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RESEARCH

Spatiotemporal comparison of fatty acid profiles of four gastropod species in aquatic fields in Korea

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Background: Gastropods as primary consumer serve the principal ecological function of transporting nutrients and energy from food sources, such as phytoplankton and periphyton, to higher trophic levels in aquatic environments. In addition to their ecological roles, freshwater gastropods have long been used by humans in Korea. Owing to biosynthesis constraints, animals must consume important components, including fatty acids, from their diet. Thus, the fatty acid composition of consumers reflects that of their diets. To determine the patterns of fatty acid accumulation in gastropods in coexisting aquatic habitats, we conducted a spatiotemporal study on the fatty acid composition of four freshwater gastropods associated to humans collected from reservoirs, rivers, and rice paddy fields in Korea.
Results: Our results showed that the four gastropod species [Chinese mystery (*Cipangopaludina chinensis malleata*), melanian (*Semisulcospira gottschei*), European ear (*Radix auricularia*), and golden apple (*Pomacea canaliculata*) snails] had differentiated fatty acid compositions according to sampling site based on the result of cluster analysis. Furthermore, principal component analysis showed that coexisting gastropods displayed intraspecific variations in fatty acid profiles, even when inhabiting same areas and were provided similar potential food sources. By comparing biomarkers, it appears that fatty acid accumulation patterns in gastropods are affected by their feeding strategies.
Conclusions: Taxonomic variations in fatty acid composition can be attributed to competition for trophic niches with limited resources, survival, feeding strategies, and metabolic requirements.

Keywords: aquatic ecosystems, coexistence, fatty acid, gastropods, primary consumer

Introduction

Primary consumers, including benthic organisms and zooplankton, perform important ecological functions by transporting nutrients and energy from phytoplankton, submerged plants, and periphyton to higher trophic levels in aquatic ecosystems (Lampert and Sommer 2007; Vadeboncoeur et al. 2002). Among the primary consumers, gastropods contribute to energy flow and nutrient cycling in benthic environments through feeding activity, excretion, surface sediment mixing, and trophic interactions with other benthos, such as amphipods and arthropods (Covich et al. 1999). In addition to their ecological roles, gastropods are utilized as human food and aquaculture feed, similar to other primary consumers such as brine shrimp or bivalves (Jeong et al. 1999; Sorgeloos et al. 2001).

Gastropoda, the largest group in the phylum Mollusca, has approximately 78,000 valid described species. They live in diverse environments including freshwater (~4,000 species), terrestrial (~24,000 species), and marine (~50,000 species) habitats, globally (Strong et al. 2008). In Korea, the National Institute of Biological Resources of the Ministry of Environment has classified 1,363 gastropod species living in those of ecosystems on the National Species List of Korea (2023). Gastropods, particularly freshwater snails, have been connected to human life in Korea for a long time. Some freshwater snail species, such as the Chinese mystery (*Cipangopaludina chinensis malleata*) and melanian (e.g., *Semisulcospira gottschei*) snails, which live in rivers, reservoirs, and rice paddy fields, have traditionally been used as food resources, as have marine species (Jeong et al. 1999; Lim et al. 2009; Oh et al. 2006). The effectiveness of these snails was also described in an old Korean medical encyclopedia known as the “Donguibogam” by

Heo (1613). Recently, they were explored for investigated biological activities such as antioxidant and antibacterial properties from melanian snail extract in medical applications (Kim et al. 2009; Nam et al. 2021). An exotic species, the golden apple snail (*Pomacea canaliculata*) was introduced into Korea for weed control in organic rice farming and was also tested for use in human food and feed products (Bae et al. 2012; Ghosh et al. 2017). On the contrary, lymnaeid snails such as the European ear snail (*Radix auricularia*), which is often found in freshwater lakes, ponds, and rivers of Korea, serve as intermediate vectors for a wide variety of parasites, particularly trematodes that are harmful to humans through food chains (Chai and Lee 2002).

Gastropods utilization for food and medicinal resources is linked to the make-up of crucial components in the body, which is connected to feeding characteristics and accumulation patterns. Owing to their constraints on locomotion using their ventral feet, gastropods have a narrow range of habitats. They compete with other benthos for nutrients, including essential metabolic components such as fatty acids (FAs) and amino acids, which are transported to higher consumers, including humans, within their limited habitats. Animals, including gastropods, have restricted biological synthesis pathways for essential compounds such as FAs (Müller-Navarra 2008). The conversion rates from C18 ω3-polyunsaturated FAs (PUFAs) to highly unsaturated FAs (HUFAs) are poor, and therefore, animals are unable to synthesize ω3 PUFAs (Cook and McMaster 2002). Thus, consumers obtain the required FAs from their diets and their FA profiles mirror those of their diets (Brett et al. 2006; Galloway and Budge 2020).

The trophic interactions among these gastropods must be understood in terms of their ecological significance as primary consumers and human food sources. FA variation in gastropods is largely unknown in terms of its ecological aspects in natural aquatic fields in Korea, despite studies on their edible food items (Moon et al. 2015; Surh et al. 2003). To better understand the FA accumulation patterns of gastropods commonly found in Korean aquatic fields, we examined the spatiotemporal variation in FA in four gastropod species, namely *C. chinensis malleata*, *S. gottschei*, *R. auricularia*, and *P. canaliculata*, collected from freshwater environments, such as reservoirs, rivers, and rice paddy fields.

