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Organotropism of metals and Zn—Cu isotope ratios in hydrothermal vent mussels (*Bathymodiolus*) and sea snails (*Ifremeria* and *Alviniconcha*): Implications for bioaccumulation mechanisms

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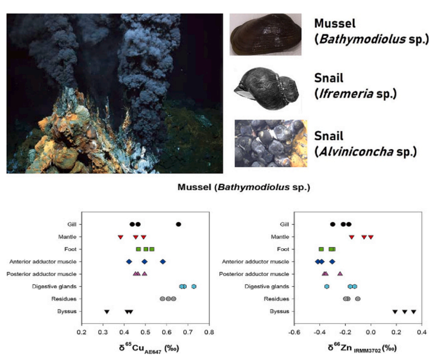
HIGHLIGHTS

- Metal accumulation varies by organ and species in hydrothermal vent mollusks.
- Zn isotopes show greater intratissue variability than Cu in vent mollusks.
- *Alviniconcha* exhibits distinct Zn isotope signatures from other vent mollusks.
- Isotope fractionation relates to species-specific metal uptake and detoxification.
- Isotopic signatures shed light on understanding bioavailability in vent organisms.

GRAPHICAL ABSTRACT



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ABSTRACT

This study investigated metal organotropism and Zn—Cu isotopic compositions in hydrothermal vent mussels (*Bathymodiolus* sp.) and sea snails (*Ifremeria* sp. and *Alviniconcha* sp.). In mussels, bioaccumulation of Al, V, Cr, Mn, Fe, Co, Ni and Zn occurred mainly in the byssus and digestive gland, whereas Cu, As, Ag, Cd, and Pb were found in the gills, suggesting that bioaccumulation of these metals occurs via the respiratory system. In sea snails, the digestive glands tended to have higher metal concentrations than other organs. Zn showed higher intratissue isotope variability than Cu. For Cu isotopes, the digestive glands of vent mollusks had the highest δ^{65}Cu values. However, while Zn concentrations were consistently elevated in the digestive glands, δ^{66}Zn values did not exhibit a corresponding trend. In vent mussels, during sequenced transport or metal partitioning processes after accumulation via the gills and digestive glands, Zn and Cu concentrations decreased with isotopic fractionation, indicating that lighter isotopes are preferentially used. Both sea snail species differed from mussels in that they preferentially accumulated lighter Zn isotopes in the digestive glands with higher Zn content. The metal and isotopic signatures accumulated in the internal organs of hydrothermal vent mollusks suggest species-dependent dietary strategies and mechanisms of uptake, accumulation, and detoxification. Our findings related to the

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organotropism of Zn and Cu isotopes offer new insights into the bioavailability and bioaccumulation processes of hydrothermal vent mollusks.

1. Introduction

Deep-sea constitutes the paramount realm of uncharted ecological inquiry on our planet, encompassing >90 % of the Earth's biosphere by volume (Mat et al., 2020). Hydrothermal environments are characterized by extreme environmental conditions such as hypoxia, the absence of sunlight, and high temperatures and pressures (Yan et al., 2022; Zhou et al., 2020). Fluids released from the hydrothermal vents contain high concentrations of metals that can accumulate in surrounding organisms through direct exposure (Chen et al., 2018; Lough et al., 2019).

Diverse mollusks, including gastropods, bivalves, and vestimentiferan tubeworms have evolved intricate and efficacious physiological adaptations to withstand excessive metal exposure and bioaccumulation near hydrothermal vent systems (Perez et al., 2021; Ramirez-Llodra et al., 2015; Zhou et al., 2020). In particular, deep-sea mussels uptake metals through the filtration of large volumes of seawater, and are therefore pivotal organisms for investigating biogeochemical cycles (Cosson et al., 2008; Koschinsky et al., 2014; Ma and Wang, 2020; Martinez et al., 2019; Martins et al., 2011; Zhou et al., 2020). Hydrothermal vent mollusks have managed to acclimate to the distinctive features of their deep-sea surroundings, allowing them to thrive and establish habitats (Laming et al., 2018; Van Dover, 2014). Due to their sedentary nature, gastropods accumulate trace metals from various environmental compartments, including the aqueous medium and through the ingestion of food and inorganic particulate matter, resulting in significant metal concentrations in tissues (Krupnova et al., 2018; León et al., 2021; Pérez et al., 2019; Primost et al., 2017). The sea snail (*Hexaplex trunculus*) was found to exhibit biomagnification of the trace metals (As, Cd, Cu, Pb, Zn) through predation on the cockle (*Cerastoderma glaucum*) (León et al., 2021). Another study observed the highest bioaccumulation factors for Zn and Cu in soft tissues of the gastropods (*Contectiana listeri*, *Lymnaea stagnalis* and *Bithynia tentaculata*) in the Southern Ural lakes of Russia (Krupnova et al., 2018). However, the application of metallic isotopic systems, to understand the accumulation of trace elements in deep-sea biospheres, remains underexplored (Ma and Wang, 2021).

Copper (Cu) and zinc (Zn) play essential roles in key biochemical processes in marine organisms, which have developed homeostatic mechanisms to regulate their internal concentrations. During these processes, stable isotopes of Cu and Zn exhibit uneven distribution (i.e., isotopic fractionation), depending on underlying mechanisms such as membrane transport, complexation, intracellular storage, and detoxification (Araújo et al., 2024; Fujii et al., 2013; Jeong et al., 2024; Köbberich and Vance, 2019; Wanty et al., 2017). Thus, these crucial metals for living organisms are employed in research to investigate their bioaccumulation and bioavailability with their isotopic ratios (Araújo et al., 2021, 2023; Chifflet et al., 2022; Jeong et al., 2021b, 2023; Jouvin et al., 2012; Köbberich and Vance, 2019; Little et al., 2017; Ma et al., 2019; Vance et al., 2008). In coastal environments, the isotope compositions of bivalve mollusks (such as mussels and oysters) have been associated with dietary and anthropogenic sources (Araújo et al., 2021; Ma et al., 2019). The Zn isotopic signatures of hydrothermal vent mollusks revealed differential Zn uptake pathways despite the similarity in their environmental habitats (Ma and Wang, 2021). However, sampling hydrothermal vent organisms presents challenges, and approaches vary among related studies, complicating direct comparisons of their results and leaving many open questions, with hypotheses yet to be tested (Demina and Galkin, 2016).

Additionally, extant inquiries have primarily focused on delineating the causal nexus between metal contamination within entire soft tissues of organisms and the surrounding environment, including seawater and sediment. Modulation by a spectrum of biotic and abiotic determinants affects the dynamics of metal accumulation and depuration which are inherently non-constants (Gestin et al., 2023; Zhang and Reynolds, 2019). However, differential isotopic compositions across organotropism and the pathways of bioaccumulation remain to be comprehensively elucidated.

Therefore, this study investigated the organotropism of Zn and Cu isotopes in hydrothermal vent mussels and sea snails using a two-dimensional approach to elucidate their metal accumulation mechanisms. Our results provide valuable insights into the utility of metallic isotopes as indices to detect patterns of metal bioaccumulation in hydrothermal settings.

2. Materials and methods

2.1. Mussel and sea snail sampling and sample treatment

Mussel (*Bathymodiolus* sp.; N = 3) and two sea snail species (*Ifremeria* sp.; N = 3 and *Alviniconcha* sp.; N = 3) were collected from hydrothermal chimneys in November 2016 in the South Pacific Ocean (18°51.4878′ S and 173°29.9447′ E; depth 2721 m) using a remotely operated vehicle. After sample collection, mussels were measured to obtain their shell length, shell height, shell width, and wet weight. Sea snail samples were measured for shell height, shell width, aperture height, aperture width, spiral length and wet weight. Morphological parameters for the measured values are summarized in Table S1. Samples were stored in deep freezer at −80 °C and transported to the laboratory.

In the laboratory, mussel and sea snail samples were washed with deionized water and the shell and soft tissues were separated. For mussels, soft tissues were dissected using titanium and ceramic knives into eight different organs: gill, mantle, foot, anterior adductor muscle (AAM), posterior adductor muscle (PAM), digestive glands (DG), residues, and byssus. Snail species were dissected into five parts: mantle skirt, mantle (roof of ctenidium), foot, body of foot, and digestive glands. The dissected samples were placed in acid-cleaned polyethylene bottles, freeze-dried and pulverized using an agate mortar.

