

Article

Seasonal Dietary Shifts of the Gammarid Amphipod *Gondogeneia antarctica* in a Rapidly Warming Fjord of the West Antarctic Peninsula

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Abstract: The amphipod *Gondogeneia antarctica* is among the most abundant benthic organisms, and a key food web species along the rapidly warming West Antarctic Peninsula (WAP). However, little is known about its trophic strategy for dealing with the extreme seasonality of Antarctic marine primary production. This study, using trophic markers, for the first time investigated seasonal dietary shifts of *G. antarctica* in a WAP fjord. We analyzed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in *G. antarctica* and its potential food sources. The isotopic signatures revealed a substantial contribution of red algae to the amphipod diet and also indicated a significant contribution of benthic diatoms. The isotope results were further supported by fatty acid (FA) analysis, which showed high similarities in FA composition (64% spring–summer, 58% fall–winter) between *G. antarctica* and the red algal species. *G. antarctica* $\delta^{13}\text{C}$ showed a small shift seasonally (-18.9 to -21.4‰), suggesting that the main diets do not change much year-round. However, the relatively high $\delta^{15}\text{N}$ values as for primary consumers indicated additional dietary sources such as animal parts. Interestingly, *G. antarctica* and its potential food sources were significantly enriched with $\delta^{15}\text{N}$ during the fall–winter season, presumably through a degradation process, suggesting that *G. antarctica* consumes a substantial portion of its diets in the form of detritus. Overall, the results revealed that *G. antarctica* relies primarily on food sources derived from benthic primary producers throughout much of the year. Thus, *G. antarctica* is unlikely very affected by seasonal Antarctic primary production, and this strategy seems to have allowed them to adapt to shallow Antarctic nearshore waters.

Keywords: *Gondogeneia antarctica*; seasonal dietary shift; macroalgae; benthic diatoms; C and N stable isotopes; West Antarctic Peninsula; King George Island; Marian Cove ($62^{\circ}13' \text{S}$; $58^{\circ}47' \text{W}$)



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1. Introduction

Antarctic marine ecosystems are rapidly changing, particularly along the West Antarctic Peninsula (WAP), due to regional warming and glacier melt [1–4]. The changes are most prominent in shallow coastal waters where marine-terminating glaciers have been rapidly retreating over the last half-century [5]. Aside from the ongoing climate impacts, ice disruptions are prevalent year-round in the intertidal and shallow subtidal zones, and benthic communities end up with low abundance and low diversity [6–8].

Amphipods are one of the few benthic fauna frequently observed in highly disturbed shallow habitats. Vagile amphipods aggregate in gravel or macroalgal beds, utilizing them as shelter and/or potential food sources [9–15]. Amphipod crustaceans are among the most specious fauna, with more than 800 species in the Southern Ocean; >500 are strictly endemic to the Antarctic [16] and remarkably abundant along the Antarctic Peninsula [9,17,18].

Amphipods also show a highly diverse lifestyle associated with a variety of food sources and habitats [13,19–21].

The gammaridean amphipod *Gondogeneia antarctica* (Chevreux, 1906) is one of the most abundant species, particularly in shallow (<40 m) nearshore habitats, and is usually associated with macroalgal beds, which frequently form dense canopies in shallow waters along the WAP [9,11,22–26]. Nearshore Antarctic benthic communities rely on various food sources obtained through multiple pathways from both pelagic and benthic primary producers [27–31]. *G. antarctica* feeds primarily on benthic diatoms and macroalgae [10,13,32,33], although its gut contents indicated that it also consumes some animal parts (e.g., crustacean parts and sponge spicules) [9,10,13,34]. In turn, this species is preyed upon by various benthic invertebrates and demersal fishes, among other taxonomic groups [26,35–40]. Thus, *G. antarctica* plays an important role in shallow Antarctic marine food webs [40]. Therefore, the trophic response of *G. antarctica* to climate change and consequent constraints may be a good indication of the adaptability of this species, as well as of trophically related key organisms.

However, little is known about the trophic strategy of *G. antarctica* for dealing with the extreme seasonality in primary production of the Antarctic marine environment, and almost all feeding studies have been carried out during the summer when food availability is highest. A prerequisite to evaluate the adaptations or constraints of a key species to climate change is to understand its seasonal trophic characteristics (e.g., feeding preferences and the ability to mobilize energy during food-constrained periods). The Antarctic marine environment is characterized by small seasonal variations in seawater temperature and salinity, whereas primary phytoplankton production is extremely seasonal with explosive blooms occurring during a relatively short time in summer [41].

In this study, using trophic markers, we for the first time investigated dietary shifts in *G. antarctica* over 1 year in Marian Cove, a typical nearshore habitat for this species in the WAP. We analyzed carbon and nitrogen stable isotopes (SIs) and fatty acids (FAs) of *G. antarctica* along with its potential food sources (macroalgae, benthic diatoms, and suspended particulate organic matter (SPOM)), and examined any seasonal shifts in their trophic signatures. The findings from this study will enhance our understanding of the *G. antarctica* trophic strategy to deal with extremely seasonal food availability in its habitat and provide insight into likely future changes in the trophic relationships of nearshore benthic communities in the WAP.

2. Materials and Methods

2.1. Study Area

The King Sejong Station (62°13' S, 58°47' W) is located in Marian Cove, which is a glacial embayment (4.5 km long, ~1.5 km wide, ~130 m deep) within Maxell Bay bounded by the Weaver Peninsula and Barton Peninsula (Figure 1). Surface seawater freezes frequently in winter, although not every year, with variable cover of drifting ice throughout much of the year. Seawater temperature varies seasonally, from a maximum of ca. +1.5 °C in February to a minimum of ca. −1.8 °C in August; salinity varies much less, from 33.8 to 34.1 psu [42]. Further details of the hydrographic features and other environmental conditions of this area have been described elsewhere [43,44].

In addition to macroalgae and benthic diatom, SPOM was also selected as a potential food source, as it likely reflects organic detritus on the bottom, which are available to the amphipods in the study area. In general, SPOM, the most important form of organic particulate matter in the water column, is indicative of pelagic primary production. SPOM eventually settles to the bottom after bloom and constitutes part of sedimentary organic deposit, which is available to benthic fauna. In shallow nearshore waters, however, organic detritus settled on the bottom can be easily resuspended by tides or waves. Previous studies in this area reported that a substantial portion of SPOM in the shallow nearshore waters (<30 m) was frequently derived from benthic sources, such as benthic diatoms detached from their biotic and abiotic substrates and resuspended by wind-generated vertical mixing [60]. SPOM $\delta^{13}\text{C}$ values reported in a previous study in the same area during austral summer ($-24.1 \pm 0.2\text{‰}$, $n = 6$) [61] were even close to the benthic diatom values ($-23.3 \pm 0.3\text{‰}$ in [30]), while the reported SPOM $\delta^{13}\text{C}$ values derived from phytoplankton ranged from -28.0 to -30.4‰ [59]. Thus, findings from previous studies suggest that SPOM in shallow nearshore Antarctic waters could consist of a mixture of organic matter derived from various sources resuspended from the sea floor, and it reflect organic detritus on the bottom available to the amphipods.

2.3. Sample Collection and Processing

G. antarctica, SPOM, and macroalgae were collected between January and November 2015 from intertidal and shallow subtidal waters (<0.5 m below low tide level) adjacent to the station. To obtain the SPOM, surface seawater was collected using 2 L sterile LDPE collapsible water bottles (DAIHAN, Wonju, South Korea), and the collected water was filtered (300–500 mL for each $\delta^{13}\text{C}$ replicate and 700–1000 mL for each $\delta^{15}\text{N}$ replicate) using a vacuum pump onto pre-combusted (450 °C, 4 h) glass fiber filters (25-mm in diameter; Whatman, Florham Park, NJ, USA). The filters were immediately frozen.

