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Lanthanum anomalies provide constraints on macrofaunal predation at methane seeps

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Abstract



The feeding habits and predation behaviour of organisms can exert significant control on the dynamics of local food webs. Yet, little is known about the effects of predation on the material and trophic transfer dynamics in chemosynthesis-based ecosystems. Here, we investigated the rare earth element (REE) composition of soft tissues and hardparts for thiotrophy-dependent vesicomyid clams (*Archivesica marissinica*), aerobic methanotrophy-dependent bathymodiolin mussels (*Gigantidas haimaensis*), in addition to turrid gastropods (*Phymorhynchus buccinoides*) and parasitic scale worms (*Branchiopolynoe pettiboneae*) from the Haima seeps of the South China Sea; the latter two species are predators feeding on mussels. Our goal was to determine if the specific, microbially-derived, light REE enrichment characteristics of seep mussels can be transferred to the biomass of their predators. The vesicomyid clams were found to exhibit light REE patterns similar to that of seawater. In contrast, the bathymodiolin mussels, turrid gastropods, and scale worms revealed pronounced lanthanum (La) enrichment, agreeing with substantial transfer of La within the local food web. The observed enrichment of La in seep dwelling predators represents an independent method for monitoring the dynamics within seep ecosystems and potentially for assessing faunal interactions in ancient chemosynthesis-based ecosystems.

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Introduction

Understanding food web structures is essential for comprehending the composition, functionality, and stability of ecosystems. Predation is a crucial component of food web structures and plays a vital role in regulating the population dynamics and maintaining population equilibrium within an ecosystem. Predator-prey interactions also influence species distribution across trophic levels, affecting the flow of energy and matter within the ecosystem. These interactions, in conjunction with adaptation and evolution, contribute to the complexity of food webs and ecological networks. Overall, predator-prey relationships are recognised as important mechanisms in structuring ecosystems (van Denderen *et al.*, 2018).

Submarine seep ecosystems are found worldwide along continental margins (Levin *et al.*, 2016). Unlike ecosystems that rely on photosynthesis, seeps are typified by chemosynthesis-based ecosystems that primarily obtain energy from the

oxidation of reduced compounds like methane and hydrogen sulfide. These ecosystems are typified by a low diversity but high abundance of the dominant species (Jørgensen and Boetius, 2007). The community structure is influenced by the availability of energy sources, as well as other factors such as predation, water depth, substrate type, and ecological succession (MacAvoy *et al.*, 2002; Morganti *et al.*, 2022).

The impact of predation on the community structure of seep ecosystems is still not fully understood (Levin *et al.*, 2016). Previous studies have suggested that predators in these ecosystems do not play a dominant role and their influence is typically considered modest (Portail *et al.*, 2016). However, some studies have shown that predation can facilitate trophic transfer and regulate species diversity in seep ecosystems (MacAvoy *et al.*, 2002; Olsen *et al.*, 2014). For example, predation pressure has been found to be the main factor behind the inverse correlation between macrofauna and meiofauna/nematode densities

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among the seep benthos (Van Gaever *et al.*, 2009). Predation by metazoans may also explain the differences in copepod abundance between mussel beds and tubeworm colonies at seeps in the Gulf of Mexico (Plum *et al.*, 2015). Moreover, seeps serve as nurseries for deep sea predators, which can greatly affect the diversity of animal species along continental margins (Treude *et al.*, 2011; Danovaro *et al.*, 2022). Understanding the variables influencing the community composition of seep ecosystems, particularly the role of predation, is crucial for comprehending the succession dynamics and the evolution of chemosynthesis-based faunas in Earth history (Treude *et al.*, 2011; Kiel *et al.*, 2016).

Bathymodiolin mussels serve as an ideal focal point for investigating the trophic transfer and the turnover of material within seep ecosystems. Regarding their trophic level, mussels can be classified as primary consumers (Portail *et al.*, 2016). Seep dwelling mussels rely on endosymbiotic primary producers, such as methanotrophic and/or thiotrophic bacteria. In turn, mussels serve as prey for higher level consumers. Representative examples of these higher level consumers include the turrid gastropod *Phymorhynchus buccinoides* and the scale worm *Branchipolynoe pettiboneae* at the Haima seeps of the South China Sea (Fujikura *et al.*, 2009; Takahashi *et al.*, 2012).