2.2. Trace metal(oid)s analysis

The homogenized samples (50–100 mg) were weighed on a Teflon digestion vessel. After adding concentrated HNO_3 (Ultrapure; Kanto Chemical Co., Japan) and H_2O_2 (Ultrapure; Kanto Chemical Co., Japan), the lid was loosely closed and CO_2 gas was purged in a PVC hood overnight. After most of the powdered sample was dissolved, the sample was decomposed on a hot plate at 185 °C for 48 h (Jeong et al., 2021a). The decomposed mussel and snail samples were evaporated to dryness and redissolved in 2 % HNO_3. This final extract was split for isotope and elemental analyses. Trace metals and metalloids were determined using inductively coupled plasma mass spectrometry (ICP-MS; iCAP-Q, Thermo Fisher Scientific Co., Germany). Three certified reference materials representing mussel (NIST SRM2976), oyster (NIST SRM1566b), and fish protein (NRCC DORM-4) were decomposed following the same procedure used for the samples, accompanied by blanks. The recovery of trace metals and metalloids analysis deviated within ±10 % of certified values. Detailed recovery data are presented in Table S2.

2.3. Zn and Cu isotope analyses

Aliquots of mussel and snail sample extracts were proceeded using an ion exchange chromatography column packed with AG-MP1 resin (100–200 mesh, Bio-Rad) to separate the Cu and Zn analytes from matrix interferents, following a previously developed protocol (Jeong et al., 2021a). Briefly, the aliquot was evaporated and redissolved in chloridric medium (7 mol/L) followed by the sequential separation of Cu (19 mL of 7 mol/L HCl + 0.001 % H_2O_2) and Zn (10 mL of 0.5 mol/L HNO_3). For Cu, this process was repeated to remove completely interferences such as Na, Mg, Ti, and Ba. The final Cu and Zn purified fractions were evaporated and redissolved with 3 % HNO_3. Elemental analysis of a small aliquot confirmed recoveries close to 100 % within analytical uncertainty.

Cu and Zn isotopic compositions were determined using multi-collector ICP-MS (MC-ICP-MS; Neptune Plus, Thermo Fisher Scientific, Germany) at the Korea Institute of Ocean Science and Technology (KIOST). Standard-sample bracketing (SSB) and external normalization (Zn spike for Cu and vice-versa) were applied for the mass bias correction of raw ratios. Cu and Zn doping was performed at a 1:1 ratio, with concentration of 100 μg/L each. Each sample was analyzed three times. Cu and Zn isotopic compositions were expressed as delta (δ) values in per mil (‰) relative to reference materials for Cu (ERM-AE647, IRMM, Belgium) and Zn (IRMM-3702, IRMM, Belgium):

$$\delta^{65}\text{Cu}\ (‰) = \left(\frac{^{65/63}\text{Cu}_{\text{sample}}}{^{65/63}\text{Cu}_{\text{AE647}}} - 1\right) \times 1000$$

$$\delta^{66}\text{Zn}\ (‰) = \left(\frac{^{66/64}\text{Zn}_{\text{sample}}}{^{66/64}\text{Zn}_{\text{IRMM-3702}}} - 1\right) \times 1000$$

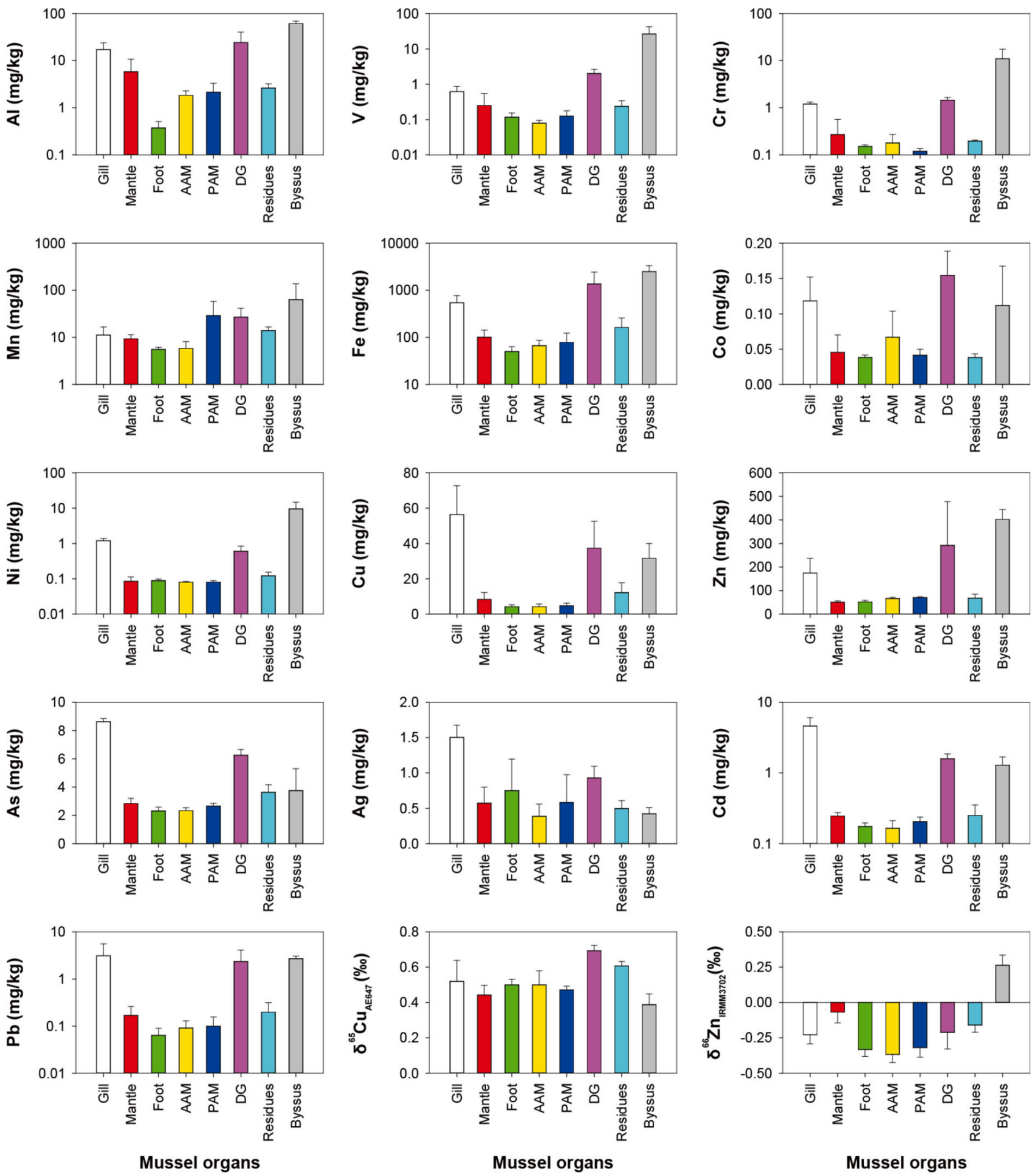

Fig. 1. Comparison of mean metal concentrations and isotopic compositions for Cu and Zn in different organs of the hydrothermal vent mussel (*Bathymodiolus* sp.). Error bars represent standard deviation (1sd). AAM, anterior adductor muscle; DG, digestive gland; PAM, posterior adductor muscle.

In every analytical sequence, we routinely verified the δ-zero value to ensure the accuracy and precision of Cu and Zn isotope analyses. Three CRMs were analyzed using the same procedure as the samples to verify the accuracy of the isotope data. The mean δ^{65}Cu values for SRM2976 (n = 12), SRM1566b (n = 6) and DORM-4 (n = 6) were 0.03 ± 0.02 ‰, 0.08 ± 0.02 ‰ and 0.44 ± 0.02 ‰ (2sd), respectively. The corresponding δ^{66}Zn values were 0.30 ± 0.01 ‰ for SRM2976, 0.45 ± 0.01 ‰ for SRM1566b and −0.17 ± 0.01 ‰ (2sd) for DORM-4, which are consistent with previously reported values (Jeong et al., 2021a). All labware was acid-cleaned with high-purity acid (Ultra-100 grade, Kanto Chemical Co., Japan), and the entire chemical process and analyses were performed in a clean room (Class 1000) at KIOST.

