
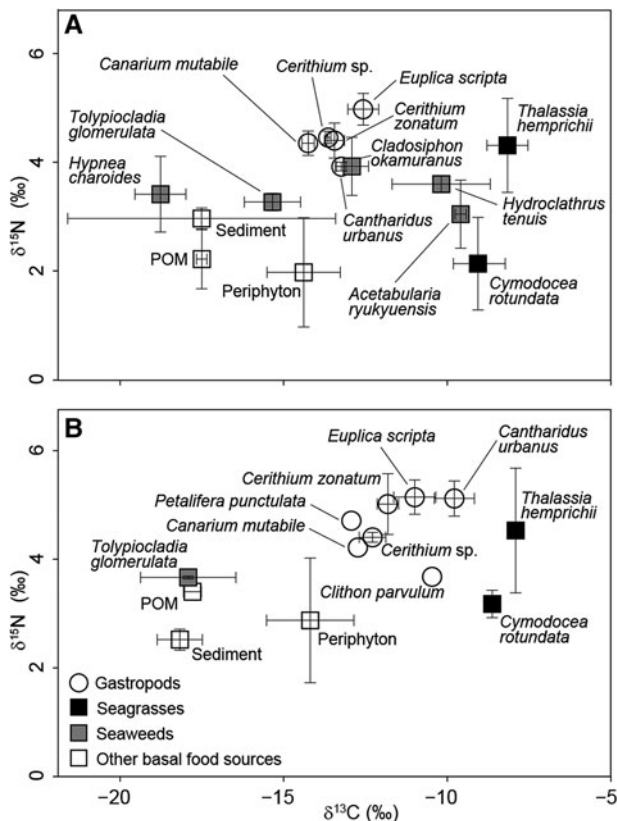
Fig. 2. Mean (± SD) δ¹³C and δ¹⁵N values of seagrasses (black squares), seaweeds (grey squares), other basal food sources (white squares) and herbivorous gastropods (white circles) collected in the seagrass bed in Nagura Bay in spring (a) and in summer (b), 2015.

where $X = {}^{13}$C or ^{15}N and $R = {}^{13}$C/^{12}C or ^{15}N/^{14}N, respectively. International standards of Pee Dee Belemnite and atmospheric N_2 were used as standards. Glycine was used as a reference material and run every 10 samples. The analytical error of δ¹³C and δ¹⁵N measured by glycine were both 0.24‰ in standard deviation.

Gastropods with δ¹⁵N values lower than the averaged δ¹⁵N value of macrophytes plus 2.4, the fractionation factor of δ¹⁵N (Mittermayr et al., 2014), were regarded as herbivores. The food sources of the herbivorous gastropods were estimated using the mixing models in siarmcmcdirichletv4 function of package SIAR (Stable Isotope Analysis in R; Parnell et al., 2010) in R version 3.3.3 (R Development Core Team, 2017). The number of possible food sources for the herbivorous gastropods was too large to estimate the contribution rates of all possible food sources. Therefore, we used isotopic values of Cy. rotundata and Th. hemprichii (seagrass), Hypnea charoides and To. glomerulata (rhodophyte), Hyd. tenuis and Cladosiphon okamuranus (phaeophyte), and Acetabularia ryukyuensis (chlorophyte) for estimating the contribution rates for herbivorous gastropods in spring. In addition, the isotopic values of periphyton were used to estimate the contribution rates for Cant. urbanus, Ce. zonatum, Ce. sp., Cl. parvulum, E. scripta and Petalifera punctulata as these gastropods were abundant on the seagrasses and seaweeds, and the isotopic values of sediment were used for Canarium mutabile as this species was abundant on the sandy bottom. In summer, seagrass, rhodophyte calculated using only To. glomerulata and periphyton (for gastropods other than Cana. mutabile) or sediment (for Cana. mutabile) were used for estimating the contribution rates because no phaeophytes or chlorophytes were found at the study site. The fractionation factors were used as 0.5 ± 0.5 for δ¹³C and 2.4 ± 1.1 for δ¹⁵N, respectively (Mittermayr et al., 2014).

Statistical analysis

The results of estimated contribution rates in SIAR in 2015 indicate that herbivorous gastropods changed their food sources from seaweeds to seagrasses in 2015. The dietary change from seaweeds to seagrasses in the same way in 2015 would result in an increase in δ¹³C values of herbivorous gastropods because δ¹³C values of seaweeds were lower than seagrasses in 2013. Therefore, we examined whether the seasonal variation of δ¹³C values of the herbivorous gastropods was larger than the seasonal variation of the basal food sources in 2013 by testing the effect of the interaction between trophic position (basal food sources vs herbivorous gastropods) and season (spring vs summer). We first constructed the LMM with δ¹³C values of the basal food sources and the herbivorous gastropods as response variables, and season, trophic position, and the interaction between season and trophic position were included as predictor variables. Then, the above model was compared with the LMM in which predictor variables include only season and trophic position. Each species was included in the random slope and intercept. Significance of the interaction between season and trophic position was determined by ANOVA using Wald chi-square test with one degree of freedom. All LMMs were analysed using lmer function in R package lme4 (Bates et al., 2015).