Materials and Methods

Collection of samples

Four gastropod species, the Chinese mystery (*C. chinensis malleata*), melanian (*S. gottschei*), European ear (*R. auricularia*), and golden apple (*P. canaliculata*) snails, were collected at five sites of Korean aquatic fields, including a reservoir (Site B), a river (Site D), and rice paddy fields (Sites A, C, and E) in 2011 and 2012 (Fig. 1). In the rice paddy fields, we surveyed two distinct farming fields at Site C, unlike at Sites A and E. Eighteen Chinese mystery snails were collected from the reservoir (Site B) and rice paddy fields (Sites A, C, and E) in 2011 and 2012 (Table 1). Seven

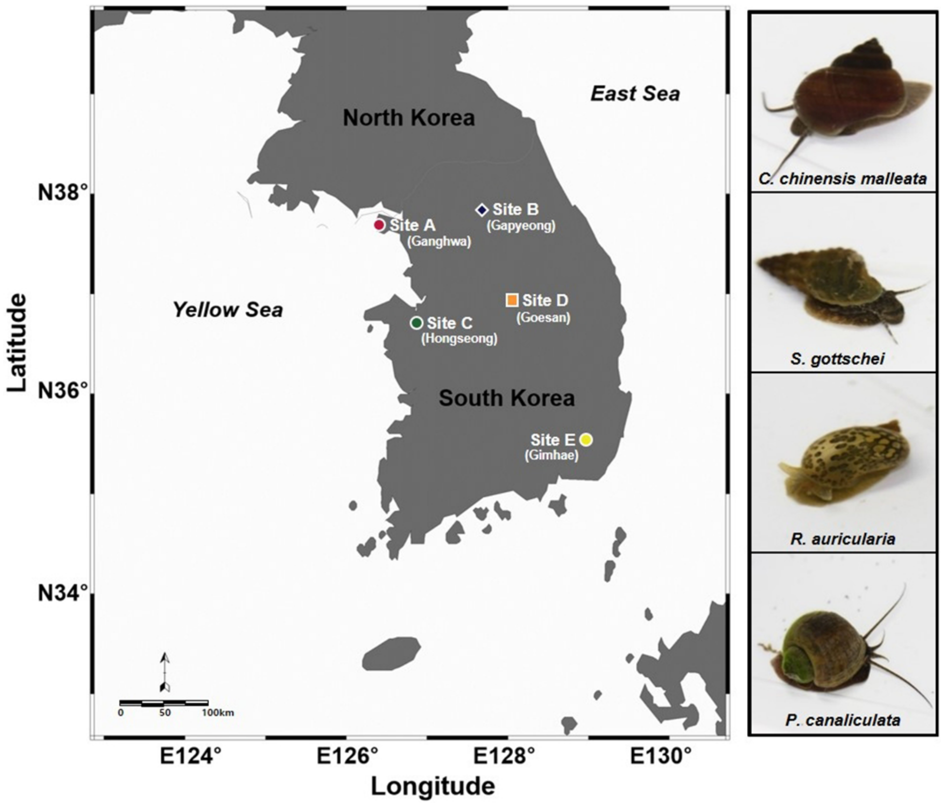

Fig. 1 Sampling sites and images of collected gastropods in this study. The symbols denote type of sampling sites; circle: rice paddy field, diamond: reservoir, and square: river.

Table 1 Overview of the sample data for four gastropods in the present study

Species (scientific name/common name)	Sampling sites	Regions	Field types	Sampling period	*n*
Cipangopaludina chinensis malleata/Chinese mystery snail	A	Songhae-myeon, Ganghwa-gun, Incheon	A rice paddy field	Apr., 2012	3
	B	Cheongpyeong-myeon, Gapyeong-gun, Gyeonggi-do	A reservoir	Jul./Aug./Sep., 2012	7
	C	Hongdong-myeon, Hongseong-gun, Chungcheongnam-do	Rice paddy fields	Jul./Aug., 2011	5
	E	Jinyoung-eup, Gimhae-si, Gyeongsangnam-do	A rice paddy field	Aug., 2012	3
Semisulcospira gottschei/melanian snail	B	Cheongpyeong-myeon, Gapyeong-gun, Gyeonggi-do	A reservoir	Aug./Sep., 2012	5
	D	Chilseong-myeon, Goesan-gun, Chungcheongbuk-do	A river	Sep., 2012	2
Radix auricularia/European ear snail	B	Cheongpyeong-myeon, Gapyeong-gun, Gyeonggi-do	A reservoir	Jul./Aug./Sep., 2012	8
Pomacea canaliculata/golden apple snail	C	Hongdong-myeon, Hongseong-gun, Chungcheongnam-do	Rice paddy fields	Jul./Aug./Sep., 2011	4
	E	Jinyoung-eup, Gimhae-si, Gyeongsangnam-do	A rice paddy field	Aug., 2012	3

n is total number of collected samples.

different individuals of melanian snails were collected from Sites B and D in 2012. In contrast, only eight European ear snails were sampled at Site B between July and September 2012. Golden apple snails were collected from rice paddy fields in two different regions (Sites C and E) in 2011 and 2012. All gastropods were sampled manually at the waterfront (Sites B and D) or inside rice paddy fields, including small irrigation ponds (Sites A, C, and E). At site B, where three gastropods (excluding the golden apple snail) coexisted, their potential diets, such as periphyton on stones, fresh/decomposed litterfall, and submerged plants (*Hydrilla verticillata*), were also collected in September 2012 to investigate the relationship between the grazers FA profiles and their food sources. All the samples were transferred to the laboratory and maintained at a low temperature in an icebox.

FA analysis

Gastropod and plant samples were rinsed with distilled water, whereas periphyton samples were scraped from the collected stones using a brush, followed by filtration with pre-combusted glass fiber paper (GF/C, Whatman, Maidstone, UK). For pretreatment, collected samples were frozen at −80°C in a deep freezer then lyophilized for 24 hours using a freeze dryer (FD2.5, Heto LAB Equipment, Allerød, Denmark). The dried flesh of the gastropods and whole plants was ground using a ball mill (Retsch, Haan, Germany), and filtration replicates (n = 3) were extracted and methylated to FA methyl ester (FAME), according to the method described by Kattner and Fricke (1986). The FAME samples were analyzed using a gas chromatograph (5890 Series II, Hewlett Packard, Palo Alto, CA, USA) equipped with a quadrupole mass spectrometer (5972A MSD Hewlett Packard). The identification and quantification of the extracted FAs were performed by comparing the retention times and mass spectra of commercial FAME standard mixtures (Supelco 37 Component FAME Mix, Cat. No. 47885-u, and PUFA No.1, Cat. No. 47033, Sigma Aldrich, St. Louis, MO, USA) and the area ratio of the sample peaks.

Statistical analysis

For gastropods and potential food sources, the FA composition was calculated as the percentage of FAs identified to the total FA amount. To compare the similarity in FA compositions among gastropod species, hierarchical cluster analysis based on the Bray-Curtis distance was performed using PRIMER 6 (PRIMER-E) after log transformation (log(x+1)) of the data matrix. Principal component analysis (PCA) was conducted to explore the intraspecific variation in FA profiles influenced by spatiotemporal factors, such as habitat and season. Prior to PCA, log-transformed data were subtracted from the mean of each FA variable and divided by the square root of their standard deviation to improve the biological information content of the metabolomic data (van den Berg et al. 2006). Kruskal-Wallis analysis and Dunn's test with Bonferroni adjustment as post hoc tests were conducted to compare the FA content among gastropods. PCA and Kruskal-Wallis tests with post hoc tests were conducted using R software (R Core Team 2024) and the 'dunn.test' package in R (Dinno and Dinno 2017).