2.4. Statistical analysis

All statistical analyses were performed using PASW Statistics version 18. The Kruskal-Wallis non-parametric test was applied to assess the significance of differences in chemical composition (metal concentrations, Cu and Zn isotope values) among various organs of mussels and sea snails. Pairwise comparison results and their significance values (p) are provided in Tables S3–S43. Pearson's correlation analysis was conducted to assess the relationships between metal concentrations and isotopic compositions (Cu and Zn) in different hydrothermal vent mollusks. The results are presented as Pearson's correlation coefficients (r), where bold values indicate statistical significance at the 0.01 level (2-tailed) (Tables S44–S46).

3. Results and discussion

3.1. Organotropism of metals in hydrothermal vent mollusks

3.1.1. Mussels

Al, V, Cr, Mn, Fe, Ni, and Zn showed the highest concentrations in the byssus (Fig. 1). The byssus of mussels is a protein-based fiber structure composed of individual threads that are anchored to other substances to avoid displacement by currents and waves. This material is composed of four regions and has a unique chemical and molecular structure that is very rich in binding sites for metal ions (Harrington et al., 2010; Suhre et al., 2014; Xu et al., 2019). The byssus of mussels was reported to exhibit higher metal accumulation than other organs (Zhang et al., 2017). Several studies have shown that byssus threads, which are metal-polymer complexes, have the potential to purify polluted environments with metal ions (Anand and Shibu Vardhanan, 2023; Montroni et al., 2020; Zhang et al., 2019).

Cu, As, Ag, Cd, and Pb have the highest concentrations in the gills (Fig. 1). Our results showed lower metal concentrations in the gills compared to mussel *Bathymodiolus azoricus* from five different hydrothermal vent sites along the Mid-Atlantic Ridge (Cosson et al., 2008). Mussel gills are organs that filter seawater; therefore, they can adsorb and accumulate metals from both dissolved phase and fine particles due to their strong chelating ability (Dragun et al., 2004; Langston et al., 1998; Xu et al., 2022). Additionally, a mucous substance is excreted from the gills, which can lead to increased metal accumulation. Previous studies reported that the gills accumulate higher or similar metal levels than the digestive glands (Cosson et al., 2008; Sakellari et al., 2013). Our findings indicate that the gills of hydrothermal vent mussels accumulate both essential (Cu) and toxic (As, Cd, and Pb) metals discharged from hydrothermal activity.

Given that hydrothermal vent mussels rely on gill function not only for respiration but also for hosting symbiotic bacteria, their metal uptake may be closely linked to microbial activity. Deep-sea bathymodioline mussels (*Bathymodiolus* spp.) that live in chemosynthetic habitats depend on organic carbon produced by sulfur- and/or methane-oxidizing symbionts within their gills (Jang et al., 2022; Yu et al., 2019). Symbiotic bacteria in the gills of *Bathymodiolus* spp. play important roles in metal uptake, bioaccumulation, and detoxification (Hardivillier et al., 2006). In a previous study, metal accumulation such as Al in the gills is closely linked to the presence of symbionts (Kádár et al., 2006). These symbionts may also undergo lysosomal digestion within the host, thereby potentially redistributing metals (Kádár et al., 2005, 2006). Moreover, *Bathymodiolus azoricus* shows strong physiological responses to metal exposure in the gills, which indicates a symbiont-mediated mechanism for metal regulation (Hauton et al., 2017).

The digestive glands exhibited the second highest concentrations among mussel organs for most metals, in the decreasing order: Fe > Zn > Cu > Mn > Al > As > Pb > V > Cd > Cr > Ag > Ni > Co (Table 1). Like the gills, the digestive glands are major organs for metal accumulation in mussels and contain numerous blind-ended epithelial tubules and digestive cells (Dimitriadis et al., 2003). The lysosomes of the digestive cell are the main organelles for toxic metal sequestration (Faggio et al., 2018; Marigómez et al., 2002; Owen, 1972). A previous study showed that Zn accumulated in mineralized lysosomes within mussel digestive glands (Etxeberria et al., 1994). Metals in hydrothermal vent mussels were found to be associated with soluble compounds in the gills and insoluble compounds in the digestive glands (Cosson et al., 2008). The Ag, Fe, Mn and Zn concentrations determined in the digestive glands of mussels in the present study were higher than those of mussels inhabiting hydrothermal vents in Mid-Atlantic Ocean (Cosson et al., 2008). The bioaccumulation of metals in mussel organs appears to be influenced by the metal content of mussel habitats.

Elements typically enriched in hydrothermal fluids, such as Fe, Cu, Zn, Pb, and Cd, were significantly accumulated in the gills and digestive glands of vent mussels (*Bathymodiolus* spp.), consistent with our findings (Koschinsky et al., 2014). However, metal concentrations tend to vary across different geographical locations (Colaço et al., 2006; Demina and Galkin, 2008). For example, spatial variation in metal accumulation has been observed in *Bathymodiolus azoricus* from different vent sites, with mussels from metal-rich environments, such as the Rainbow hydrothermal vent field, exhibiting higher bioaccumulation levels compared to those from other hydrothermal vent sites including Menez Gwen and Snake Pit (Demina and Galkin, 2008). This pattern aligns with differences in the chemical compositions of hydrothermal fluids, as high-temperature venting at the Rainbow vent field results in elevated metal concentrations, influencing the bioaccumulation potential of the local fauna. Furthermore, a study on *Bathymodiolus azoricus* demonstrated that spatial variation in metal accumulation at the Eiffel Tower edifice was linked to fine-scale environmental factors affecting mussel physiology and metal regulation (Martins et al., 2011). Additionally, Fe—Mn hydroxide films on mussel shells may act as secondary metal reservoirs, further impacting metal availability and accumulation patterns (Demina and Galkin, 2008). Such processes, combined with species-specific physiological adaptations, contribute to differences in metal uptake and retention among vent organisms. These findings suggest that metal accumulation in vent mussels is shaped by a combination of hydrothermal fluid properties, local environmental dynamics, and physiological adaptations. Further comparative studies across different vent ecosystems are necessary to enhance our understanding of the extent of these variations and their implications for metal cycling in chemosynthetic communities.

3.1.2. Sea snails

The metal concentrations of different organs in hydrothermal vent sea snails are presented in Fig. 2. In the snail *Ifremeria* sp., the highest concentrations of all metals were observed in the digestive glands (Table 1). The Cu (477 mg/kg) and Zn (1048 mg/kg) concentrations in the digestive glands of *Ifremeria* were approximately nine times higher than those in the body of the foot and mantle skirt, respectively, which exhibited the lowest concentrations among the organs. The digestive glands of *Alviniconcha* exhibited Zn (1971 mg/kg), As (47.2 mg/kg), and Pb (133 mg/kg) concentrations that were approximately 2-, 2-, and 7-fold higher, respectively, than those of *Ifremeria*. Unlike *Ifremeria*,

Table 1
Analytical results for mean metal concentrations (mg/kg, dry weight) in different organs of the hydrothermal vent mussel (*Bathymodiolus* sp.) and the sea snails (*Ifremeria* sp. and *Alviniconcha* sp.).