Macroalgae stranded on the shore were randomly collected by hand in February, March, May, and October but not in winter (June–September), during which the shallow seabed was covered by pack ice. The collected macroalgae seemed to have been recently detached by waves and were fresh at the time of collection onshore. The collected macroalgal fronds were washed with filtered seawater. All visible encrusted fauna and flora were removed from the surface and placed into plastic bags after being cut into pieces, and then frozen. *G. antarctica* was randomly collected using a hand net (20 cm diameter, 100 μm mesh) in the shallow subtidal zone (<50 cm). The collected SPOM, macroalgae, and animals were stored at -80 °C for up to 9 months at the station and then transported to the KOPRI for analysis. Isotopic data for benthic diatoms and additional data for macroalgae were obtained from a previous study performed in this area [30].

2.4. Stable Isotope Analysis (SIA)

The macroalgae and amphipods were freeze-dried and ground with a mortar and pestle into a homogenous powder at the KOPRI. Aliquots (0.60–0.80 mg each) of the homogenized samples were used for the SIA. The amphipod samples for each sampling time included both juveniles (body length < 0.9 cm) and adults (>0.9 cm) [10]. Among them the samples with body size (0.5–1.5 cm) were pooled to ensure a sufficient amount for reliable and representative composite samples.

The samples for the organic carbon isotope analysis were rapidly acidified with two or three drops of 1 N HCl to remove inorganic carbonates, and rinsed with Milli-Q water [62]. Because acid washing can affect the nitrogen isotope ratios of organic material [63], samples for the nitrogen isotope analysis were not acidified. Lipids were removed using the chloroform/methanol procedure outlined in [64]. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses were performed with an isotopic mass spectrometer (Isoprime 100; Elementar, Manchester, UK) coupled with an elemental analyzer (Euro EA3028; EuroVector, Milan, Italy) following the procedure in [30].

The isotopic ratios were expressed in parts per thousand (‰) according to the following equation:

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

where X is ^{13}C or ^{15}N and R is the corresponding $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ ratio. The R_{standard} values for ^{13}C and ^{15}N are from V-PDB and atmospheric N_2 , respectively.

2.5. Fatty Acid (FA) Analysis in *Gondogeneia antarctica* and Red Algae

FAs were determined using a protocol slightly modified from those used in previous studies [65–67]. Aliquots (approximately 15 mg) of freeze-dried and homogenized amphipod and red algal samples were extracted with a mixture of dichloromethane: methanol (3:1, *v:v*). The extract was separated into three fractions (neutral lipids, free fatty acids (FFAs), and polar lipids) by column chromatography using an aminopropyl mini-column (Waters Sep-Pak[®] Cartridges; Waters Inc.; Milford, MA, USA). The FFA fraction was methylated with 20% BF₃ in methanol (90 °C for 1 h), and the FAs were recovered as fatty acid methyl esters (FAMES). The FAMES were analyzed by gas chromatography (Agilent 5890 Series II; Agilent Technology Inc.; Santa Clara, CA, USA) equipped with a flame ionization detector. The FAMES were identified and quantified based on retention times and a calibration curve using external standards (37 Component FAME Mix C4-C24; Supelco, Bellefonte, PA, USA). The peaks areas of each compound were integrated using ChromQuest 4.1 software, and total FA content ($\mu\text{g}\cdot\text{mg}^{-1}$) and composition (%) were determined.

2.6. Data Analysis and Statistics

Seasonal trends in the environmental parameters were analyzed by regression analysis using PASW Statistics (version 18.0; SPSS Inc.; Chicago, IL, USA). Univariate non-parametric (Kruskal-Wallis test and the Mann-Whitney *U* test) and correlation analyses were also performed using PASW. Multivariate analyses were performed using PRIMER version 6 [68]. We tested for differences in FA composition between the amphipod and red algal groups, and between the amphipod groups during different seasons using the analysis of similarity (ANOSIM). Similarities between the groups were further identified in a non-metric multi-dimensional scaling (MDS) ordination plot based on the Bray-Curtis similarity index. The relative contributions of the FAs to the similarity/dissimilarity identified in the MDS plot were analyzed using the similarity percentages program (SIMPER).

2.7. Supporting Data

Seawater temperature, as well as salinity and chlorophyll (Chl) data, were obtained from year-round monitoring at the station [69].

3. Results

3.1. Seasonal Variations in Salinity, Seawater Temperature, and Chl-*a* Concentrations

Salinity (psu) varied slightly (32.6 to 34.4), with a small decline seen during the summer months due to meltwater input (Figure 2a). In contrast, seawater temperature exhibited distinct variation (+1.97 to −1.87 °C) over the year, with the lowest monthly average occurring in September (−1.85 °C) and the highest in February (1.49 °C) (Figure 2b). The seawater was frozen (sea ice thickness up to 1.5 m, personal observation) for approximately 3 months from June 21 through October 2. During this period, the temperature was almost stable, remaining at the seawater freezing point (−1.8 °C).

Chl-*a* concentrations in the surface seawater peaked several times during summer (January–March) with the highest monthly average occurring in January ($0.64 \mu\text{g}\cdot\text{L}^{-1}$) (Figure 2c). The highest daily peak ($1.28 \mu\text{g}\cdot\text{L}^{-1}$) occurred on February 25. In addition, unusually late blooms occurred in May (monthly mean = $0.48 \mu\text{g}\cdot\text{L}^{-1}$ with several daily peaks of $\sim 1.05 \mu\text{g}\cdot\text{L}^{-1}$). Thereafter, Chl-*a* concentrations declined sharply and remained at very low levels ($<0.1 \mu\text{g}\cdot\text{L}^{-1}$) during winter (June–August), with the lowest monthly average occurring in July ($0.046 \mu\text{g}\cdot\text{L}^{-1}$). The Chl-*a* values started to increase again in early September, reaching levels similar to summer during late November ($0.64\text{--}0.67 \mu\text{g}\cdot\text{L}^{-1}$).

Overall, the variation in Chl-*a* closely followed the variation in seawater temperature ($r = 0.66, n = 66, p < 0.001$), while salinity was negatively correlated with temperature ($r = -0.67, n = 266, p < 0.001$).