Results

The FA profiles of the four gastropods were categorized by species using hierarchical cluster analysis at approximately 90% similarity, and further separated according to the sites under study as their habitat, except for the European ear snail, which was collected only at Site B (Fig. 2).

Interspecific variations in the indicated FA content that contributes to the assemblage are represented by the grouping of the FA composition. Comparison of the FA content of gastropod species across sites and sampling periods revealed considerable differences in selected FAs based on the results of the similarity percentage (SIMPER) analysis (Fig. 3, $p < 0.001$). The Chinese mystery and melanian snails showed higher gondoic (20:1ω9, Fig. 3A) and docosapentaenoic (DPA, 22:5ω3, Fig. 3B) acid contents than the other snails, respectively. The oleic acid (18:1ω9) content of the European ear snail differed from those of the Chinese mystery and melanian snails (Fig. 3C). The golden apple snail had higher palmitic acid (16:0) content than the other species (Fig. 3D).

The FA profiles of the gastropods were separated by sampling period and site depending on the first and second principal components (PC1 and PC2) based on the PCA score plot (Fig. 4). The PCA score plot explained 66.3% to 90.7% of the total variance using PC1 and PC2 for all gastropods. For the Chinese mystery snails, the FA composition showed more spatial than seasonal variations along the PC1 and PC2 axes in the PCA score plot (Fig. 4A). PCA loadings showed that saturated FAs, including stearic (18:0), palmitic, and arachidic (20:0) acids, correlated positively with PC1, while the contents of oleic and eicosapentaenoic acids (EPA, 20:5ω3) in the Chinese mystery snails increased along the axis of PC2. In the melanian and golden apple snails, the FA compositions were grouped by site along the PC1 axis with a higher proportion of variance (60.7% and 80.8%, respectively) than the PCA results for the other species (Fig. 4B, D, respectively). According to PC1 loadings, both linoleic (18:2ω6) and arachidonic (20:4ω6) acids in the melanian and golden apple snails had a positive correlation with the axis. In contrast, the European ear snails, collected from Site B showed that the FA profiles were separated into seasons by the PC1 and PC2 axes (Fig. 4C). Linoleic and oleic acids are important FAs for the PC1 axis, whereas linoleic acid and EPA are important FAs for the PC2 axis, according to the PCA loadings of European ear snail FAs.

At Site B, where three species coexisted, excluding the golden apple snail, the gastropods showed distinct FAs composition among the species in the PCA score plot during the study period (Fig. 5). PC1 and PC2 in the PCA score plot explained 71.7% of the total variance (44.8% and 26.9% for PC1 and PC2, respectively). PC1 and PC2 loadings indicate that gadoleic acid (20:1ω11), DPA, and oleic acid are the main FAs that differentiate species groups on the PCA score plot. To study the interactions between prey and gastropod consumers, the FAs contents of potential prey and coexisting gastropods were compared seasonally at Site B (Fig. 6). Potential prey were collected only in September, and FAs, such as oleic and linoleic acids, with a

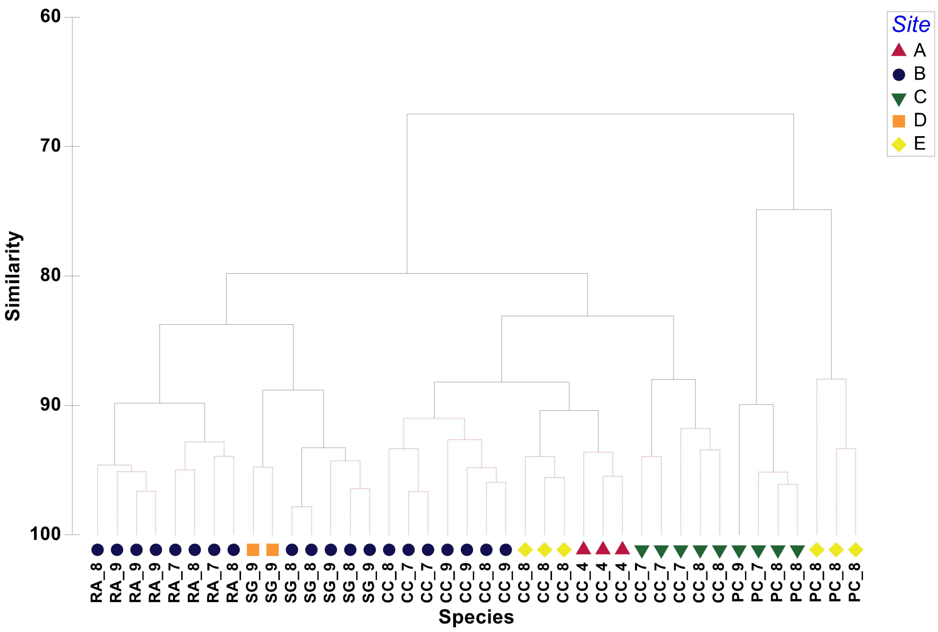

Fig. 2 Results of cluster analysis showing four gastropod fatty acid compositions. CC: Chinese mystery snail (*Cipangopaludina chinensis malleata*); SG: melanian snail (*Semisulcospira gottschei*); RA: European ear snail (*Radix auricularia*); and PC: golden apple snail (*Pomacea canaliculata*). Numbers represent sampling periods (month), while symbols denote sampling sites.