Organs	Al	V	Cr	Mn	Fe	Co	Ni	Cu	Zn	As	Ag	Cd	Pb
Mussel (*Bathymodiolus* sp; n = 3)													
Gill	17.2	0.62	1.20	11.2	544	0.12	1.19	56.4	175	8.62	1.50	4.61	3.10
Mantle	5.85	0.25	0.27	9.36	102	0.05	0.09	8.36	50.7	2.84	0.57	0.25	0.17
Foot	0.37	0.12	0.15	5.56	50.2	0.04	0.09	4.19	52.1	2.31	0.75	0.17	0.06
Anterior adductor muscle	1.83	0.08	0.18	5.88	66.9	0.07	0.08	4.25	66.6	2.33	0.39	0.17	0.09
Posterior adductor muscle	2.15	0.13	0.12	29.1	78.4	0.04	0.08	4.76	70.4	2.65	0.58	0.20	0.10
Digestive glands	24.2	2.02	1.45	26.9	1368	0.15	0.61	37.4	292	6.25	0.93	1.59	2.35
Residues	2.63	0.24	0.20	14.0	162	0.04	0.12	12.2	67.9	3.63	0.50	0.25	0.20
Bysuss	61.3	26.7	11.0	63.4	2480	0.11	9.57	31.7	402	3.75	0.42	1.29	2.70
Sea snail (*Ifremeria* sp.; n = 3)													
Mantle skirt	1.42	0.22	5.24	6.53	158	0.01	0.05	67.5	117	2.70	2.06	0.33	0.35
Mantle (roof of lung)	67.8	0.98	8.16	11.2	1055	0.01	0.48	212	317	5.11	2.26	5.15	2.12
Foot	8.16	0.29	4.33	5.64	316	0.01	0.08	109	223	3.12	0.11	0.21	0.31
Body of foot	3.41	0.09	3.06	3.79	179	0.004	0.04	51.0	169	2.66	1.78	0.19	0.13
Digestive glands	175	5.11	30.7	31.2	5004	0.32	1.13	477	1048	25.1	8.02	14.6	19.6
Snail (*Alviniconcha* sp.; n = 3)													
Mantle skirt	0.45	5.18	1.30	3.58	249	0.05	0.20	227	126	73.4	2.23	0.41	17.3
Mantle (roof of lung)	0.21	2.18	0.57	2.68	277	0.02	0.12	139	94.2	17.0	2.06	0.06	2.87
Foot	2.69	11.4	4.26	6.46	2042	0.03	0.62	491	1434	360	2.27	6.90	321
Body of foot	1.06	3.36	0.87	4.97	436	0.03	0.27	557	84.5	6.03	0.51	0.12	5.95
Digestive glands	1.28	4.18	1.76	14.0	2652	0.09	0.27	166	1971	47.2	1.68	6.90	133

Alviniconcha exhibited the highest concentrations of all metals in the foot, except for Fe, Co, and Zn. While Fe (2652 mg/kg), Co (0.09 mg/kg), and Zn (1971 mg/kg) were most concentrated in the digestive glands, Fe and Zn showed similar concentrations to those in the foot. Aquatic organisms exposed to metals in the environment accumulate excess metals by sequestering them in either metabolically available (metallothionein) or unavailable (phosphate granules) forms (Mason and Nott, 1981). This process may explain the high concentrations of Zn and Cu found in the digestive glands of mussels and snails in this study. High metal concentrations in the viscera of vent snails (*Gigantopelta aegis*) have also been reported (Ma and Wang, 2020). Toxicity experiments of Cd, Cu, Ni, Pb, and Zn were conducted using the freshwater snail *Pomacea insularum* (Yap et al., 2023); the results indicated that Cu was the most toxic metal, with snail mortality increasing with both Cu concentration and exposure time. Hoang et al. (2008) reported that most of the Cu accumulated in apple snails (*Pomacea paludosa*) was concentrated in the soft tissues, with about 60 % in the digestive glands.

Previous studies have shown that sulfide- and/or methane-oxidizing endosymbiotic bacteria live in the gills of the mixotrophic-feeding snail, *Ifremeria nautilei*, allowing it to host chemoautotrophic symbionts (Bojar et al., 2018; Warèn and Bouchet, 1993). Generally, freshwater snails accumulate metals in their bodies through several exposure routes such as water exposure, ingestion, dermal contact with soil, and dietary uptake (Heng et al., 2004; Hoang et al., 2008). Therefore, the higher metal enrichment observed in the digestive glands of *Ifremeria* gastropod mollusks than in *Bathymodiolus* mussels may be due to intrinsic species-specific physiologies related to diet, bioaccumulation routes, and homeostasis. Further investigations are needed to identify mechanisms of metal accumulation in hydrothermal vent mollusks related to feeding and respiration.

3.2. Organotropism of Zn—Cu isotopes in hydrothermal vent mollusks

The Zn and Cu isotope variations among organs (Δ_{organs} = maximum − minimum δ values) were ~0.3 ‰ ($\Delta^{66}Zn_{organs}$) and ~0.3 ‰ ($\Delta^{65}Cu_{organs}$) in *Bathymodiolus*, ~0.6 ‰ ($\Delta^{66}Zn_{organs}$) and ~0.1 ‰ ($\Delta^{65}Cu_{organs}$) in *Ifremeria*, and ~0.5 ‰ ($\Delta^{66}Zn_{organs}$) and ~0.3 ‰ ($\Delta^{65}Cu_{organs}$) in *Alviniconcha* (Fig. 3). Zn isotope values in mussel organs excluding the byssus ranged from −0.37 ‰ (anterior adductor muscle) to −0.07 ‰ (mantle) (Table 2). These values are similar to the −0.37 ± 0.33 ‰ for *Bathymodiolus marisindicus* reported by Ma and Wang (2021). The $\delta^{66}Zn$ values in the various mussel organs in this study were lighter than those of mussels collected from coastal regions of Korea (mean: 0.09 ‰ for *Mytilus edulis*; Jeong et al., 2021b), France (mean: 0.28 ‰ for *Mytilus galloprovincialis*; Shiel et al., 2013) and Brazil (mean: 0.55 ‰ for *Perna perna*; Araújo et al., 2017).

The gills and digestive glands of mussels provide primary avenues for Cu uptake, facilitated by respiration and dietary assimilation (Chen et al., 2023; Nugroho and Frank, 2011; Raftopoulou and Dimitriadis, 2011). Additionally, gills can uptake metals through both seawater filtration and respiration processes (Dragun et al., 2004; Xu et al., 2022). Cu isotopic compositions and concentration in the gills and digestive glands of mussels were higher than those in all other organs (Fig. 3). Although the gills exhibited the highest Cu content (mean: 56.4 mg/kg), their isotopic compositions were similar to those of other organs, including the mantle, foot, and adductor muscle, which were characterized by lower Cu content and isotope values. For Zn, the byssus showed a high concentration (402 mg/kg) and isotopic signature ($\delta^{66}Zn$: 0.26 ‰), which were clearly distinguished from those of other organs (Fig. 4). Although the gills (−0.23 ‰) and digestive glands (−0.21 ‰) showed similar Zn isotopic compositions ($\delta^{66}Zn$), their Zn concentrations differed. As previously noted, the mussel byssus has different characteristics to those of the gills and digestive glands (Inoue et al., 2021; Yap and Al-Mutairi, 2023). Our data showed that the foot and adductor muscles also had lower Zn levels and isotopic composition than the gills and digestive glands. These findings suggest that, in hydrothermal vent mussels, metal detoxification processes may influence isotope fractionation of Cu and Zn not only in the digestive glands but also in the gills, potentially contributing to the preferential release of lighter isotopes via symbiont-mediated mechanisms. Hence, the transfer of Cu and Zn accumulated in the gills and digestive glands to other organs involves processes that decrease their concentration, accompanied by the preferential utilization of lighter isotopes. Furthermore, mussels accumulate Cu in their soft tissues at different rates depending on the bioaccumulation process and residence time (Araújo et al., 2021). The mean $\delta^{65}Cu_{AE647}$ in the whole soft tissues of mussels was 0.97 ‰, with a substantial annual variation of 0.94 ‰ in a French coastal area (Araújo et al., 2021). The $\delta^{65}Cu$ values of *Bathymodiolus* were lower than those of *Mytilus edulis*. The variations in Cu isotopes among different organs or individuals were smaller than regional or temporal differences.