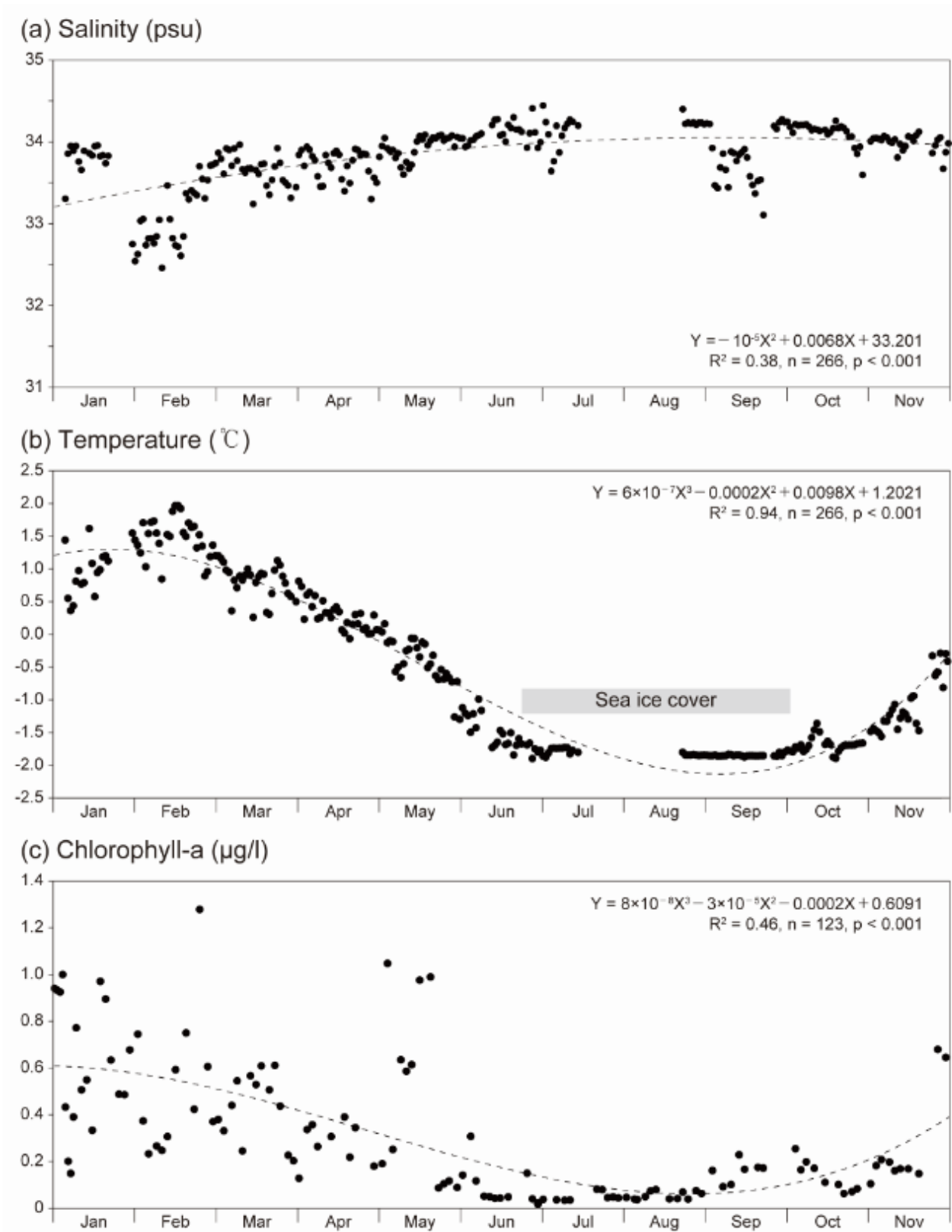


Figure 2. Seasonal variations in the surface seawater at the Marian Cove sampling site in 2015.

3.2. Seasonal Variations in the Isotopic Signatures of *Gondogeneia antarctica* and Its Potential Food Sources

Seasonal variations in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for *G. antarctica* and SPOM are displayed in Figure 3a–d. The monthly average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for *G. antarctica*, and its potential food sources during different months, are summarized in Table 1.

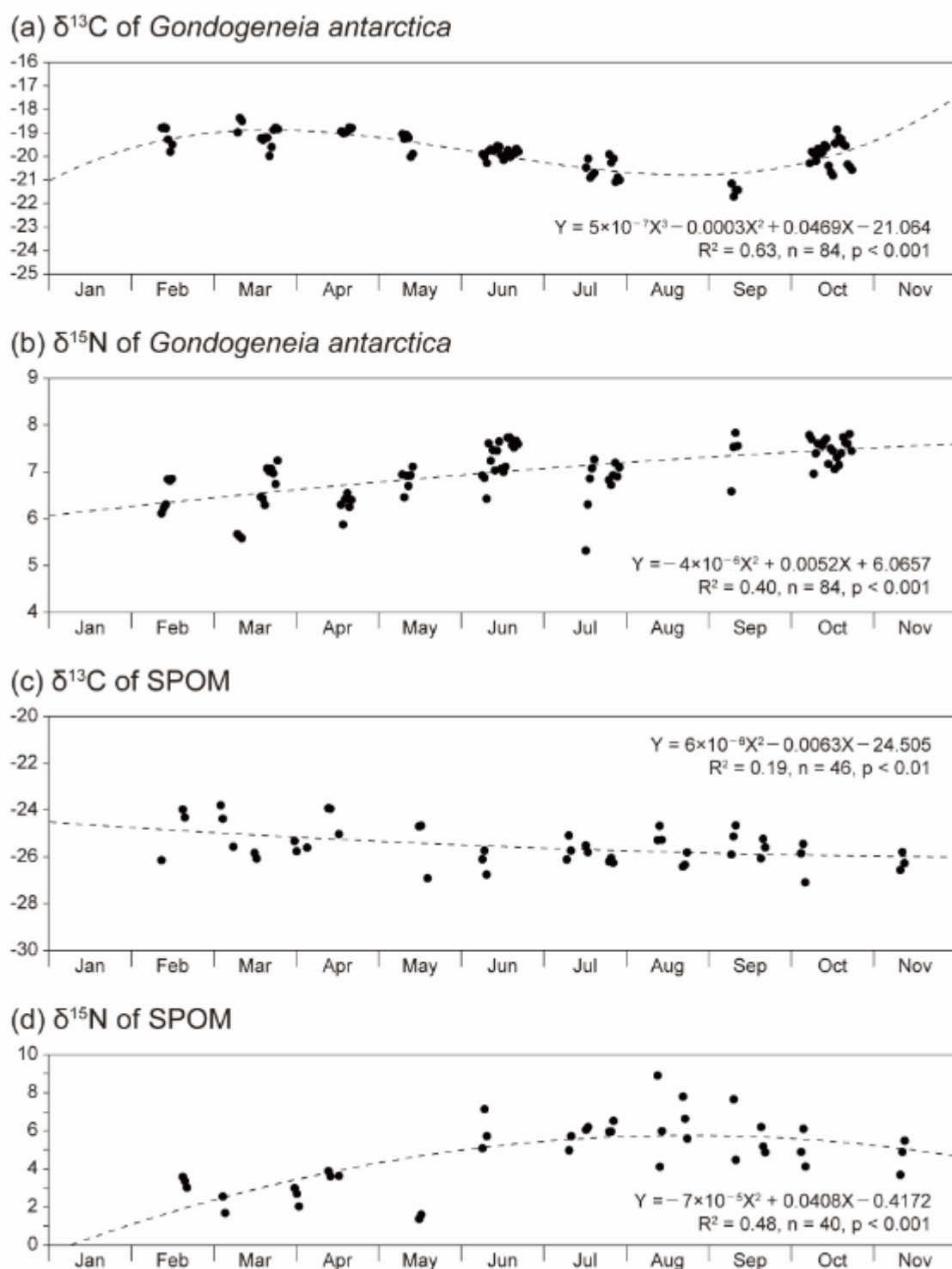


Figure 3. Seasonal variations in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for *Gondogeneia antarctica* (a,b) and suspended particulate organic matter (SPOM) (c,d) in the surface water of the sampling site in 2015.

Table 1. C and N stable isotopic ratios of the amphipod *Gondogeneia antarctica* and its potential food sources in various months. *n*, replicate numbers for the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses, except those indicated for SPOM $\delta^{15}\text{N}$ values. Numbers in parentheses for *G. antarctica* indicate the total number of individuals pooled for analysis. Mean and standard deviation (SD) values are presented. R: red algae; Br: brown algae. *n*: replicates of analysis. The data with * was cited from [30].