Turrid gastropods of the genus *Phymorhynchus* are common in various deep sea habitats such as hydrothermal vents, hydrocarbon seeps, and sunken wood, where they are unspecialised predators that benefit from the high mass of available food in these ecosystems (Sasaki *et al.*, 2010). Stable carbon and nitrogen isotope analysis conducted on *P. buccinoides* specimens collected at the Haima seeps indicated a dependence on local chemosynthetic carbon sources, with the gastropods taking up methane-derived carbon through predation (Ke *et al.*, 2022). *Phymorhynchus* has a well developed, funnel-shaped rhynchostome that facilitates its predatory behaviour (Warén and Bouchet, 2001), and fragments of various organisms in the gut of *Phymorhynchus* have been documented (Sasaki *et al.*, 2010). Its predation on mussels has been demonstrated by *in situ* behavioural observations and bait trap experiments as well as anatomic examination (Fujikura *et al.*, 2009).

Scale worms can thrive in a wide range of habitats and frequently engage in a ‘parasitic’ relationship with mussels within seep ecosystems (Becker *et al.*, 2013; Yao *et al.*, 2022). Previous stable isotope analyses conducted on scale worms from hydrocarbon seeps indicated their reliance on chemosynthesis-based biomass (Becker *et al.*, 2013; Ke *et al.*, 2022). Based on their jaw structure, it has been inferred that the scale worms exhibit predatory behaviour (Fauchald and Jumars, 1979). Likewise, mussel fragments have been discovered among the stomach contents of the parasitic scale worm *Branchipolynoe symmytilida* (Desbruyères *et al.*, 1985). Nitrogen stable isotope compositions of amino acids of the scale worm *B. pettiboneae* and its host mussel indicate that the mussel serves as the primary source of amino acids for the adult parasitic worm (Takahashi *et al.*, 2012). Parasitism of *B. pettiboneae* within *G. haimaensis* was confirmed and described in detail by Yao *et al.* (2022).

Here, we developed a new approach to quantify the trophic transfer among seep macrofauna (the thiotrophy-dependent vesicomyid clam *Archivesica marissinica*, the aerobic methanotrophy-dependent bathymodiolin mussel *Gigantidas haimaensis*, the heterotrophic turrid gastropod *P. buccinoides*, and the scale worm *B. pettiboneae*) from the Haima seeps of the South China Sea (Fig. 1, Table S-1), with the latter two species known to be feeding on mussels. We analysed the contents of rare earth elements (REEs), particularly lanthanum (La), of these species to evaluate the predation dynamics in seep ecosystems. This

approach is based on the facts that (1) the occurrence of La anomalies in seep dwelling metazoans is a robust fingerprint of methanotrophy since the second step in the aerobic oxidation of methane ($\text{CH}_3\text{OH} \rightarrow \text{HCHO}$) can be catalysed by La (Semrau *et al.*, 2018; Wang *et al.*, 2020), and (2) aerobic methanotrophy-dependent mussels are ubiquitous in seep ecosystems (Wang *et al.*, 2022).

Results

The contents of light REEs in the four examined metazoan species vary from several ng/g to several hundred ng/g. Notably, only two samples of bathymodiolin mussels exhibit contents at the $\mu\text{g/g}$ level (Tables S-2 to S-5). The distribution patterns of REEs in the chemosymbiotic bivalves align with previous studies – the REE compositions of the clams fall between the compositions of terrigenous sediments and seawater, lacking light REE enrichment (Fig. S-2), while the light REE contents in the gills of the mussels are one order of magnitude higher than contents in the clams, particularly with respect to La (Fig. S-3). The scale worms as a whole and some of types of soft tissue (gills and visceral mass) of the turrid gastropods reveal an enrichment of La (Figs. S-4, S-5). However, no such enrichment was observed in the shells of the turrid gastropods (Fig. S-4).