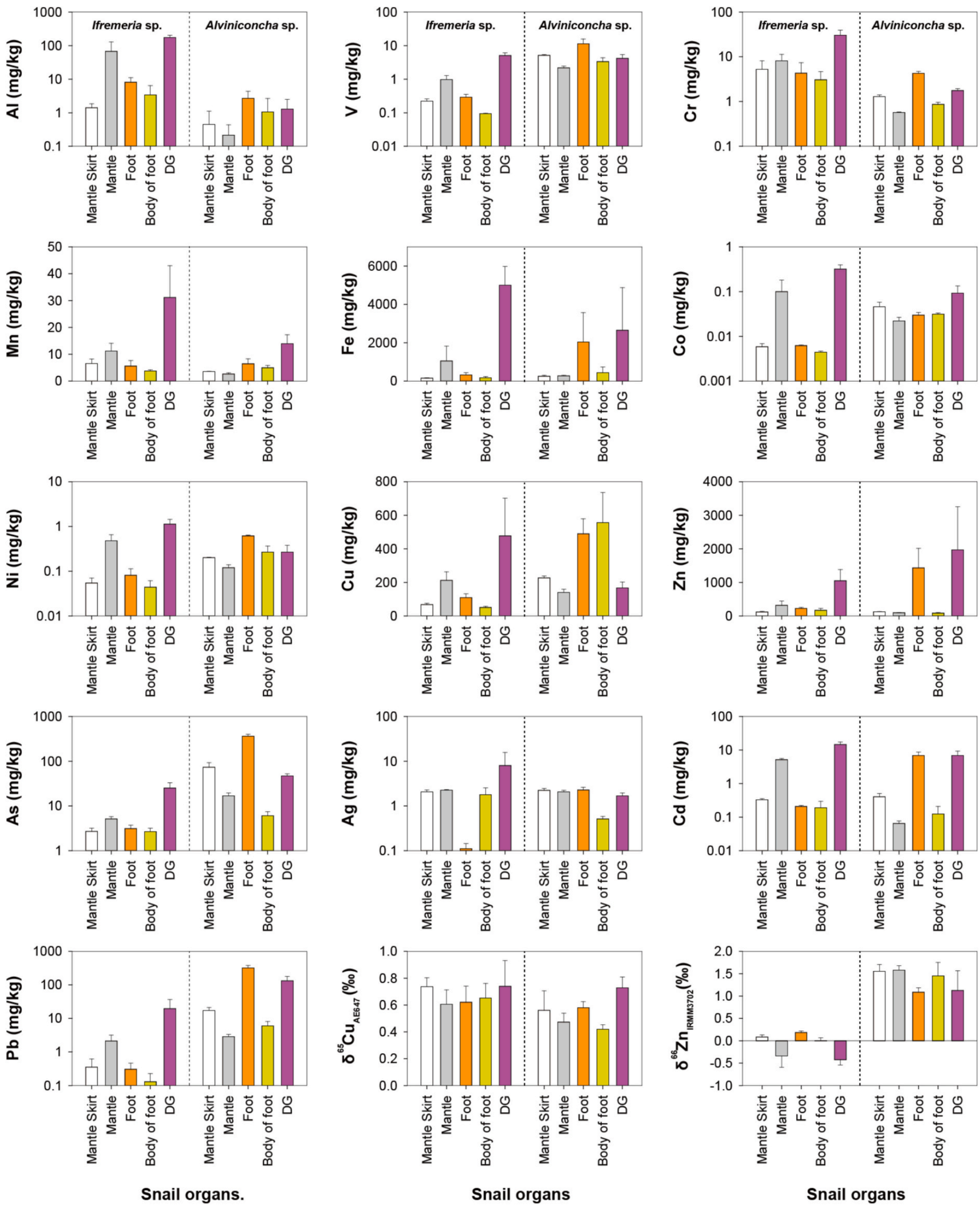

Fig. 2. Comparison of mean metal concentrations and isotopic compositions for Cu and Zn in different organs of the hydrothermal vent sea snails (*Ifremeria* sp. and *Alviniconcha* sp.). Error bars represent standard deviation (1sd). DG, digestive gland.

For sea snails, the mantle and digestive glands of *Ifremeria* showed negative δ^{66}Zn values, contrasting with those of other organs (Fig. 2). The Cu isotopic composition exhibited only a 0.13 ‰ difference among organs, whereas the Zn isotopic composition displayed a larger isotopic difference of 0.61 ‰ (Table 2). Compared with the δ^{66}Zn values of different organs in *Ifremeria*, *Alviniconcha* tissues appeared enriched in heavier isotopes, ranging from 1.09 ‰ in the foot to 1.58 ‰ in the mantle. The Zn isotope values were lower in the digestive glands of both sea snail species than in other organs. A previous study of the sea snails (*Chrysomallon squamiferum* and *Gigantopelta aegis*) collected from the Longqi hydrothermal vent fields found no discernible differences in δ^{66}Zn values across species and organs, concluding that no isotope fractionation occurs during the internal distribution of Zn (Ma and Wang, 2021). Nevertheless, our study revealed considerable disparity in δ^{66}Zn values between *Ifremeria* and *Alviniconcha*, despite the slight isotopic variation observed among organs.

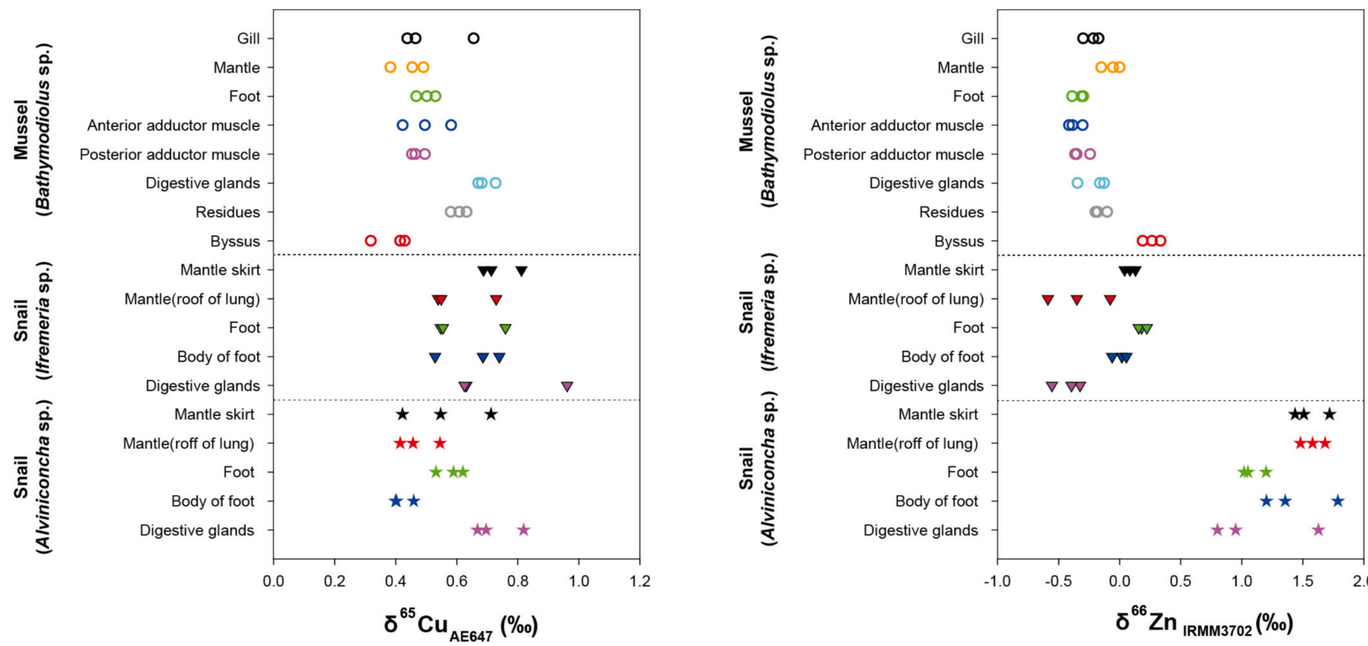

Fig. 3. Cu ($\delta^{65}Cu_{AE647}$) and Zn ($\delta^{66}Zn_{IRMM3702}$) isotopic compositions in different organs of hydrothermal vent mussels and sea snails.

Table 2
Mean ± standard deviation (1sd), minimum and maximum values (in parentheses) for Cu ($\delta^{65}Cu_{AE647}$) and Zn ($\delta^{66}Zn_{IRMM3702}$) isotopic compositions in the hydrothermal vent mussel (*Bathymodiolus* sp.) and the sea snails (*Ifremeria* sp. and *Alviniconcha* sp.).