Results

Each basal food source had similar isotopic values between the two seasons (Table 1, Figure 2). The δ¹³C values of seagrasses, Cymodocea rotundata and Thalassia hemprichii, ranged from −7.9‰ to −10.4‰ and were higher than values of seaweeds, periphyton and sediment (Table 1). The δ¹³C values of seaweeds varied between −9.6‰ and −18.8‰, although phaeophytes and the chlorophyte were more enriched in ¹³C than rhodophytes (Table 1). The δ¹³C values of periphyton ranged from −14.2‰ to −14.4‰ and in between those of seagrasses and seaweeds (Table 1).

Seven species of gastropods, Canarium mutabile, Cantharidus urbanus, Cerithium zonatum, Ce. sp., Clithon parvulum, Euplica scripta and Petalifera punctulata, were considered as herbivores. The δ¹³C values of the herbivorous gastropods varied from −8.5‰ to −14.3‰ and differed among the gastropod species (Table 1). All the herbivorous gastropod species in summer were more enriched in ¹³C than those in spring (Table 1, Figure 3).

The mixing models in SIAR showed that the contribution rates of seagrass for all herbivorous gastropod species increased from spring to summer in 2015 (Figure 4). The mean contribution rates of seagrass in spring ranged from 12% in Ce. zonatum to 16% in E. scripta, and those in summer ranged from 32% in P. punctulata to 60% in Cant. urbanus. In contrast, those of rhodophyte slightly decreased from spring to summer although there was a large overlap in the posterior distribution. The mean contribution rates of phaeophyte in spring for herbivorous gastropods ranged from 10% in Ce. zonatum to 15% in E. scripta and Cant. urbanus. Those of chlorophyte were from 11% in Ce. zonatum to 18% in E. scripta. The contribution rates of respective food sources were also different among gastropod species (Figure 4). For example, the contribution rate of seagrass for Cant. urbanus was higher than for the other herbivores in summer although the between-species-difference was less clear in comparison to the between-season-difference. The increase of δ¹³C from spring to summer was larger in herbivorous gastropods than those of the basal food sources in 2013 according to the results of LMMs (season × trophic position, $\chi^2 = 8.15$, $P < 0.01$).
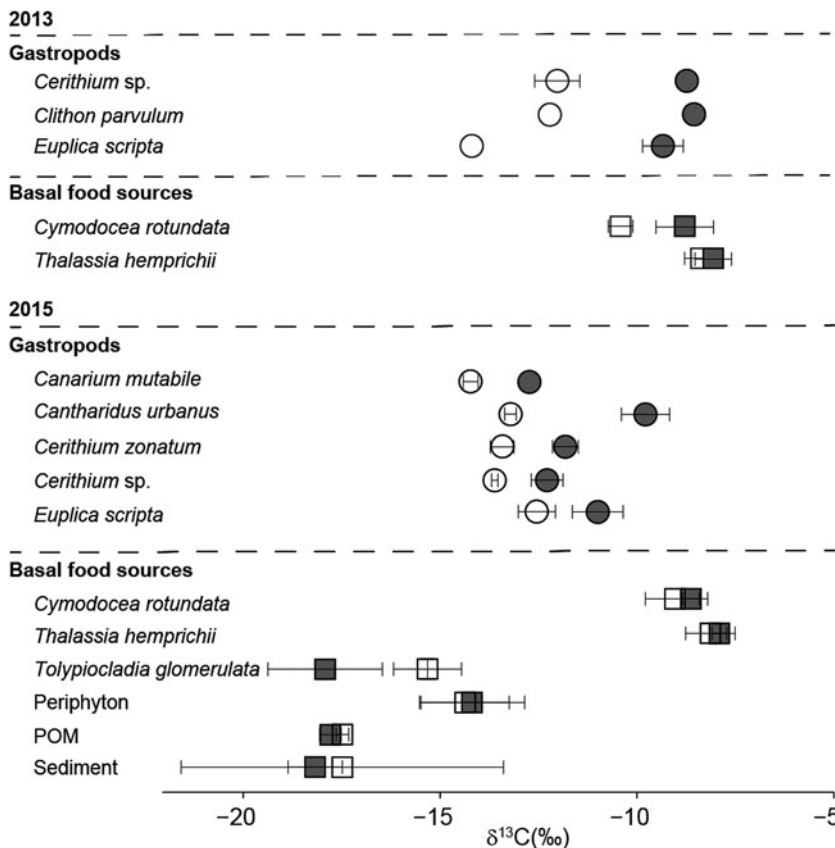
Fig. 3. Comparison of $\delta^{13}C$ values (mean ± SD) for basal food sources (squares) and herbivorous gastropods (circles) between spring (white) and summer (grey) in 2013 and 2015.