Discussion

By determining the La and Ce anomalies (La/La^* and Ce/Ce^* ; Eq. 1 and 2; cf. Barrat *et al.*, 2023)

$$\text{La/La}^* = \text{La}_{\text{sn}} \times \text{Nd}_{\text{sn}}^2 / \text{Pr}_{\text{sn}}^3 \quad \text{Eq. 1}$$

$$\text{Ce/Ce}^* = \text{Ce}_{\text{sn}} \times \text{Nd}_{\text{sn}} / \text{Pr}_{\text{sn}}^2 \quad \text{Eq. 2}$$

for four invertebrate species from the Haima seeps, we find that the REE patterns of the thiotrophy-dependent *A. marissinica* resemble the REE compositions of other seep dwelling clams (Wang *et al.*, 2020). Additionally, the La anomaly ($\text{La/La}^* = 1.15\text{--}2.64$) observed for *A. marissinica* is similar to that of thiotrophy-dependent mussels from seeps on the Costa Rica margin (Barrat *et al.*, 2022a). The Ce anomaly in *A. marissinica* soft tissue ($\text{Ce/Ce}^* = 0.23\text{--}1.02$) is typically lower than that of its shells ($\text{Ce/Ce}^* = 1.08\text{--}1.42$). The presence of positive Ce anomalies in shells, agreeing with reducing conditions, is likely indicative of the clams’ semi-infaunal lifestyle. In contrast, the shells of the epifaunal mussel *G. haimaensis* yielded minor negative Ce anomalies ($\text{Ce/Ce}^* = 0.90\text{--}1.03$), reflecting their exposure to oxic seawater. The La anomalies of mussel shells ($\text{La/La}^* = 2.10\text{--}3.71$) are similar to previous findings ($\text{La/La}^* = 2.50\text{--}3.92$, Wang *et al.*, 2020) – slightly higher than the La anomalies of *Gigantidas* shells from the Brine Pool and Bush Hill sites of the Gulf of Mexico ($\text{La/La}^* = 1.73\text{--}2.70$), but significantly lower than the anomalies of two *Bathymodiolus* shells from Edison Seamount ($\text{La/La}^* = 7.88\text{--}11.89$; Barrat *et al.*, 2022a). While the magnitude of the mussels’ La anomaly could possibly relate to the efficiency of La utilisation during aerobic oxidation of methane by their symbiotic bacteria (Lin *et al.*, 2023), understanding the cause of the variability of La enrichment in seep mussels requires further investigation.

Although the observed patterns suggest that aerobic methanotrophy-dependent mussels are typified by a distinctive accumulation of light REEs (Fig. S-3), it appears that these mussels cannot be differentiated from thiotrophy-dependent clams solely based on the extent of the La anomaly. We therefore suggest employing a $(\text{La/Nd})_{\text{sn}}$ vs $(\text{Pr/Nd})_{\text{sn}}$ diagram as a means of differentiation (Fig. 2; cf. Wang *et al.*, 2020; Barrat *et al.*, 2022a, 2023). In this diagram, clam soft tissues are primarily situated