Organs	$\delta^{65}Cu_{AE647}$ (‰)	$\delta^{66}Zn_{IRMM3702}$ (‰)
Mussel (*Bathymodiolus* sp; n = 3)		
Byssus	0.39 ± 0.06 (0.32 to 0.43)	0.26 ± 0.07 (0.19 to 0.34)
Gill	0.52 ± 0.12 (0.44 to 0.66)	−0.23 ± 0.06 (−0.30 to −0.17)
Mantle	0.44 ± 0.06 (0.38 to 0.49)	−0.07 ± 0.08 (−0.15 to 0.00)
Foot	0.50 ± 0.03 (0.47 to 0.53)	−0.33 ± 0.05 (−0.39 to −0.30)
Anterior adductor muscle	0.50 ± 0.08 (0.42 to 0.58)	−0.37 ± 0.06 (−0.41 to −0.30)
Posterior adductor muscle	0.47 ± 0.02 (0.45 to 0.50)	−0.32 ± 0.07 (−0.36 to −0.24)
Digestive glands	0.69 ± 0.03 (0.67 to 0.73)	−0.21 ± 0.12 (−0.34 to −0.13)
Residues	0.61 ± 0.03 (0.58 to 0.63)	−0.16 ± 0.05 (−0.20 to −0.10)
Sea snail (*Ifremeria* sp.; n = 3)		
Mantle skirt	0.74 ± 0.07 (0.71 to 0.81)	0.09 ± 0.04 (0.04 to 0.13)
Mantle (roof of lung)	0.61 ± 0.11 (0.54 to 0.73)	−0.34 ± 0.26 (−0.59 to −0.08)
Foot	0.62 ± 0.12 (0.55 to 0.76)	0.19 ± 0.03 (0.16 to 0.22)
Body of foot	0.65 ± 0.11 (0.53 to 0.74)	0.00 ± 0.06 (−0.06 to 0.05)
Digestive glands	0.74 ± 0.19 (0.63 to 0.96)	−0.42 ± 0.12 (−0.55 to −0.32)
Snail (*Alviniconcha* sp.; n = 3)		
Mantle skirt	0.56 ± 0.15 (0.42 to 0.71)	1.55 ± 0.15 (1.51 to 1.72)
Mantle (roof of lung)	0.47 ± 0.07 (0.41 to 0.55)	1.58 ± 0.10 (1.48 to 1.68)
Foot	0.58 ± 0.04 (0.53 to 0.62)	1.09 ± 0.10 (1.02 to 1.20)
Body of foot	0.42 ± 0.03 (0.40 to 0.46)	1.45 ± 0.30 (1.20 to 1.79)
Digestive glands	0.73 ± 0.08 (0.67 to 0.82)	1.13 ± 0.44 (0.80 to 1.63)

Given that *Ifremeria* and *Alviniconcha* host different symbionts and occupy distinct microhabitats, we hypothesize that symbiont-mediated metabolism plays a role in Zn isotope fractionation between these species. *Ifremeria* harbors a single Gammaproteobacterial sulfur-oxidizing symbiont, whereas *Alviniconcha* hosts both Gammaproteobacteria and Campylobacteria, which utilize different electron donors for energy metabolism (Beinart et al., 2019; Podowski et al., 2009). The ability of *Alviniconcha*'s Campylobacterial symbionts to metabolize hydrogen in addition to sulfur may alter Zn uptake pathways compared to the sulfur-oxidizing symbionts in *Ifremeria*, potentially contributing to the heavier Zn isotope signatures observed in *Alviniconcha*. Habitat differences may also influence Zn isotope fractionation. *Alviniconcha* inhabits regions closer to hydrothermal vent orifices, where metal concentrations are higher, whereas *Ifremeria* is found in slightly more peripheral environments with lower metal fluxes (Beinart et al., 2019; Podowski et al., 2009). These different environmental exposures may affect Zn bioavailability and uptake mechanisms, further contributing to interspecies differences. Given these factors, we propose that symbiont metabolism plays an important role in shaping Zn isotope compositions in hydrothermal vent gastropods. However, many uncertainties remain regarding the specific mechanisms by which symbionts mediate metal uptake, distribution, partitioning, and regulating processes. Further investigation into symbiont-related Zn assimilation pathways and their influence on metal isotope fractionation would provide deeper insight into these interspecies differences.

Furthermore, mussels and snails adopt different dietary strategies; while adults of most *Bathymodiolins* species are mixotrophic, relying on bacterial partners for much of their nutrition, gastropods primarily depend on symbionts (Laming et al., 2018; Ma and Wang, 2021). Thus, the elemental and isotopic compositions of metals accumulated within the internal organs of hydrothermal mollusks offer valuable insights into their diverse dietary sources, as well as the respective uptake and accumulation mechanisms that are contingent upon species, organs, and metals.

3.3. Statistical analysis of interorgan variability in metal content and Zn—Cu isotope ratios

Significant differences ($p < 0.050$) in metal concentrations and isotope ratios were observed among different organs within each species (Tables S3–S43). In *Bathymodiolus* sp., significant differences were observed for V ($p = 0.018$) and δ^{66}Zn ($p = 0.031$) between AAM and byssus, for Fe ($p = 0.028$) between the foot and byssus, for Ni ($p = 0.048$) between PAM and byssus, for Zn ($p = 0.034$) between the mantle and byssus, for As ($p = 0.042$) between the foot and gill, for Cd ($p = 0.042$) between AAM and gill, and for δ^{65}Cu ($p = 0.015$) between the byssus and digestive glands. In *Ifremeria* sp., significant differences were found for