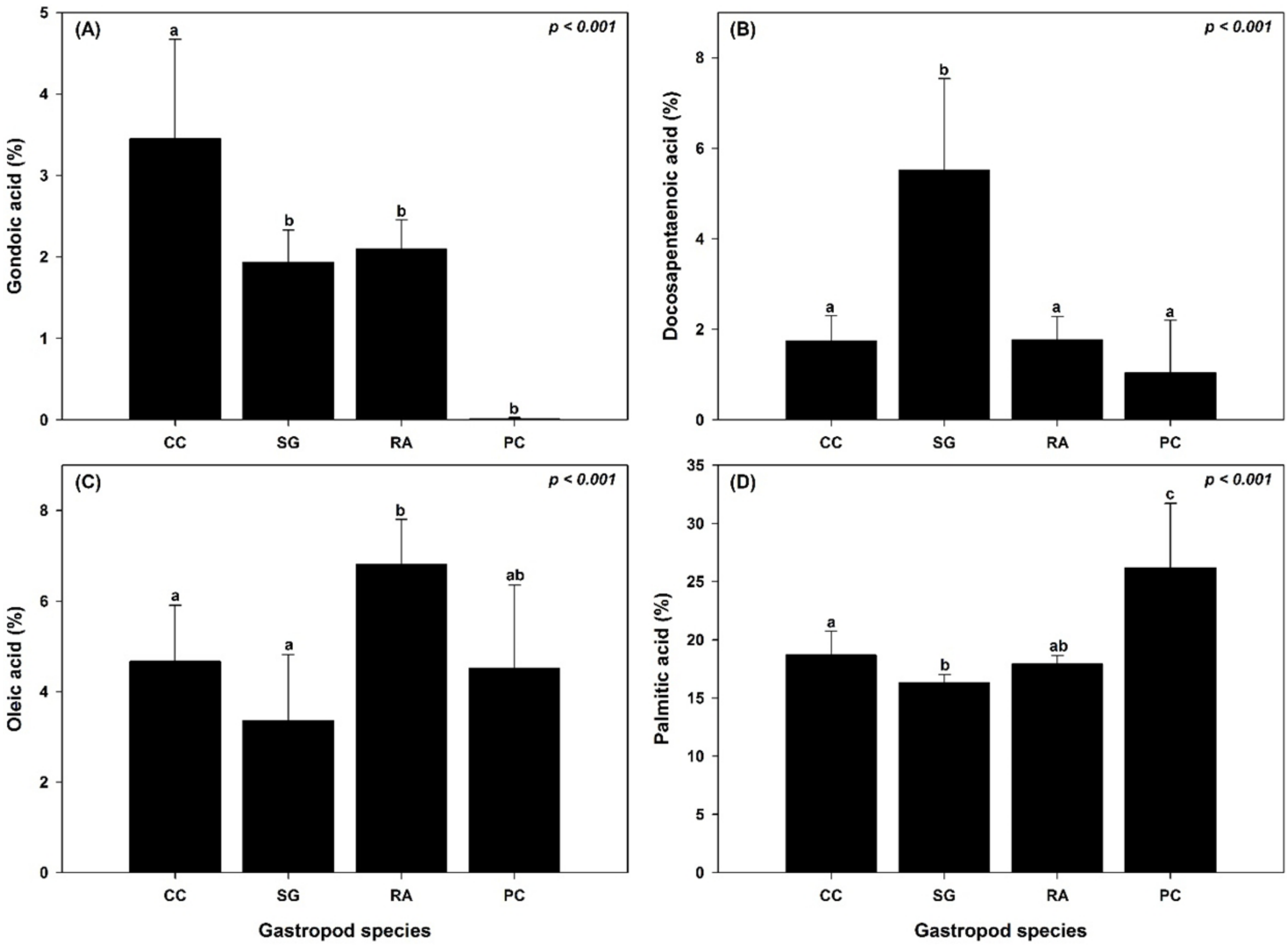

Fig. 3 Comparison of important fatty acid contents of the gastropods across all collected sites and sampling period in this study (mean ± standard deviation). (A) Gondoic acid: 20:1ω9, (B) Docosapentaenoic acid: 22:5ω3, (C) Oleic acid: 18:1ω9, and (D) Palmitic acid: 16:0. CC: Chinese mystery snail (*Cipangopaludina chinensis malleata*); SG: melanian snail (*Semisulcospira gottschei*); RA: European ear snail (*Radix auricularia*); and PC: golden apple snail (*Pomacea canaliculata*). Bars labeled with the same letter show no significant difference across species according to Kruskal-Wallis test and Dunn's pairwise comparisons.

content of more than 1%, were selected for comparison. FAs contents of potential food sources were separated into two types: waterthymes (*H. verticillata*) and fresh fallen leaves of oak trees, which had higher content of alpha-linolenic acid (ALA, 18:3ω3), and decomposed fallen leaves of oak trees and periphyton on stones, which had higher contents of palmitoleic acid (16:1ω7) and EPA than other food sources (Fig. 6A). Furthermore, among the potential prey, decomposed leaves contained the most oleic acid, whereas linoleic acid was found in the periphyton. Oleic acid, linoleic acid, and EPA contents in the Chinese mystery and European ear snails were higher than those of the other selected FAs (Fig. 6B, D). From July to September, ALA and EPA contents of the Chinese mystery snail declined slightly, whereas oleic acid content of the European ear snail increased. In contrast, melanian snails had high linoleic acid and EPA contents, which increased over time (Fig. 6C).

Discussion

Our results demonstrate that the FA composition of aquatic gastropods is influenced by certain environmental conditions, particularly their habitat (Fig. 2). Mollusk FA composition is affected by a variety of environmental factors, including diet and temperature. As a result, the FA content of storage organs fluctuates according to the diet, whereas that of membranes varies with temperature (Voogt 1983). In the present study, the FA content of gastropods was comparable to that of a given diet source in a restricted habitat (Fig. 6). Consumers retain essential nutritional biomolecules, including FA, for physiological purposes, somatic growth, and reproduction through de novo synthesis or feeding in the ecosystem (Ruess and Müller-Navarra 2019). Owing to the limited FA synthesis in animals, some FAs produced by algae, bacteria, and fungi are used as taxonomic and trophic biomarkers (de Carvalho and Caramujo 2018). In controlled experiments, some filter-feeding consumers, *Branchinella kugenumaensis* and *Daphnia*