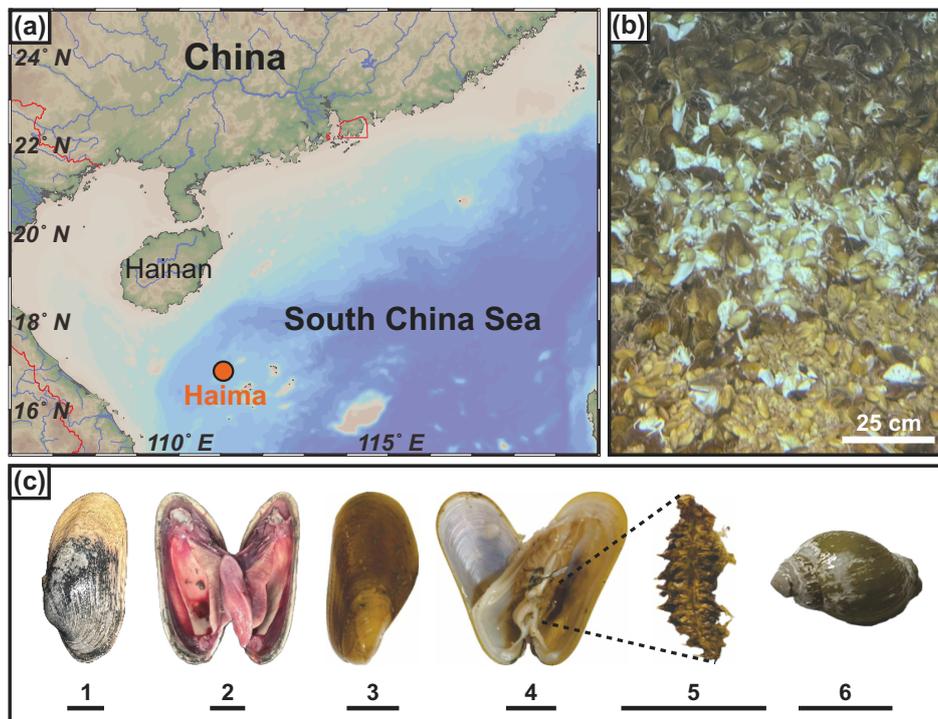


Figure 1 (a) Approximate sampling location (Haima seeps). (b) Coexisting *Gigantidas haimaensis* (periphery) and *Phymorhynchus buccinoides* (centre) on the seabed. (c) Species investigated in this study. (c1-c2) *Archivesica marissinica*; (c3-c4) *G. haimaensis*; (c5) *Branchipolynoe pettiboneae*; (c6) *P. buccinoides*. Note that in c4, *B. pettiboneae* is parasitic in *G. haimaensis*. Scale bars are 3 cm.

in the lower left corner, with $(\text{La}/\text{Nd})_{\text{sn}}$ ranging from 0.93 to 2.14 and $(\text{Pr}/\text{Nd})_{\text{sn}}$ ranging from 0.85 to 1.05. Similarly, clam shells occupy the same region of the diagram, with $(\text{La}/\text{Nd})_{\text{sn}}$ ratios ranging from 0.99 to 1.22 and $(\text{Pr}/\text{Nd})_{\text{sn}}$ ratios ranging from 0.84 to 0.91. In contrast, mussel soft tissue – $(\text{La}/\text{Nd})_{\text{sn}} = 1.25\text{--}16.51$, $(\text{Pr}/\text{Nd})_{\text{sn}} = 0.83\text{--}2.22$ – and shells – $(\text{La}/\text{Nd})_{\text{sn}} = 3.60\text{--}8.28$, $(\text{Pr}/\text{Nd})_{\text{sn}} = 1.20\text{--}1.35$ – tend toward the upper right quadrant of the diagram.

With mussels being part of the diet of the predatory gastropod *Phymorhynchus* (Fujikura *et al.*, 2009; Sasaki *et al.*, 2010), it is likely that the gastropod assimilates some components of the mussels, and consequently could also acquire the mussels' La enrichment. Indeed, our findings show that the La ($\text{La}/\text{La}^* = 1.08\text{--}3.39$) and Ce anomalies ($\text{Ce}/\text{Ce}^* = 0.40\text{--}1.01$) of *P. buccinoides* closely resemble those of mussels. Predation on mussels is further in accord with the $(\text{La}/\text{Nd})_{\text{sn}}$ ratios from 1.02 to 3.43, and the $(\text{Pr}/\text{Nd})_{\text{sn}}$ ratios from 0.88 to 1.14 found in the gills of *P. buccinoides*. The same argument applies to the composition of the gastropod's visceral mass with $(\text{La}/\text{Nd})_{\text{sn}}$ ratios ranging from 2.86 to 4.05 and $(\text{Pr}/\text{Nd})_{\text{sn}}$ ratios ranging from 1.04 to 1.25. The shells of *P. buccinoides* ($n = 5$), with $(\text{La}/\text{Nd})_{\text{sn}}$ ratios ranging from 1.04 to 1.40 and $(\text{Pr}/\text{Nd})_{\text{sn}}$ ratios ranging from 0.81 to 0.89, do not exhibit significant enrichment of light REEs. Further measurements of additional predatory species with fossilisable hard parts would be needed to test whether this approach can be applied to ancient seep deposits (Kiel *et al.*, 2016).

Scale worms of the genus *Branchipolynoe* are known to parasitise within bathymodiolin mussels (Desbruyères *et al.*, 1985; Becker *et al.*, 2013), and it can therefore be anticipated that they will exhibit positive La anomalies similar to those observed in *P. buccinoides*. Indeed, specimens of *B. pettiboneae* are found to exhibit positive La anomalies ($\text{La}/\text{La}^* = 2.55\text{--}14.23$, $(\text{La}/\text{Nd})_{\text{sn}} = 2.18\text{--}17.42$), likely due to the long term parasitic relationship between the scale worm and mussels, where the

scale worm's diet is essentially mussel based. *Phymorhynchus* gastropods, on the other hand, display more omnivorous feeding habits. Interestingly, the degree of the La anomaly in the scale worms is found to be even higher than that of its host mussels (Fig. 2). A potential and simple explanation is that in predator-prey relationships, metal elements become more enriched in organisms of higher trophic levels (biomagnification effect), as in the case of mercury accumulation in the food chain of aquatic organisms (Sun *et al.*, 2020). In summary, *B. pettiboneae* and some of the soft tissues of *P. buccinoides* (gills and visceral mass) exhibit significant enrichment of La. The corresponding La anomalies reflect the interaction between these predatory metazoan species and the aerobic methanotrophy-dependent *G. haimaensis* mussels within the food web structure of the Haima seep ecosystem (Fig. 3).