Specimens	Month	<i>n</i>	$\delta^{13}\text{C}$ (‰)		$\delta^{15}\text{N}$ (‰)		
			Mean	SD	Mean	SD	
<i>Gondogeneia antarctica</i>	Feb	6 (137)	−19.2	0.44	6.53	0.35	
	Mar	12 (174)	−19.1	0.45	6.52	0.61	
	Apr	6 (107)	−18.9	0.10	6.30	0.23	
	May	6 (151)	−19.4	0.42	6.85	0.23	
	Jun	18 (449)	−19.9	0.19	7.32	0.37	
	Jul	11 (94)	−20.6	0.42	6.78	0.55	
	Sep	4 (27)	−21.4	0.23	7.38	0.55	
	Oct	21 (598)	−19.9	0.53	7.49	0.24	
SPOM	Feb	3	−24.8	1.17	3.32	0.29	
	Mar	5	−25.1	0.99	2.12	0.61	
	Apr	6	−24.9	0.81	3.14	0.70	
	May	3	−25.4	1.29	1.48	0.16	(<i>n</i> = 2)
	Jun	3	−26.2	0.52	5.98	1.05	
	Jul	8	−25.8	0.40	5.91	0.48	(<i>n</i> = 7)
	Aug	6	−25.6	0.68	6.50	1.69	
	Sep	6	−25.4	0.52	5.68	1.28	(<i>n</i> = 5)
	Oct	3	−26.1	0.85	5.04	1.00	
	Nov	3	−26.2	0.39	4.69	0.91	
	Macroalgae <i>Iridaea cordata</i> (R)	Mar	2	−19.4	2.69	5.21	0.26
May		4	−23.1	2.00	5.03	0.39	
<i>Palmaria decipiens</i> (R)	May	1	−19.4		5.12		
	Oct	2	−22.3	2.65	4.18	0.06	
<i>Gigartina skottsbergii</i> (R)	Jan *	2	−23.1	0.94	3.33	0.75	
	May	1	−21.1		4.90		
	Oct	1	−23.4		3.55		
<i>Curdiea racovitzae</i> (R)	Jan *	2	−23.1	1.32	3.26	0.36	
	May	1	−17.4		5.87		
<i>Phaeurus antarcticus</i> (Br)	Jan *	2	−14.2	0.63	4.46	0.44	
	May	2	−32.0	1.22	2.78	0.06	
<i>Desmarestia</i> sp. (Br)	Oct	1	−27.3		3.45		
Benthic diatom	Jan *	3	−23.3	0.26	3.55	0.30	

The *G. antarctica* $\delta^{13}\text{C}$ values (monthly averages: max = −18.9‰ in April, min = −21.4‰ in September) were positively correlated with seawater temperature (Pearson’s correlation coefficient, $r = 0.67$, $n = 84$, $p < 0.001$) and the Chl-*a* concentration ($r = 0.62$, $n = 84$, $p < 0.001$). The overall variations were small but showed more significant enrichment (Mann–Whitney *U*-test, $p < 0.001$) during the summer–early fall period (February–April) ($-19.1 \pm 0.4\text{‰}$, $n = 24$) than during the fall–winter period (May–September) ($-20.2 \pm 0.7\text{‰}$, $n = 39$). In contrast, the *G. antarctica* $\delta^{15}\text{N}$ value (6.3‰ in April to 7.5‰ in October) was negatively correlated with seawater temperature ($r = -0.60$, $n = 84$, $p < 0.001$) and Chl-*a* concentrations ($r = -0.47$, $n = 84$, $p < 0.001$), with significant enrichment ($p < 0.001$) seen in the winter–spring period (May–October) ($7.2 \pm 0.5\text{‰}$, $n = 60$) compared to the summer–fall period (February–April) ($6.5 \pm 0.4\text{‰}$, $n = 24$).

The seasonal variation patterns in SPOM $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Figure 3c,d) were similar to those of *G. antarctica*. The SPOM $\delta^{13}\text{C}$ showed a small but significant variation over the year (monthly means = −24.8‰ to −26.2‰) and was positively correlated with seawater temperature (Pearson’s correlation coefficient (r) = 0.43, $n = 46$, $p < 0.01$) and Chl-*a* concentrations ($r = 0.36$, $n = 46$, $p < 0.05$). In contrast, the SPOM $\delta^{15}\text{N}$ values (1.5‰ to 6.5‰) were negatively correlated with seawater temperature ($r = -0.74$, $n = 40$, $p < 0.001$)

and Chl-*a* concentrations ($r = -0.78, n = 40, p < 0.001$). The SPOM $\delta^{15}\text{N}$ value showed a relatively large ($p < 0.001$) increase in the winter season (June–September) ($6.1 \pm 0.9\text{‰}$, $n = 21$) compared to the summer–fall period (February–April) ($3.0 \pm 0.7\text{‰}$, $n = 11$). The SPOM $\delta^{15}\text{N}$ value sharply declined in May, during which unusual Chl-*a* peaks occurred.

Isotopic values of macroalgae were compared only for the two contrasting seasons (May vs. January, March, and October), as sampling was impossible during the winter season (June–September), due to the formation of sea ice (pack ice, fast ice) in the sampling site. The macroalgae $\delta^{13}\text{C}$ values varied widely among species, particularly between red and brown algae. Within the red algal species, *C. racovitzae* (-15.6 to -17.4‰) was much more enriched with $\delta^{13}\text{C}$ ($p < 0.001$) than the other three species (*I. cordata* -21.3 to -22.3‰ , *P. decipiens* -19.4 to -20.5‰ , and *G. skottsbergii* -21.1 to -23.4‰). The brown algae *Desmarestia* sp. and *P. antarcticus* were most depleted with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (*Desmarestia* sp. -27.3‰ and 3.5‰ , *P. antarcticus* -32.0‰ and 2.8‰). The macroalgae $\delta^{13}\text{C}$ varied little seasonally, despite the wide variation among species. On the other hand, the macroalgae $\delta^{15}\text{N}$ values were significantly (Mann-Whitney *U*-test, $p = 0.008$) enriched in May ($5.1 \pm 0.4\text{‰}$, $n = 7$) compared to the other months (January, March, and October) ($4.0 \pm 0.8\text{‰}$, $n = 11$).

3.3. Isotopic Signatures of *Gondogeneia antarctica* and Its Potential Food Sources

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of *G. antarctica* and its potential carbon sources are displayed in a dual plot (Figure 4). The amphipod and groups of potential food sources (SPOM, red algae, brown algae, and benthic diatoms) during different months were well distinguished by their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. The monthly *G. antarctica* $\delta^{13}\text{C}$ values ranged from -18.9 to -21.4‰ , which were close to those of three red algal species (-19.4 to -23.4‰) and benthic diatom (-23.3‰). On the other hand, the SPOM (monthly means = -24.8‰ to -26.2‰) and the brown algae (*Desmarestia* sp. -27.3‰ and *P. antarcticus* -32.0‰) exhibited far more depleted $\delta^{13}\text{C}$ values.

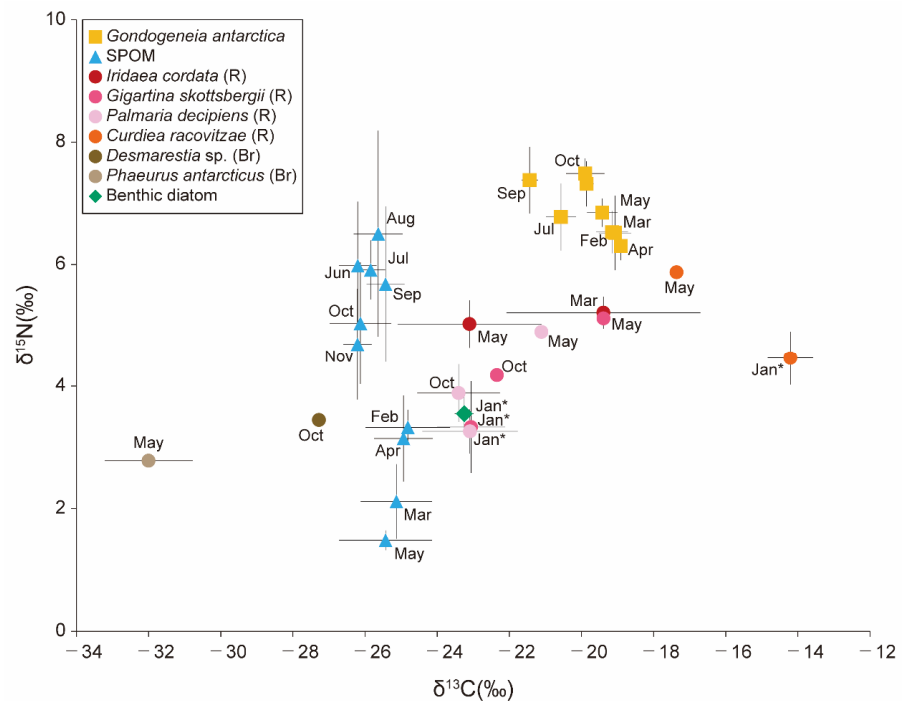


Figure 4. Seasonal variations in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of *Gondogeneia antarctica* and its potential food sources (suspended particulate organic matter, SPOM; red algae, R, and brown algae, Br). Sampling was conducted from February to November 2015. The data for benthic diatom and additional data for macroalgae (* marked) were obtained from a previous study performed in the study area [30]. Mean \pm standard deviation values are presented. Refer to Table 1 for details.