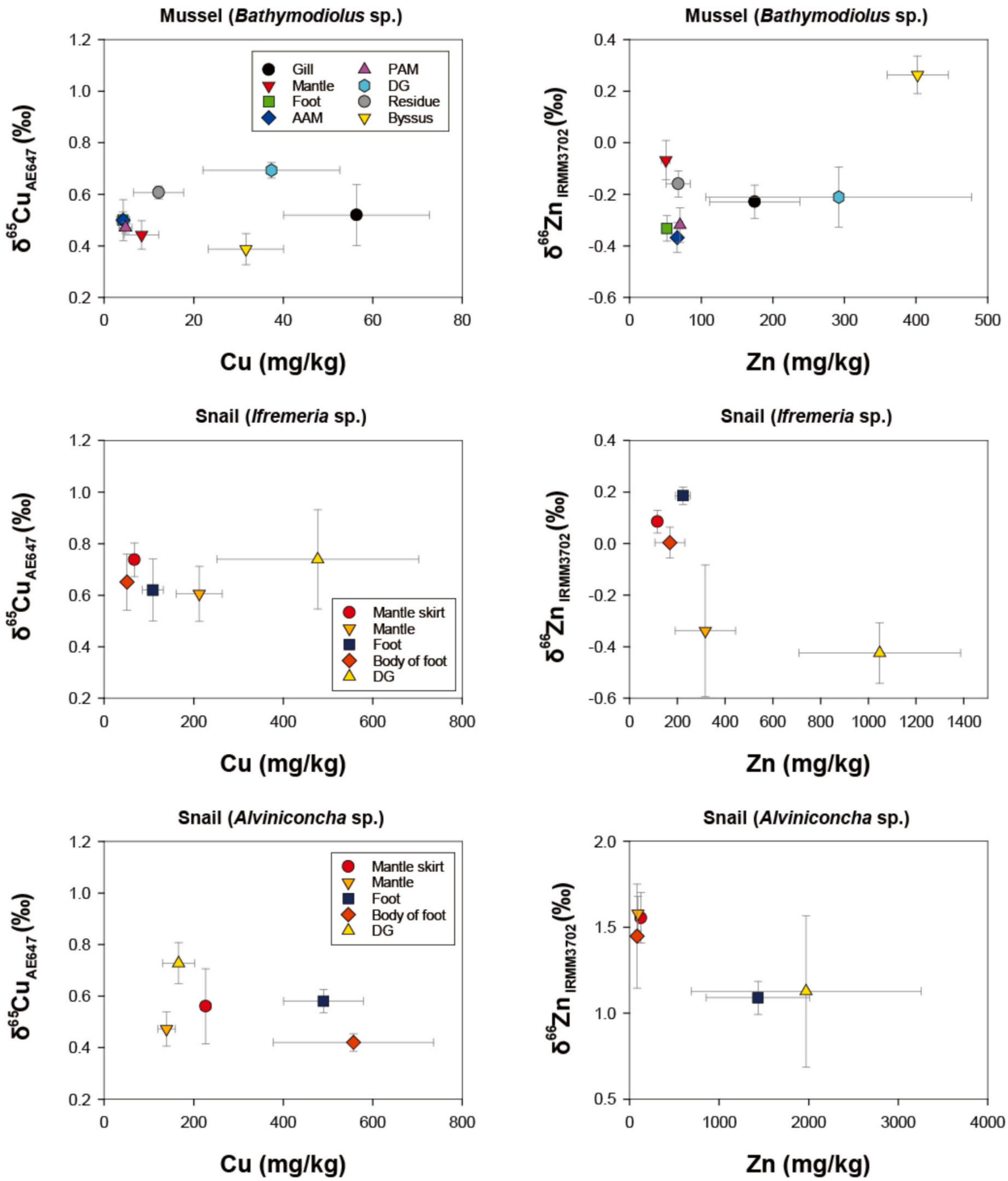

Fig. 4. Relationships between mean concentrations and isotopic values of Cu and Zn in the hydrothermal vent mussel (*Bathymodiolus* sp.) and the sea snails (*Ifremeria* sp. and *Alviniconcha* sp.). Error bars represent standard deviation (1sd). AAM, anterior adductor muscle; DG, digestive gland; PAM, posterior adductor muscle.

Al ($p = 0.014$), Fe ($p = 0.047$), and Zn ($p = 0.014$) between the mantle skirt and digestive glands, V ($p = 0.010$), Cr ($p = 0.035$), Mn ($p = 0.010$), Fe ($p = 0.047$), Co ($p = 0.012$), Ni ($p = 0.025$), Cu ($p = 0.010$), As ($p = 0.047$), Cd ($p = 0.034$), and Pb ($p = 0.022$) between the body of the foot and digestive glands, Ag ($p = 0.010$) and δ^{66}Zn ($p = 0.035$) between the foot and digestive glands, and δ^{66}Zn ($p = 0.047$) between the mantle and foot. In *Alviniconcha* sp., significant differences were detected for V ($p = 0.014$), Cr ($p = 0.010$), Ni ($p = 0.010$), and Pb ($p = 0.010$) between mantle and foot, Mn ($p = 0.010$) and Co ($p = 0.013$) between the mantle and digestive glands, As ($p = 0.010$) between body of the foot and foot; and δ^{65}Cu ($p = 0.039$) between body of the foot and digestive glands. However, across all organ comparisons within each species, Ag in *Bathymodiolus* sp. ($p = 0.071$), Cu in *Ifremeria* sp. ($p = 0.632$), and Al in *Alviniconcha* sp. ($p = 0.\ 291$) showed no statistically significant differences. These results indicate species-specific differences in metal distributions and isotope fractionation across organs within gastropods, suggesting physiological variation among species and differences in metal uptake, storage, detoxification, and biochemical processes.

3.4. *Environmental implications in hydrothermal ecosystems: a focus on metal and isotope signatures*

The δ^{66}Zn of mussels was positively correlated with Zn concentration (*Bathymodiolus*, $r = 0.67$, $p < 0.01$; Fig. 5), however, sea snails showed a

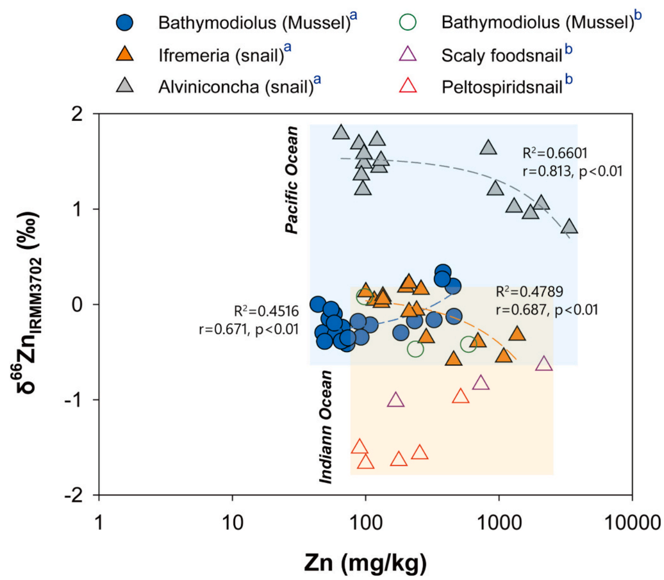

Fig. 5. Relationships between concentration and isotope signatures of Zn in hydrothermal vent mollusks (a: this study, b: Ma and Wang, 2021).

negative correlation between isotope and concentration of Zn (*Ifremeria*, $r = -0.69$, $p < 0.01$; *Alviniconcha*, $r = -0.81$, $p < 0.01$; Fig. 5). Coastal mussels tend to regulate Cu by stabilizing its concentration independently of its environmental bioavailability. Therefore, no correlation was observed between isotope values and concentrations of Cu in French mussels (Araújo et al., 2021). Marine mussels, distributed from nearshore zones to the deep-sea, exhibit diverse physiological adaptations to their respective environments (Beyer et al., 2017; Qian et al., 2024; Zhao et al., 2024). Coastal mussels, such as *Mytilus edulis* rely primarily on their gills for respiration and filter-feeding, whereas the digestive gland functions as the main detoxification organ (Regoli and Principato, 1995; Zhao et al., 2024). These mussels regulate Cu homeostasis efficiently, stabilizing Cu concentrations in their tissues independently of environmental bioavailability, which explains the lack of correlation between Cu isotope values and Cu concentrations in French coastal mussels (Araújo et al., 2021). In contrast, deep sea *Bathymodiolus* mussels have enlarged gills that harbor sulfur- and/or methane-oxidizing symbionts within specialized bacteriocytes (Duperron et al., 2019; Ikuta et al., 2021). These symbionts facilitate metal bioaccumulation and detoxification, influencing metal uptake pathways differently from coastal mussels. Hydrothermal vent mussels in the Pacific and Indian Oceans have similar Zn isotopic compositions, whereas sea snails have distinct isotopic signatures depending on their species and geographical region (Ma and Wang, 2021) (Fig. 5). In *Bathymodiolus*, Cu exhibited significant correlations with Al, Fe, Co, Zn, As, Ag, Cd, and Pb ($p < 0.01$) (Table S44). Zn isotope values were significantly correlated with Al, V, Cr, Fe, Ni, and Zn concentrations; however, the Cu isotopic compositions of mussels showed no correlation with other metals (Table S44). Bivalve mollusks can regulate internal accumulated metal concentrations within certain limits, and possess an effective mechanism for the detoxification of excess accumulated metals, which involves the metallothionein protein (Amiard et al., 2006; Baltaci et al., 2018; Raftopoulou and Dimitriadis, 2011). Additionally, metal-containing phosphate granules that form in lysosomes of digestive cells are also involved in metal accumulation and detoxification in mussel tissues (Marigómez et al., 1990; Slobodskova et al., 2022; Soto et al., 1997). In addition to metal uptake from the surrounding environment through the gills and digestive glands, another possible uptake or transport pathway of metals is from the gills toward the digestive glands via hemocytes (Giamberini et al., 1996; Weng et al., 2022). A previous study reported that the hydrothermal vent mussel (*Bathymodiolus marisindicus*) had a greater capacity to detoxify metals than the snail (*Gigantopelta aegis*) (Ma and Wang, 2021). Fig. 6 shows the relationship between Cu and Zn isotopic compositions for mussel organs. Differences among organs were greater for Cu than for Zn, and no correlation was observed between the two isotopes.