Discussion

The mixing models in SIAR showed that the total contribution rates of seaweeds, that is rhodophyte, phaeophyte and chlorophyte, for all herbivorous gastropod species decreased from spring to summer in 2015; in contrast, those of seagrasses increased (Figure 4). This was supported by the results of LMMs which showed that the seasonal variations in $\delta^{13}C$ of the herbivorous gastropods were larger than those of the basal food sources in 2013, indicating that the food sources of the herbivorous gastropods changed seasonally. Many herbivorous gastropods do not depend on any particular food source (Jaschinski *et al.*, 2008; Doropoulos *et al.*, 2009) and this ability of generalistic food use would be responsible for the temporal dietary change in the herbivorous gastropods.

There is a time lag for animal isotopic values to reflect the diet isotopic value. However, the turnover rate generally depends on the metabolic rate and growth of the organisms, and thus body mass and water temperature (McIntyre & Flecker, 2006; Thomas & Crowther, 2015). Therefore, the half-life time of the small gastropods in subtropical areas is much shorter than one season, which is 3 months (Thomas & Crowther, 2015; Vander Zanden *et al.*, 2015), and the stable isotopes of the herbivorous gastropods in this study must have reflected the isotopic values of relatively recent food sources. This supported the result of this study that the increase in isotopic values of the herbivorous gastropods from spring to summer was caused by the change in food sources.

Seasonal changes in food sources of the herbivorous gastropods corresponded with the change in food availability. In Nagura Bay, abundance of seagrasses such as *Cymodocea rotundata* and *Thalassia hemprichii* did not change much through the year. In contrast, as in the case of other areas of Indo-Pacific tropical or subtropical regions (Agawin *et al.*, 2001; Paula *et al.*, 2001; Tsai *et al.*, 2004; Titlyanov *et al.*, 2014;

Tytlyanov *et al.*, 2014), abundance of seaweeds such as *Tolypiocladia glomerulata* and *Hydroclathrus tenuis* fluctuated seasonally. As seaweeds are superior to seagrasses in food value (Nienhuis & Van Ierland, 1978; Van Montfrans *et al.*, 1982; Jernakoff *et al.*, 1996), contribution rates of seaweeds are expected to be high when the abundance of seaweeds is high, which was consistent with the results of this study.

The contribution of seagrasses as food sources for herbivorous invertebrates in seagrass beds is controversial. Although early observations led to the generalized view that seagrasses are rarely consumed by herbivorous invertebrates (Nienhuis & Van Ierland, 1978; Van Montfrans *et al.*, 1982; Jernakoff *et al.*, 1996) and some recent studies also reported minimal contribution of seagrasses (Jaschinski *et al.*, 2008; Douglass *et al.*, 2011), other studies showed that seagrasses contributed substantially to herbivorous invertebrates as food sources (Kharlamenko *et al.*, 2001; Vonk *et al.*, 2008). One cause of the difference in contribution rates of seagrasses for herbivores among the studies must be the difference in feeding organs or digestive ability of inhabiting herbivores. The present study also showed that the contribution rate of seagrass differed between the two seasons even for the same gastropod species (Figure 4). The availability of food sources other than seagrass may be another factor leading to the differences in the contribution rate of seagrasses for herbivores.