3.4. Total FA Content and Composition in *Gondogeneia antarctica* and Red Algae

The FA contents and composition of *G. antarctica* and its presumptive major diet, red algae are shown in Table 2. The most dominant FAs in the amphipod throughout the year were C16:0 (mean = 26.2% in June, 33.5% in March), followed by C20:5_(n-3) (14.6%–23.9%), C18:2_(n-6) (10.6%–15.3%), C18:1_(n-9) (7.0%–11.8%), C16:1_(n-9) (4.6%–10.3%), and C22:6_(n-3) (3.5%–5.5%).

The total FA contents in *G. antarctica* continued to increase from mid-summer (February) until reaching a peak in May ($60.5 \pm 22.1 \mu\text{g}\cdot\text{mg}^{-1}\text{dw}$, $n = 6$). The total remained at similar levels during the winter season and then declined to its lowest level in October ($23.2 \pm 7.8 \mu\text{g}\cdot\text{mg}^{-1}\text{dw}$, $n = 13$) (Figure 5a). Among the major FAs, C16:0 and C20:5_(n-3) showed relatively large variations. Of note, C20:5_(n-3) distinctly increased in the winter period in terms of both the absolute and relative composition. (Figure 5b,c). C16:0 and C18:1_(n-9), C20:5_(n-3), and C20:4_(n-6) were the major FAs in the red algae analyzed in this study. However, the FA composition varied among algal species. C16:0 and C18:1_(n-9) were most abundant in *I. cordata* and *P. decipiens*, while C16:0 and C20:5_(n-3) were detected as the most dominant in *G. skottsbergii* and *C. racovitzae*, respectively.

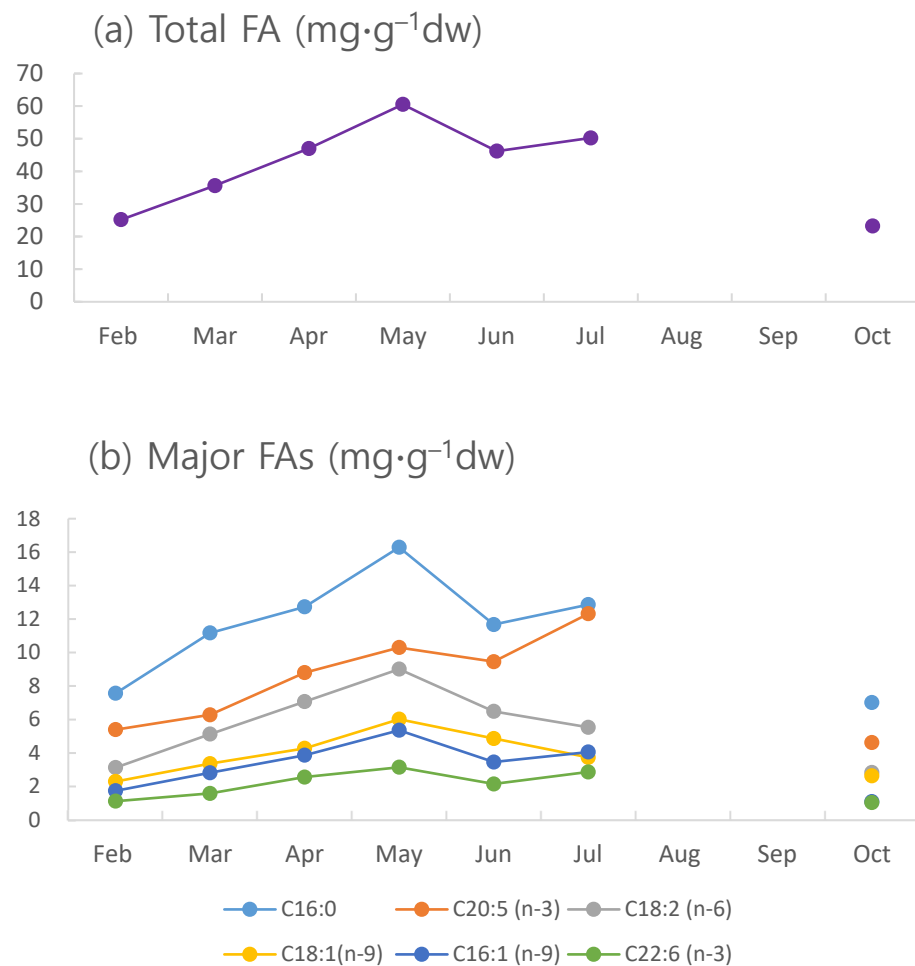


Figure 5. Cont.

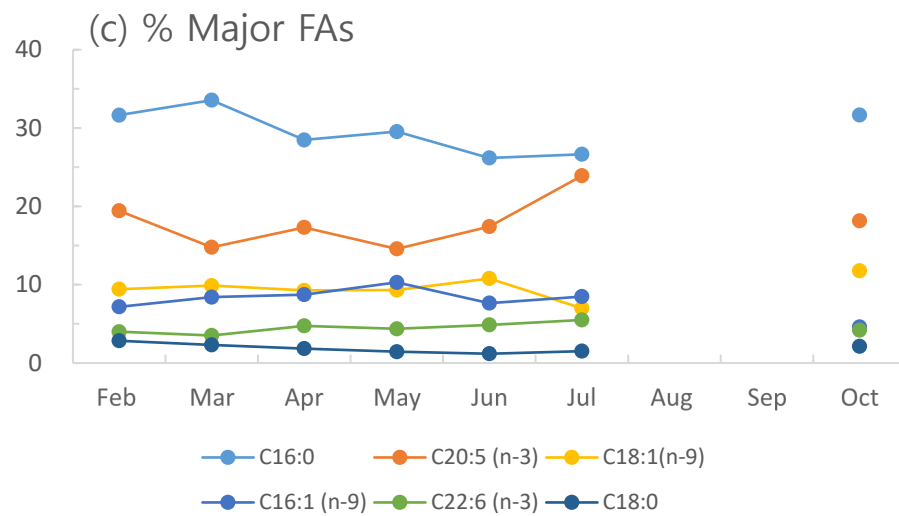


Figure 5. Seasonal variations in the *Gondogeneia antarctica* fatty acids (FAs). (a) Total contents; (b) absolute concentration of major FAs; (c) % composition of the major FAs. Mean values are presented. Refer to Table 2 for details.

Nonparametric MDS analysis (Figure 6) revealed that a small but distinct shift in *G. antarctica* FA composition occurred from spring–summer (February, October) to fall–winter (March, April, June, and July) (ANOSIM test: Global R = 0.17, $p = 0.014$). The MDS plot also showed that the spring–summer composition was closer to the red algal FA composition. The SIMPER analysis (Table 3) showed that the dissimilarity between the amphipod and red algae FA compositions decreased slightly from 42% during fall–winter to 36% during spring–summer.