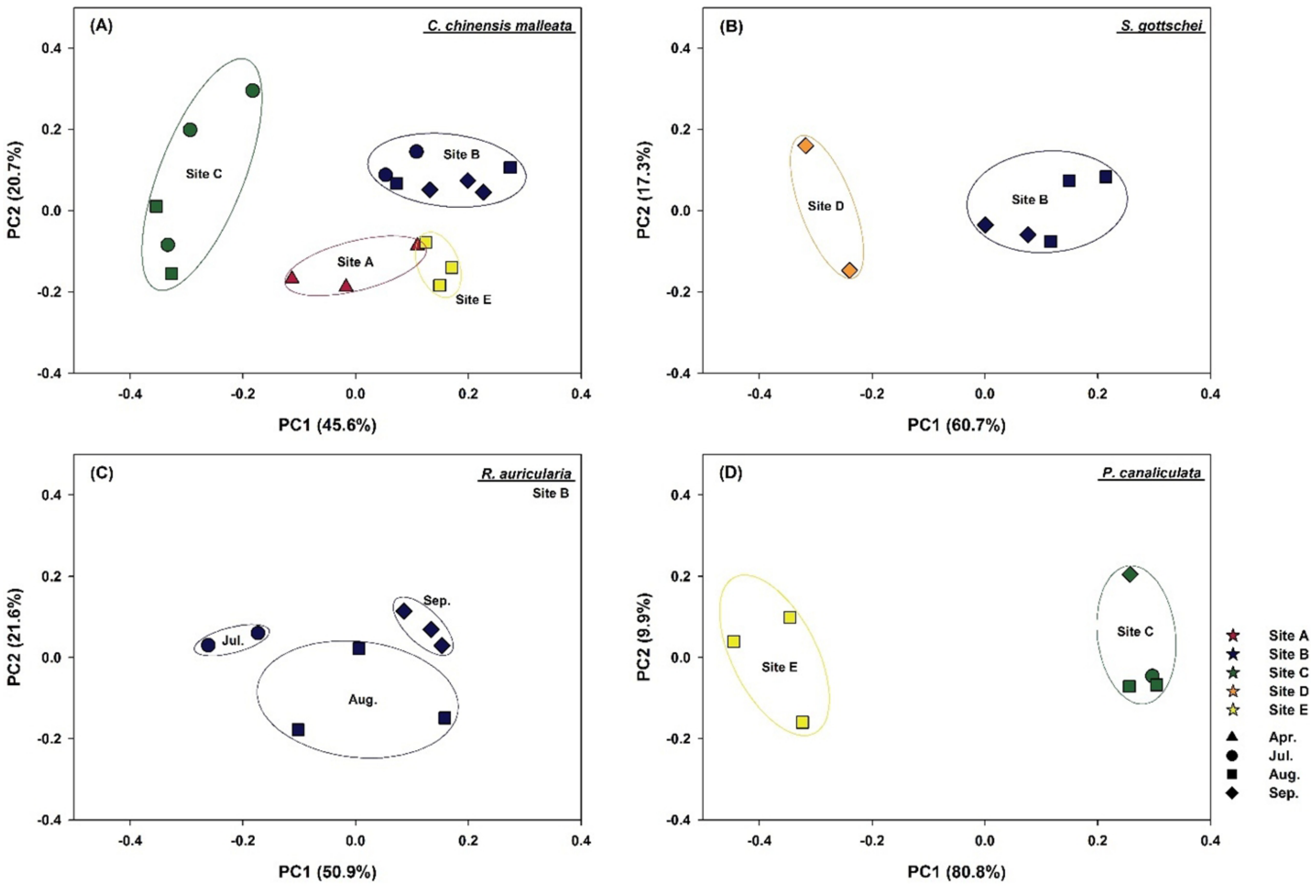

Fig. 4 Score plots of principal component analysis of fatty acid composition of four gastropods across all collected sites during the study period. (A) Chinese mystery snail: *Cipangopaludina chinensis malleata*, (B) melanian snail: *Semisulcospira gottschei*, (C) European ear snail: *Radix auricularia*, and (D) golden apple snail: *Pomacea canaliculata*. The symbols indicate sampling sites and periods.

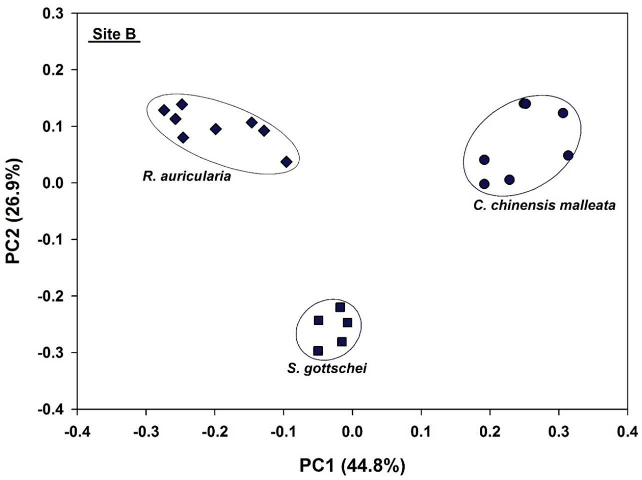

Fig. 5 Score plots of principal component analysis of fatty acid composition of coexisting gastropods collected from July to September 2012 at Site B. The symbols indicate gastropod species; circle: Chinese mystery snail (*Cipangopaludina chinensis malleata*), square: melanian snail (*Semisulcospira gottschei*), and diamond: European ear snail (*Radix auricularia*).

magna, reflected the FA profiles of heterogeneous phytoplankton diets, such as Chlorophyceae, Bacillariophyceae, and Cyanophyceae (Yang et al. 2016, 2022). Freshwater gastropods are typically micro-herbivorous or -omnivorous and consume diatoms, algae, and bacterial films (Strong et al. 2008). According to our results, gastropods mostly ingested periphyton and decomposed materials on the substrate beds at the reservoir site, as shown by the FA biomarkers (Fig. 6). Although some FAs represent diverse sources, others are employed as taxonomic biomarkers, such as palmitoleic acid for bacteria and diatoms, linoleic acid for cyanobacteria and fungi, oleic acid for green algae and gram-positive bacteria, and EPA for diatoms and cryptomonads (de Carvalho and Caramujo 2018).