Cu isotope values (δ^{65}Cu) in vent mussels and sea snails in this study were comparable to those of South Pacific deep seawater (~0.49 ‰, converted to AE647; Gueguen et al., 2022), however, they are significantly heavier than those observed in hydrothermal crust (~−0.01 ‰, converted to AE647; Gueguen et al., 2022). The similarity in Cu isotope composition between deep-sea organisms and seawater implies that Cu accumulated in vent mollusks may be more associated with the soluble phase. Conversely, the Zn isotope signatures in vent mollusks exhibited different characteristics depending on the species. *Bathymodiolus* and *Ifremeria* species had lighter Zn isotopic compositions (δ^{66}Zn) than those of the hydrothermal crust (~0.49 ‰, converted to IRMM3702; Gueguen et al., 2022) and South Pacific deep seawater (~0.9 ‰, converted to IRMM3702; Gueguen et al., 2022). In contrast, *Alviniconcha* sp. displayed heavier Zn isotopic values than these references. Zn isotopes in mussels (*Bathymodiolus*) were positively correlated with Al, V, Cr, Fe, Ni and Zn concentrations, whereas *Ifremeria* sp. was negatively correlated with most metals (Table S45). Unlike *Bathymodiolus* and *Ifremeria*, *Alviniconcha* showed very weak correlations between metals (Table S46). These findings suggest notable disparities in metal uptake and accumulation mechanisms among species, even when they inhabited the same geographical region.

Hydrothermal vent mollusks, including *Bathymodiolin* mussels, *Ifremeria nautilei*, and *Alviniconcha* sp., exhibit distinct ecological and physiological adaptations driven by differences in their symbiotic relationships, metabolic pathways, and habitat preferences (Beinart et al., 2015, 2019; Petersen and Dubilier, 2009; Podowski et al., 2009; Sanders et al., 2013; Waite et al., 2008). *Bathymodiolin* mussels host symbiotic bacteria within specialized gill bacteriocytes, with most species harboring sulfur-oxidizing symbionts, while only some also host methane-oxidizing symbionts (Duperron et al., 2008; Petersen and Dubilier, 2009). These mussels have reduced digestive systems, relying primarily on their symbionts for nutrition (Gustafson et al., 1998). *Ifremeria* harbors a single Gammaproteobacterial sulfur-oxidizing symbiont and primarily inhabits peripheral vent areas, whereas *Alviniconcha* hosts multiple symbiont lineages, including Campylobacteria, in more extreme, hydrogen- and sulfur-rich vent environments (Beinart et al., 2019; Podowski et al., 2009). These species-specific differences in symbiotic metabolism and host physiology contribute to their niche partitioning within hydrothermal vent ecosystems. Additionally, variation in metal accumulation may be linked to species-specific nutrient acquisition strategies and anatomical adaptations. According to Ma and Wang (2021), Zn uptake mechanisms differ among hydrothermal vent mollusks due to symbiont-mediated processes, which may influence Zn transport and distribution within host tissues. These physiological distinctions are likely to drive the interspecies differences observed in our isotope data.

Previous biomonitoring studies of metals in bivalve mollusks were conducted by separating the soft and hard tissues, and focused on analyzing metal concentration in various soft tissue organs (Abderrahmani et al., 2020; Akagi and Edanami, 2017; Giarratano et al., 2010; Xu et al., 2022). To date, such studies using Zn and Cu isotopes have been limited to understanding their relevance to environmental pollution in connection to the whole soft tissues of mussels and oysters (Araújo et al., 2021; Jeong et al., 2021b). In the present study, elemental and Zn—Cu isotopic signatures of hydrothermal vent mollusks suggested organ- and species-specific differences in metal accumulation mechanisms within extreme marine ecosystems. Our findings highlight variation in metal bioaccumulation and isotopic fractionation associated with biological processes, shedding light on uptake pathways across different species and organs. Notably, Zn exhibited greater intratissue isotopic variability than Cu in gastropods, suggesting its potential as a sensitive

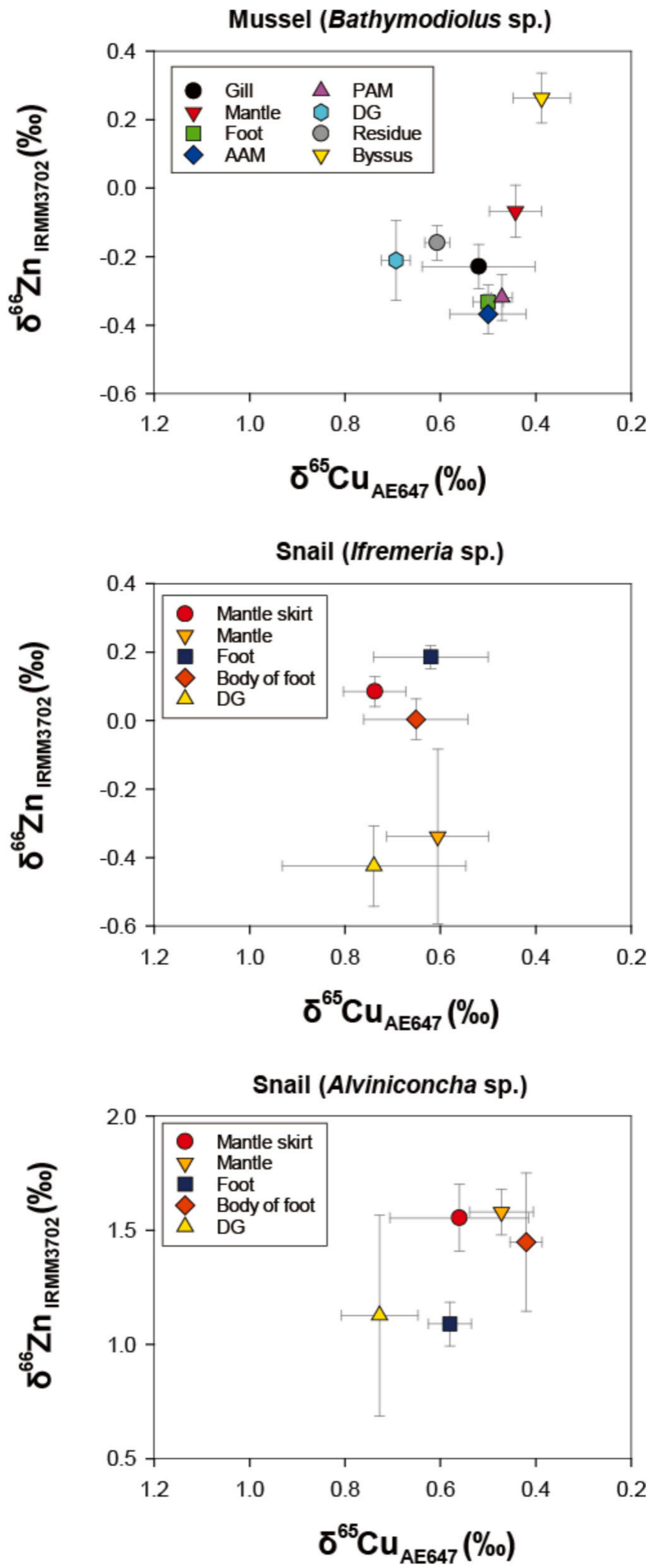

Fig. 6. Relationships between Cu and Zn mean isotopic compositions in the hydrothermal vent mussel (*Bathymodiolus* sp.) and the sea snails (*Ifremeria* sp. and *Alviniconcha* sp.). Error bars represent standard deviation (1sd).

tool for tracing metabolic pathways and metal bioaccumulation mechanisms. The morphological and/or functional classification of mollusk organs, combined with the application the Zn and Cu isotopes, will improve our understanding of the mechanisms of metal uptake, accumulation and detoxification in marine organisms.

CRediT authorship contribution statement

Hyeryeong Jeong: Writing – review & editing, Writing – original draft, Visualization, Validation, Investigation, Formal analysis, Conceptualization. **Kongtae Ra:** Writing – review & editing, Visualization, Methodology, Funding acquisition, Formal analysis. **Daniel F. Araújo:** Writing – review & editing, Validation. **Se-Jong Ju:** Writing – review & editing, Validation, Resources.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2025.179599.

Data availability

Data will be made available on request.

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