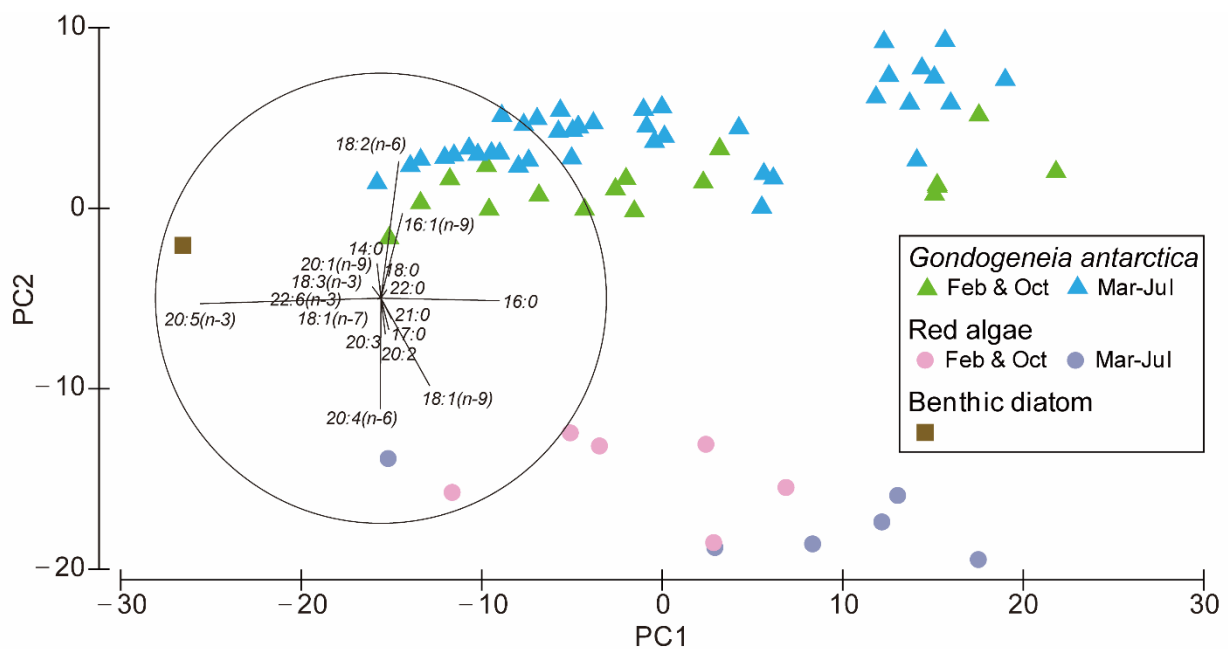


Figure 6. Non-parametric multidimensional scaling (MDS) based on the Bray–Curtis similarity matrix for the fatty acid (FA) compositions of *Gondogeneia antarctica* and red algae during the two contrasting seasons. Small but distinct differences in the FA composition were detected in *G. antarctica* between the spring–summer (February and October) and fall–winter (March–July). The FA composition of *G. antarctica* was closer to the red algal FA composition during spring–summer than early winter (March–May). Benthic diatom data are from [13].

Table 2. Total fatty acid (FA) content and % composition in *Gondogeneia antarctica* and its major diet, namely four red algal species (*Iridaea cordata*, *Palmaria decipiens*, *Curdiea racovitzae*, and *Gigartina skottsbergii*). The figures in bold indicate major FAs. FAs with mean values <0.5% are not shown in the table. (-) FA not detected. Mean and standard deviation (SD) values are presented.

	<i>Gondogeneia antarctica</i>							Red Algae			
	Feb (n = 4)	Mar (n = 3)	Apr (n = 6)	May (n = 6)	Jun (n = 22)	Jul (n = 3)	Oct (n = 13)	<i>Iridaea cordata</i> (n = 4)	<i>Palmaria decipiens</i> (n = 3)	<i>Gigartina skottsbergii</i> (n = 3)	<i>Curdiea racovitzae</i> (n = 2)
Total free FA (mg·g ⁻¹ dw)	25.2 ± 6.59	35.6 ± 14.7	47.0 ± 14.3	60.5 ± 22.1	46.2 ± 19.2	50.2 ± 12.1	23.2 ± 7.77	60.6 ± 10.5	59.9 ± 4.54	63.2 ± 1.78	46.5 ± 1.14
% of FAs											
C14:0	1.49 ± 0.21	2.85 ± 0.71	3.29 ± 0.66	4.89 ± 1.01	3.27 ± 0.73	3.2 ± 0.73	1.5 ± 0.44	-	0.22 ± 0.38	-	0.28 ± 0.4
C16:1 (n-9)	7.17 ± 1.45	8.41 ± 2.67	8.72 ± 2.29	10.3 ± 4.76	7.64 ± 1.68	8.48 ± 2.51	4.61 ± 1	0.95 ± 1.09	0.62 ± 1.07	0.24 ± 0.05	1.99 ± 2.82
C16:0	31.6 ± 8.15	33.6 ± 7.93	28.5 ± 6.07	29.5 ± 8.68	26.2 ± 4.53	26.7 ± 6.59	31.7 ± 7.3	31.8 ± 4.55	26.2 ± 2.3	42.7 ± 2.7	20.0 ± 1.7
C17:0	1.08 ± 0.25	1.03 ± 0.27	0.6 ± 0.08	0.7 ± 0.08	0.88 ± 0.23	0.67 ± 0.25	1.33 ± 0.36	4.21 ± 1.64	5.83 ± 5.05	0.56 ± 0.04	4.72 ± 4.15
C18:3 (n-3)	1.84 ± 1.02	1.45 ± 0.79	2.8 ± 1.55	3.06 ± 1.4	2.7 ± 1.25	4.07 ± 0.4	1.05 ± 0.69	1.52 ± 0.45	2.07 ± 0.45	1.21 ± 0.25	0.52 ± 0.06
C18:2 (n-6)	12.9 ± 2.05	14.9 ± 2.05	15.3 ± 3.39	14.1 ± 4.14	14.2 ± 2.25	10.6 ± 2.95	12.6 ± 2.01	2.21 ± 1.12	1.81 ± 1.16	0.81 ± 0.07	2.72 ± 1.72
C18:1(n-9)	9.42 ± 1.56	9.87 ± 1.54	9.26 ± 1.76	9.3 ± 2.97	10.8 ± 1.71	7 ± 2.97	11.8 ± 2.25	24.9 ± 3.64	21.1 ± 2.19	9.31 ± 0.7	12.5 ± 0.51
C18:1(n-7)	0.53 ± 0.3	0.47 ± 0.1	0.45 ± 0.13	1.25 ± 1.03	0.56 ± 0.3	0.25 ± 0.23	1.08 ± 2.96	1.11 ± 0.48	0.3 ± 0.51	0.22 ± 0.04	1.09 ± 1.22
C18:0	2.84 ± 0.58	2.31 ± 0.29	1.84 ± 0.29	1.44 ± 0.73	1.19 ± 0.62	1.5 ± 0.34	2.12 ± 0.7	-	0.47 ± 0.82	-	-
C20:5 (n-3)	19.4 ± 10.4	14.8 ± 10.4	17.3 ± 8.2	14.6 ± 8.57	17.4 ± 9.33	23.9 ± 3.86	18.2 ± 9.33	6.14 ± 1.52	11.8 ± 1.39	27.3 ± 3.38	27.8 ± 3.91
C20:4 (n-6)	1.05 ± 0.31	0.67 ± 0.17	0.58 ± 0.21	0.57 ± 0.18	1.27 ± 0.44	1.46 ± 0.03	1.61 ± 0.45	10.0 ± 1.46	11.5 ± 2.85	11.4 ± 1.51	14.9 ± 0.86
C20:3	0.94 ± 0.49	0.77 ± 0.39	1.29 ± 0.5	1.23 ± 0.29	1.98 ± 1.96	1.63 ± 0.08	0.92 ± 0.42	1.45 ± 0.32	4.33 ± 1.57	0.41 ± 0.03	0.46 ± 0.29
C20:2	0.6 ± 0.05	0.56 ± 0.05	0.42 ± 0.04	0.43 ± 0.04	0.64 ± 0.26	0.73 ± 0.13	0.77 ± 0.24	4.43 ± 1.35	5.56 ± 3.48	1.36 ± 0.1	3.45 ± 1.41
C20:1 (n-9)	1.3 ± 0.12	1.73 ± 0.44	2.63 ± 0.94	1.57 ± 0.98	1.68 ± 0.75	1.77 ± 0.4	1.44 ± 0.4	0.26 ± 0.08	0.77 ± 0.25	0.86 ± 0.08	1.49 ± 0.83
C21:0	-	-	-	0.05 ± 0.11	1.56 ± 3.56	-	0.16 ± 0.44	3.95 ± 3.35	0.59 ± 0.56	1.32 ± 0.13	2.53 ± 0.89
C22:6 (n-3)	3.99 ± 2.65	3.52 ± 3.47	4.74 ± 3.01	4.36 ± 2.96	4.86 ± 2.36	5.5 ± 1.37	4.19 ± 1.82	4.41 ± 1.41	4.9 ± 2.17	0.82 ± 0.07	4.08 ± 1.4
C22:0	1.78 ± 0.59	1.38 ± 0.46	0.9 ± 0.24	0.78 ± 0.53	0.8 ± 0.55	0.99 ± 0.39	1.88 ± 0.67	-	-	-	-
C23:0	0.97 ± 0.32	0.74 ± 0.25	0.49 ± 0.15	0.41 ± 0.28	0.4 ± 0.24	0.54 ± 0.21	0.97 ± 0.42	-	-	-	-
sum(%)	98.9	99.0	99.1	98.5	98.0	98.9	97.8	97.4	98.0	98.5	98.5