The isotopic composition differed among the herbivorous gastropod species, which suggests that the food sources were different among the gastropod species. The mean contribution rate of seagrasses for *Cantharidus urbanus* was higher than for *Cerithium zonatum* or *Cerithium* sp. In addition, the density of *Cant. urbanus* was higher on seagrasses than on seaweeds, indicating that *Cant. urbanus* is more associated with seagrasses than the other two gastropod species. However, food partitioning among the gastropod species must be carefully interpreted because there was an overlap in contribution rates due to the
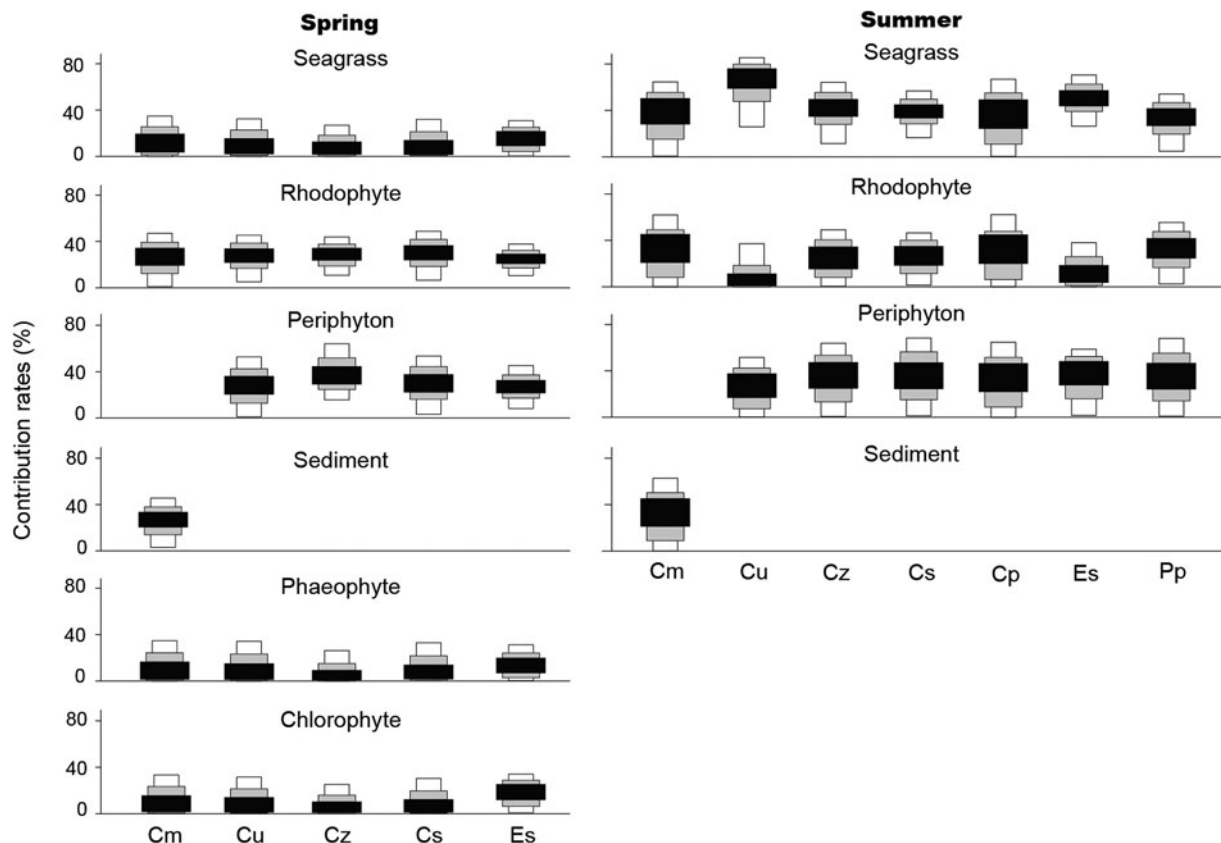
Fig. 4. Contribution rates of food sources for each herbivorous gastropod species in spring and summer of 2015. Black, grey and white boxes represent 50, 75 and 95% credibility intervals, respectively. Cm, *Canarium mutabile*; Cu, *Cantharidus urbanus*; Cz, *Cerithium zonatum*; Cs, *Ce.* sp.; Cp, *Clithon parvulum*; Es, *Euplica scripta*; Pp, *Petalifera punctulata*.

small sample size and because the isotopic composition in spring did not largely differ among the gastropod species. In order to elucidate any potential food partitioning, other analyses such as fatty acid analysis or food preference experiments should be done.

In conclusion, the results of this study indicate that food sources of herbivorous gastropods inhabiting the subtropical seagrass bed in Nagura Bay changed seasonally. This seasonal change in food use appears to correspond to the change in seaweed biomass, suggesting that the herbivorous gastropods flexibly change their diets depending on food availability. Because these herbivorous gastropods are major prey items for crabs and fishes (Duffy, 2006; Douglass *et al.*, 2008; Fukuoka & Yamada, 2015; Yamada *et al.*, 2016*a*), the origin of food materials for predators are likely to change temporally. Some herbivorous fishes such as rabbit fish prefer seaweeds to seagrasses (Pillans *et al.*, 2004; Yamada *et al.*, 2016*b*), so the food web in seagrass beds may drastically shift with the change in seaweed biomass. Our results strongly imply the importance of examining macrophyte composition in assessing the food web in seagrass beds.

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