Although they were collected from the same area and seemed to have similar foraging strategies (Bae and Park 2020; Hu et al. 2018; Kingsbury et al. 2021), the coexisting gastropods—the Chinese mystery, melanian, and European ear snails at Site B, and the Chinese mystery and golden apple snails at Sites C and E—appeared to have different FA profiles (Figs. 2 and 5). Coexisting gastropods with varied FA compositions may be associated with different metabolic demands and feeding strategies based on their morphological feeding structures. To process food mechanically, gastropods have unique radular morphologies such as chitinous membranes studded with teeth. Consequently, their dietary habits differ (Sitnikova et al. 2012). Among the investigated gastropods, the European ear snail of the lym-

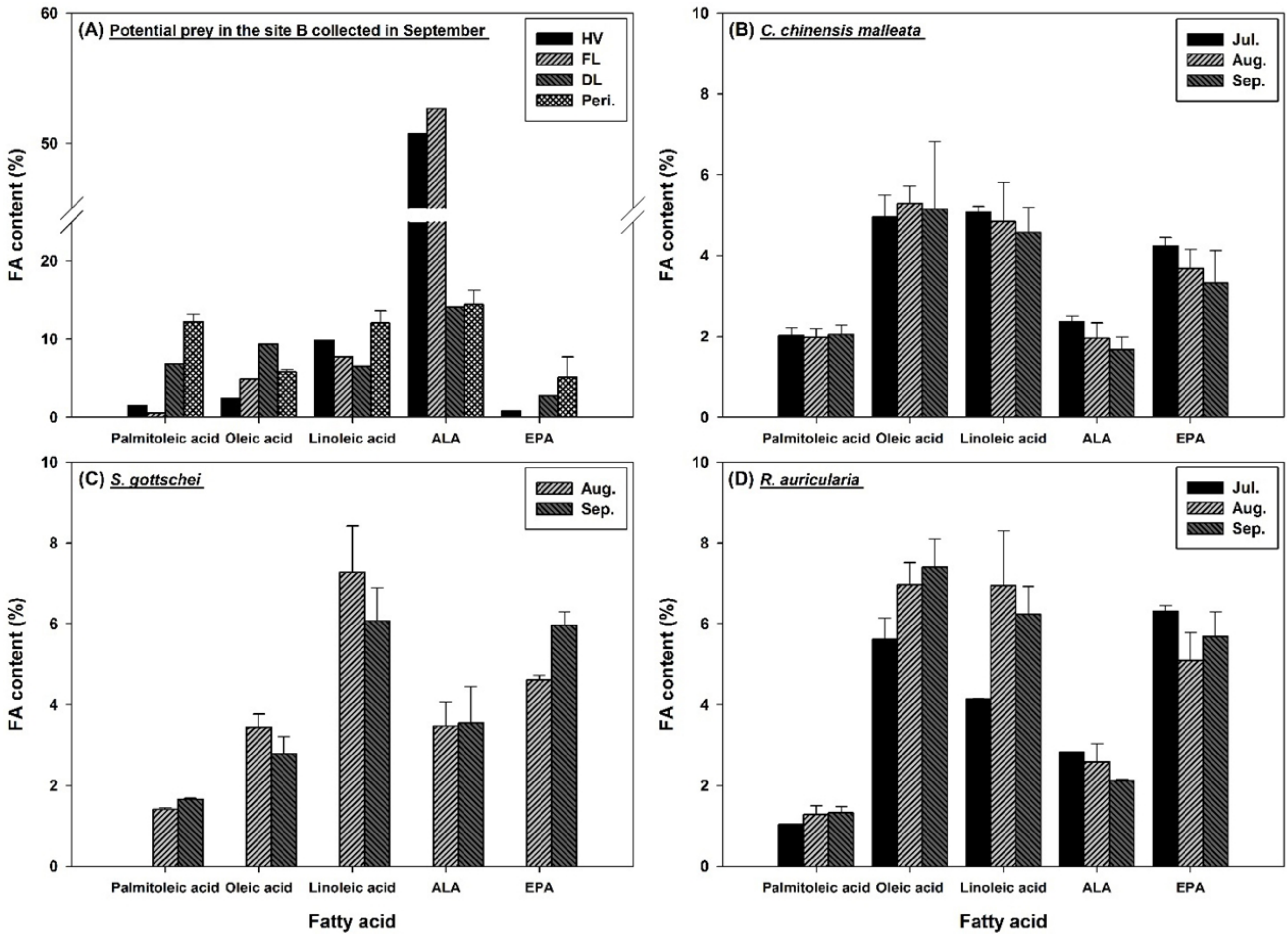

Fig. 6 Comparison of important fatty acid (FA) contents of the gastropods collected from July to September with potential food sources collected in September 2012 at site B (mean ± standard deviation). (A) Potential food sources, HV: *Hydrilla verticillata*; FL: fresh fallen leaves; DL: decomposed fallen leaves; Peri.: Periphyton on stones, (B) Chinese mystery snail: *Cipangopaludina chinensis malleata*, (C) melanian snail: *Semisulcospira gottschei*, and (D) European ear snail: *Radix auricularia*. FA denote that palmitoleic acid: 16:1ω7, oleic acid: 18:1ω9, linoleic acid: 18:2ω6, alpha-linolenic acid (ALA): 18:3ω3, and eicosapentaenoic acid (EPA): 20:5ω3.

naeid family possesses 61 radular tooth rows and a tiny center tooth that is well adapted to cropping algae (Lee et al. 1998; Pyron and Brown 2015). In contrast, the melanian snail has a Taenioglossan radula, which is appropriate for herbivores and an average of 98 tooth rows (Ko et al. 2001). In the present study, decomposed litter had a higher oleic acid content than other food sources, and European ear snails had the highest oleic acid content among the gastropods (Figs. 3 and 6). Torres-Ruiz and Wehr (2010) reported that deciduous autumn leaf litter collected from a stream had high oleic acid content after falling and decomposing, which was attributed to fungal FAs. This suggests that European ear snails fed on detritus containing a fungal diet on leaf litter using a small tooth rather than on stiff substrates such as stones.