Table 3. Results of SIMPER analyses of dissimilarities in the fatty acid (FA) composition between groups. Average dissimilarity (%) and the most discriminant FAs are presented. Spring–summer (February and October), winter (March–July). * data for benthic diatoms are from [13].

Group	Dissimilarity (%)	Most Discriminant FAs (% Contribution)
Within <i>Gondogeneia antarctica</i> Spring-summer vs. fall-winter	21.6	20:5(25)/16:0(20)/16:1(8.3)/18:2(7.0)/18:1(6.6)/22:6(6.3)
<i>Gondogeneia antarctica</i> vs. red algae Spring-summer	35.8	18:2(16)/20:4(15)/16:0(15)/20:5(14)/18:1(15)/16:1(5.9)
Fall-winter	42.1	18:1(15)/18:2(14)/20:5(14)/20:4(13)/16:1(9.3)/16:0(7.9)
<i>Gondogeneia antarctica</i> vs. benthic diatom * Spring-summer	57.3	16:0(26)/20:5(16)/18:2(13)/18:1(12)/14:0(12)/16:1(5.8)
Fall-winter	56.4	16:0(21)/20:5(18)/18:2(15)/18:1(10)/14:0(9.6)/16:1(9.4)

The SIMPER analysis showed that the FAs contributing most to the dissimilarities in *G. antarctica* between the two contrasting seasons were C20:5_(n-3) (25%) and C16:0 (20%), followed by C16:1_(n-9) (8.3%), C18:2_(n-6) (7.0%), C18:1_(n-9) (6.6%), and C22:6_(n-3) (6.3%). Of note, C20:5_(n-3) increased to its highest value in July, in terms of both the absolute and relative compositions, while the other FAs decreased or changed slightly during the same period. The MDS plot showed that the FA composition of red algae was much closer to that of *G. antarctica* than the composition of benthic diatoms. The FA composition of benthic diatoms was distinct from *G. antarctica*.

4. Discussion

4.1. Isotopic Signatures and Seasonal Dietary Shift of *G. antarctica*

The isotopic dual plot (Figure 4) indicated a higher contribution of red algae to *G. antarctica* diet relative to the other sources investigated in the study. The *G. antarctica* $\delta^{13}\text{C}$ values (−18.9 to −21.4‰) were close to the values of the 3 red algae (*I. cordata* −21.3 to −22.3‰, *P. decipiens* −19.4 to −20.5‰, and *G. skottsbergii* −21.1 to −23.4‰) and benthic diatoms (−23.3‰), while the values were much heavier than those of SPOM (−24.8‰ to −26.2‰) and brown algae (*Desmarestia* sp. −27.3‰ and *P. antarcticus* −32.0‰). It seemed that the red algae apparently contributed most to the *G. antarctica* diet throughout the investigation period, considering a fractionation factor of 0.8‰ in consumer $\delta^{13}\text{C}$ relative to its diet [59,70]. The red algae are known to be palatable to many herbivores, detritivores and omnivores [10,34,54–56]. In particular, *P. decipiens* is the most preferred by *G. antarctica* [10,56,71], and is one of the most common macroalgae in shallow waters adjacent to this study area and other similar environments around King George Island [22,53,72]. As reflected in the isotopic signatures, benthic diatoms seemed to partially contribute to the *G. antarctica* diet, while contribution of SPOM appears to be relatively small.

The *G. antarctica* $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values varied distinctly with seasonal variations in seawater temperature, salinity, and Chl-*a* concentrations. However, the overall variation was small, indicating that the main diets of the amphipod, mainly red algae and partly benthic diatoms, did not change much throughout the year. The slight enrichment of $\delta^{13}\text{C}$ in *G. antarctica* during the summer season (February–April) was likely due to increased availability of a fresh red algal diet. Around King George Island and the adjacent islands, the highest growth rates of these algal species were attained in austral spring (October–November) (*P. decipiens*) or summer (December) (*I. cordata* and *G. skottsbergii*), when the light conditions were most favorable for photosynthetic activities [24,73–75].

The *G. antarctica* isotopic values in this study were similar to those reported for the same species and other amphipod species in the WAP region [13,59]. Like other macroalgal grazers, the *G. antarctica* $\delta^{13}\text{C}$ are heavier than the values of herbivorous suspension feeders whose diets are derived mainly from phytoplankton [76], and this is consistent with the result of this study that red algae are a primary carbon source in the *G. antarctica* diet.

Thus, the results of this study revealed that the preference of *G. antarctica* for macroalgal diet persisted throughout much of the year. However, the *G. antarctica* $\delta^{15}\text{N}$ values maintained rather high (6.3~7.5‰) as for primary consumers, suggesting that dietary contribution from other food sources (e.g., crustacean parts and sponge spicules) [9,10,13,34] should be considered in future studies.

4.2. Contribution of Detrital Matter to the *Gondogeneia antarctica* Diet during the Fall-Winter

Our results also suggest that degrading organic matter is an important food source for *G. antarctica*, particularly under subdued primary production during fall and winter. The $\delta^{15}\text{N}$ values increased significantly during the winter period in *G. antarctica* and its presumptive main diet, red algae, and also in macroalgae and SPOM (Figure 3). In particular, the SPOM $\delta^{15}\text{N}$ reached the peak values ($6.1 \pm 0.9\text{‰}$, $n = 21$) in the winter season [June–September], which were two times higher than the values in the summer-early fall period [February–April] ($3.0 \pm 0.7\text{‰}$, $n = 11$). This observation indicated that, during winter, a significant portion of the diet of *G. antarctica* is in the form of detritus, which was enriched with $\delta^{15}\text{N}$ through colonization and degradation by microbes, and sometimes also by protozoans and meiofauna [77–79].

After the growth peaks in spring-summer, macroalgal growth decrease during the fall and winter seasons around King George Island and the adjacent islands, particularly under the winter sea-ice cover, when light conditions for photosynthetic activities are unfavorable [24,73–75]. Therefore, fresh algal material is likely restricted in availability during fall-winter. *G. antarctica* is known to feed year-round [32,33], and there may be other alternative food sources for *G. antarctica* during this period. Macroalgal fragments seem to create a food bank for benthic communities in shallow Antarctic waters, as degradation processes by microbes may be slow due to low temperature [79,80]. Several studies have reported that a significant amount of carbon derived from macroalgal detritus enters the benthic food web in nearshore waters of the WAP [9,59,81–84].