In contrast, the Chinese mystery snails of viviparids showed that the estimated FAs from possible food origins were not widely separated in comparison with the other coexisting species (Fig. 6). Chinese mystery snails not only graze on the habitat bed but also filter the particulate matter of water for feeding, similar to other viviparids (Hwang et al. 2008; Olden et al. 2013; Pyron and Brown 2015). Therefore, the FA profiles of Chinese mystery snails may reflect mixed diet sources as well as stone surface periphyton. The golden apple snail, which coexists with the Chinese mystery snail in rice paddy fields at Sites C and E, has robust teeth composed of large and long radular (Letelier et al. 2016). They consume detritus, diatoms, mineral particles, and vascular plants, making them apt for weed removal (López-van Oosterom et al. 2016). The different feeding characteristics of the coexisting snails may alter their FA compositions. Furthermore, biological demand may be regarded as another component that influences FA composition. The Chinese mystery snail is dioecious and ovoviviparous, whereas the golden apple snail is dioecious but oviparous (Catalán et al. 2002; Pyron and Brown 2015). These disparate reproductive systems require distinct metabolic component accumulation patterns. In a feeding experiment with two filter feeders, parthenogenetic *Daphnia* and sexually reproducing fairy shrimp demonstrated species-specific FA accumulation patterns when fed identical diets (Yang et al. 2022). Therefore, differentiated FA concentrations that do not match probable diets in gastropods may have been influenced by complex factors such as metabolic demand, ecological interaction, and environmental circumstances in the current study.

Conclusions

In conclusion, the gastropods investigated in this study showed varied FA profiles depending on their habitats, which provided different food sources. Furthermore, distinct FA compositions are displayed by coexisting gastropods in freshwater aquatic environments. The taxonomic heterogeneity in the FA composition of gastropods could be caused by competition for trophic niches with limited resources, as well as survival and feeding strategies. Additionally, it appears that physiological factors related to development and reproduction throughout the life cycle, such as metabolic requirements and metabolite accumulation patterns, have an impact. The current study focused on the link between the food source and FA composition of gastropods. To understand the accumulation pattern of each taxonomic group, a comprehensive investigation that considers variables, such as age, sex, life cycle, and relationships with higher trophic levels, is required.

Abbreviations

ALA: Alpha-linolenic acid
DPA: Docosapentaenoic acid
EPA: Eicosapentaenoic acid
FA: Fatty acid
FAME: Fatty acid methyl ester
HUFA: Highly unsaturated fatty acid
PC: Principal component
PCA: Principal component analysis
PUFA: Poly unsaturated fatty acid
SIMPER: Similarity percentage

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Not applicable.

Authors' contributions

DY designed the study, carried out the experiment, conducted the analysis, and drafted the manuscript. SP examined and revised the manuscript. All authors reviewed and approved the final manuscript.

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Availability of data and materials

The datasets used and/or analyzed in the current study are available from the corresponding author on reasonable request.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

Sangkyu Park, the corresponding author, has served as Editor-in-Chief of the Journal of Ecology and Environment since 2019. He did not participate in this article's review process. The writers state that they have no competing interests in any other case.

References

Bae MJ, Kwon YS, Park YS. Effects of global warming on the distribution of overwintering *Pomacea canaliculata* (Gastropoda: Ampullariidae) in Korea. Korean J Limnol. 2012;45(4):453-8. https://doi.org/10.11614/KSL.2012.45.4.453.

Bae MJ, Park YS. Key determinants of freshwater gastropod diversity and distribution: the implications for conservation and management. Water. 2020;12(7):1908. https://doi.org/10.3390/w12071908.

Brett MT, Müller-Navarra DC, Ballantyne AP, Ravet JL, Goldman CR. Daphnia fatty acid composition reflects that of their diet. Limnol Oceanogr. 2006;51(5):2428-37. https://doi.org/10.4319/lo.2006.51.5.2428.

Catalán NM, Fernández SN, Winik BC. Oviductal structure and provision of egg envelops in the apple snail Pomacea canaliculata (Gastropoda, Prosobranchia, Ampullariidae). Biocell. 2002;26(1):91-100.

Chai JY, Lee SH. Food-borne intestinal trematode infections in the Republic of Korea. Parasitol Int. 2002;51(2):129-54. https://doi.org/10.1016/S1383-5769(02)00008-9.

Cook HW, McMaster CR. Fatty acid desaturation and chain elongation in eukaryotes. In: Vance DE, Vance JE, editors. Biochemistry of lipids, lipoproteins and membranes. 4th ed. Amsterdam: Elsevier; 2002. p. 181-204.

Covich AP, Palmer MA, Crowl TA. The role of benthic invertebrate species in freshwater ecosystems: zoobenthic species influence energy flows and nutrient cycling. BioScience. 1999;49(2):119-27. https://doi.org/10.2307/1313537.

de Carvalho CCCR, Caramujo MJ. The various roles of fatty acids. Molecules. 2018;23(10):2583. https://doi.org/10.3390/molecules23102583.

Dinno A, Dinno MA. Package 'dunn.test'. CRAN Repos. 2017;10:1-7.

Galloway AWE, Budge SM. The critical importance of experimentation in biomarker-based trophic ecology. Philos Trans R Soc Lond B Biol Sci. 2020;375(1804):20190638. https://doi.org/10.1098/rstb.2019.0638.

Ghosh S, Jung C, Meyer-Rochow VB. Snail as mini-livestock: nutritional potential of farmed *Pomacea canaliculata* (Ampullariidae). Agric Nat Resour. 2017;51(6):504-11. https://doi.org/10.1016/j.anres.2017.12.007.

Hu Z, Chen X, Chang J, Yu J, Tong Q, Li S, et al. Compositional and predicted functional analysis of the gut microbiota of *Radix auricularia* (Linnaeus) via high-throughput Illumina sequencing. PeerJ. 2018;6:e5537. https://doi.org/10.7717/peerj.5537.

Hwang SJ, Jeon MJ, Kim NY, Kim BH. Grazing rate and pseudofaeces production of native snail *Cipangopaludina chinensis malleata* Reeve on toxic cyanobacterium *Microcystis aeruginosa*. Korean J Limnol. 2008;41:77-85.

Jeong BY, Choi BD, Moon SK, Lee JS, Jeong WG, Kim PH. Proximate composition and sterol content of 35 species of marine invertebrates. J Korean Fish Soc. 1999;32(2):192-7.

Kattner G, Fricke HSG. Simple gas-liquid chromategraphic method for the simultaneous determination of fatty acids and alcohols in wax esters of marine organisms. J Chromatogr A. 1986;361:263-8. https://doi.org/10.1016/S0021-9673(01)86914-4.

Kim YK, Moon HS, Lee MH, Park MJ, Lim CW, Park HY, et al. Biological activities of seven melania snails in Korea. Korean J Fish Aquat Sci. 2009;42(5):434-41. https://doi.org/10.5657/kfas.2009.42.5.434.