Erosion and degradation of benthic macroalgae likely occur through several processes, such as mechanical abrasion by floating icebergs, tides, waves and storms, sea ice formation, and grazing [81,84]. Grazing by herbivores, such as amphipods, also promotes microbial degradation [79]. Almost all of the brown algae are unpalatable to grazers due to their chemical defenses and/or stiff texture [34,71]. However, brown algae can be palatable in detrital form [85].

Degrading macroalgal biomass seems to reach a peak in fall–early winter in King George Island, and to be consumed as a main diet by shallow-water herbivores like *G. antarctica*. In the adjacent Admiralty Bay, a large amount of decaying macroalgae were present on the shore in late April–early June, and the peak abundance and biomass of *G. antarctica* occurred during the same period [9]. In this study, we also observed a large accumulation of decaying macroalgae on the shore in April–May right before the sea water started to freeze (Figure 7). This observation supports the isotopic results; a significant portion of the diet of *G. antarctica* is in the form of detritus during the fall and winter periods. Benthic diatoms are also likely preserved as a food bank after summer blooms and utilized as alternative food sources to support benthic communities during winter [80,86]. In addition, sea ice may provide a habit for growth of epontic algae (mostly diatoms), which are grazed by herbivores like amphipods. Several studies reported that dense populations of adult and juvenile *G. antarctica* [33] and other amphipod species [32] were associated with micro-algal blooms under sea ice during mid-winter in the WAP. In the study area, the sea surface was frozen for about 3 months (late June through September) during the investigation period (Figure 2).

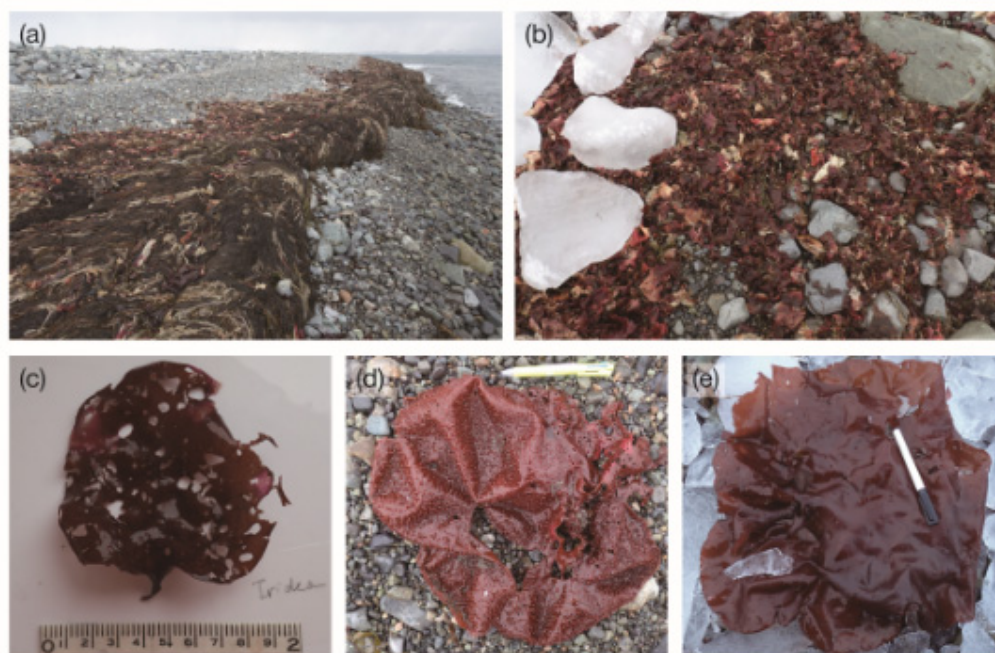


Figure 7. Macroalgal debris amassed on the shore of Marian Cove from April to early May 2015: (a) Mostly *Desmarestia* spp., (b) red algal fragments, (c) *Iridaea cordata*, (d) *Gigartina skottsbergii*, and (e) *Curdiea racovitzae*.

4.3. FA Composition in *Gondogeneia antarctica* and Its Major Food Sources

The FA results supported the isotopic results that the benthic primary producers, preferably red algae, contributed substantially to the *G. antarctica* diet throughout much of the year. The FA composition of *G. antarctica* showed small but distinct seasonal variation, particularly between the spring–summer and the fall–winter periods (Table 2, Figures 5 and 6). C20:5_(n-3) and C16:0 collectively accounted for most (45%) of the dissimilarity between the two contrasting periods (Table 3). The red algal FA composition was more similar to that of *G. antarctica* in spring–summer than winter (Figure 6, Table 3), indicating that fresh red algae were more available to the amphipod during this period.

Notably, C20:5_(n-3) in *G. antarctica* increased to its highest value in July in terms of both the absolute and relative compositions, while the other FAs decreased or changed only slightly during the same period. The increase of C20:5_(n-3) in winter may be related, in part, to the increased contribution of benthic diatoms to the *G. antarctica* diet. A previous study reported that the gut contents and FA composition of *G. antarctica* reveal an important contribution of benthic diatoms [13]. It is well known that C20:5_(n-3) occurs as a major FA in marine benthic diatoms and red algae [13,87], and has been used as a reliable dietary tracer in various marine benthic habitats from tropical to polar regions [88].

The FA composition of *G. antarctica* was similar to those of most Antarctic amphipods. Among the major FAs in *G. antarctica*, C16:0, C20:5_(n-3), C18:1_(n-9), and C22:6_(n-3) occur as major FAs in most amphipods in the peninsular region [13,89], and C16:0, C20:5_(n-3), and C18:1_(n-9) were also the major FAs in the red algae analyzed in this and other studies [13]. In particular, C20:5_(n-3) and C16:0 predominated, constituting most (41%–57%) of the FAs in this amphipod throughout the year.

Total FA content varied distinctly, with a peak seen in winter (Figure 5a). However, this pattern was unlikely to be related to variations in the diet, but rather to the reproductive cycle of *G. antarctica*, which is known to have two spawning peaks (at the end of February and at the end of September) [57]. We also observed some brooding individuals in July and early October samples, supporting the idea that reproductive development proceeded during the winter, contributing to the increase in total FA content.

4.4. Prospects for Climate Changes

The WAP is rapidly warming and deglaciating under climate change [5]. The glacial retreats are opening up new habitats for marine benthic organisms [90], and sublittoral rocky substrates are increasingly colonized by macroalgae [91], seemingly providing more food for *G. antarctica* and other herbivores. In MC, *Desmarestia* spp. and the red alga *Plocamium cartilagineum*, species unpalatable to most herbivores, have increased significantly during the last 30 years, while *P. decipiens*, a species most preferred by *G. antarctica*, has decreased [53]. In addition, a recent study indicated that climate change could alter the biochemical composition of macroalgae, but not the feeding preference of *G. antarctica* [92]. Given that only a few macroalgal species are palatable to herbivores like *G. antarctica*, the decrease in the palatable algal population could affect the survival of this species, alter food-web structures, and eventually lead to ecosystem changes.

5. Conclusions

The SI and FA results in this study revealed that *Gondogeneia antarctica* rely substantially on food sources derived from benthic primary producers, mostly red algae and their detrital forms and partly benthic diatoms. However, the relatively high $\delta^{15}\text{N}$ values in *G. antarctica*, as for primary consumers, indicated additional dietary sources such as animal parts. The isotopic signatures varied with only small shifts seen throughout the year, indicating that contribution from the main dietary sources did not change much throughout the year. The overall results suggest that *G. antarctica* is not much affected by the extreme seasonality of pelagic primary production, and this strategy seems to have allowed *G. antarctica* to adapt successfully to shallow Antarctic nearshore waters. However, ongoing climate change is altering the distribution and biochemical composition of macroalgae favored by the amphipod, which could affect its adaptation and survival.

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