Kingsbury SE, McAlpine DF, Cheng Y, Parker E, Campbell LM. A review of the non-indigenous Chinese mystery snail, *Cipangopaludina chinensis* (Viviparidae), in North America, with emphasis on occurrence in Canada and the potential impact on indigenous aquatic species. Environ Rev. 2021;29(2):182-200. https://doi.org/10.1139/er-2020-0064.

Ko JH, Lee JS, Kwon OK. Study on radulae of seven species of the family Pleuroceridae in Korea. Korean J Malacol. 2001;17(2):105-15.

Lampert W, Sommer U. Limnoecology: the ecology of lakes and streams. 2nd ed. Oxford: Oxford University Press; 2007.

Lee YS, Jeong KH, Jung YH, Jung PR. Radular teeth of six Korean freshwater pulmonates. Korean J Malacol. 1998;14(1):41-50.

Letelier S, Rebolledo A, Báez P, Fabres A, Soto-Acuña S, Jackson D, et al. The highly invasive freshwater apple snail Pomacea canaliculata (Gastropoda: Ampullariidae) in Northern Chile: morphological and molecular confirmation. J Zool Stud. 2016;3(5):119-28.

Lim CW, Kim YK, Kim DH, Park JI, Lee MH, Park HY, et al. Comparison of quality characteristics of melania snails in Korea. Korean J Fish Aquat Sci. 2009;42(6):555-60. https://doi.org/10.5657/kfas.2009.42.6.555.

López-van Oosterom MV, Ocon CS, Ferreira AC, Rodrigues-Capítulo A. The diet of Pomacea canaliculata (Gastropoda: Ampullariidae) in its native habitat based on gut content and stable isotopes analysis. Intropica. 2016;11:73-83.

Moon SK, Kim IS, Lim CW, Yoon NY, Jeong BY. Proximate and fatty acid compositions of commercial domestic and imported melania snails Semisulscospira sp. Korean J Fish Aquat Sci. 2015;48(6):977-81. https://doi.org/10.5657/KFAS.2015.0977.

Müller-Navarra DC. Food web paradigms: the biochemical view on trophic interactions. Int Rev Hydrobiol. 2008;93(4-5):489-505. https://doi.org/10.1002/iroh.200711046.

Nam HH, Yang S, Kim HS, Kim MJ, Kim JS, Lee JH. Role of *Semisulcospira gottschei* extract as medicinal food on reflux esophagitis in rats. Food Sci Nutr. 2021;9(6):3114-22. https://doi.org/10.1002/fsn3.2270.

Oh BT, Choi SG, Cho SH, Cho SH. Proximate composition, amino acid, fatty acid and inorganic matter of apple snail. Korean J Food Preserv. 2006;13(6):749-53.

Olden JD, Ray L, Mims MC, Horner-Devine MC. Filtration rates of the non-native Chinese mystery snail (*Bellamya chinensis*) and potential impacts on microbial communities. Limnetica. 2013;32(1):107-20. https://doi.org/10.23818/limn.32.11.

Pyron M, Brown K. Introduction to Mollusca and the class Gastropoda. In: Thorp JH, Rogers DC, editos. Ecology and general biology: Thorp and Covich's freshwater invertebrates. 4th ed. Cambridge: Academic Press; 2015. p. 383-421.

R Core Team. R: a language and environment for statistical computing. 2024. https://www.r-project.org/. Accessed 5 Mar 2024.

Ruess L, Müller-Navarra DC. Essential biomolecules in food webs. Front Ecol Evol. 2019;7:269. https://doi.org/10.3389/fevo.2019.00269.

Sitnikova T, Kiyashko SI, Maximova N, Pomazkina GV, Roepstorf P, Wada E, et al. Resource partitioning in endemic species of Baikal gastropods indicated by gut contents, stable isotopes and radular morphology. Hydrobiologia. 2012;682:75-90. https://doi.org/10.1007/s10750-011-0685-5.

Sorgeloos P, Dhert P, Candreva P. Use of the brine shrimp, *Artemia* spp., in marine fish larviculture. Aquaculture. 2001;200(1-2):147-59. https://doi.org/10.1016/S0044-8486(01)00698-6.

Strong EE, Gargominy O, Ponder WF, Bouchet P. Global diversity of gastropods (Gastropoda; Mollusca) in freshwater. Hydrobiologia. 2008;595:149-66. https://doi.org/10.1007/s10750-007-9012-6.

Surh J, Ryu JS, Kwon H. Seasonal variations of fatty acid compositions in various Korean shellfish. J Agric Food Chem. 2003;51(6):1617-22. https://doi.org/10.1021/jf026033a.

Torres-Ruiz M, Wehr JD. Changes in the nutritional quality of decaying leaf litter in a stream based on fatty acid content. Hydrobiologia. 2010;651:265-78. https://doi.org/10.1007/s10750-010-0305-9.

Vadeboncoeur Y, Vander Zanden MJ, Lodge DM. Putting the Lake Back Together: Reintegrating Benthic Pathways into Lake Food Web Models: lake ecologists tend to focus their research on pelagic energy pathways, but, from algae to fish, benthic organisms form an integral part of lake food webs. BioScience. 2002;52(1):44-54. https://doi.org/10.1641/0006-3568(2002)052[0044:PTLBTR]2.0.CO;2.

van den Berg RA, Hoefsloot HC, Westerhuis JA, Smilde AK, van der Werf MJ. Centering, scaling, and transformations: improving the biological information content of metabolomics data. BMC Genomics. 2006;7:142. https://doi.org/10.1186/1471-2164-7-142.

Voogt PA. Lipids: their distribution and metabolism. In: Hochachka PW, editor. The Mollusca, Volume 1: metabolic biochemistry and molecular biomechanics. New York: Academic Press; 1983. p. 329-70.

Yang D, Jeong S, Kim J, Park S. Comparisons of fatty acid accumulation patterns of two filter feeders, *Branchinella kugenumaensis* and *Daphnia magna* in a controlled environment. J Ecol Environ. 2022;46:31. https://doi.org/10.5141/jee.22.065.

Yang D, Nam S, Hwang SJ, An KG, Park YS, Shin KH, et al. Fatty acid biomarkers to verify cyanobacteria feeding abilities of herbivorous consumers. J Freshw Ecol. 2016;31(1):77-91. https://doi.org/10.1080/02705060.2015.1025304.