Finally, we put forward a Bayesian mixing model for assessing the relative contributions of various end members based on the degree of light REE enrichment, with particular focus on the La anomaly. The underlying principle of this method resembles the determination of nutritional interactions among large animals in chemosynthesis-based ecosystems using stable isotopes (Ke *et al.*, 2022). The method is described in detail in the Supplementary Information. In short, the calculation indicates that the proportion of the La anomaly originating from the bathymodiolin mussels – and consequently the food sources – of *P. buccinoides* at the Haima seep site is approximately 50.4 %. This proportion is very similar to the value obtained through the estimate based on stable carbon isotopes (51.0 %; Fig. S-6). When applied to the *B. pettiboneae* from the Haima seep site, the proportion of La anomaly originating from the bathymodiolin mussels is approximately 87.9 %; a proportion almost identical to the value obtained with carbon isotopes (~88.5 %; Fig. S-7). Such estimates suggest that the cycling of La and carbon between trophic levels in seep ecosystems is similar and conservative.

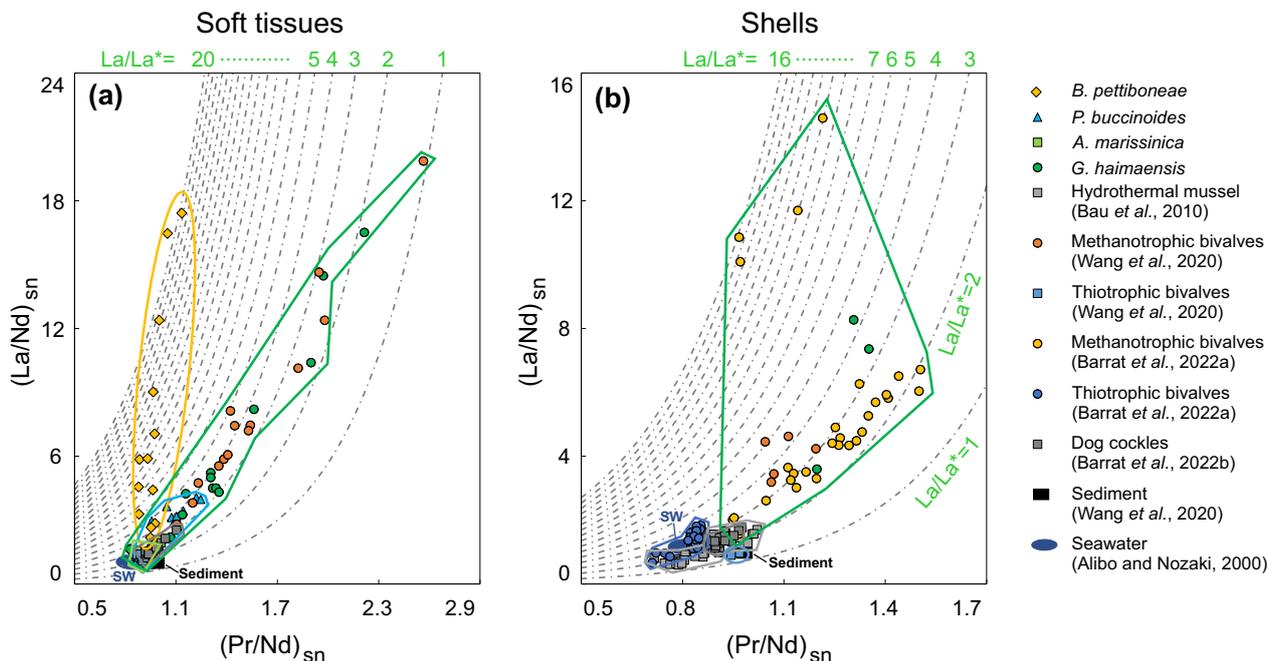


Figure 2 $(La/Nd)_{sn}$ vs. $(Pr/Nd)_{sn}$ plots for (a) soft tissues and (b) shells of various macrofauna from the Haima seeps. Previous work (Bau et al., 2010; Wang et al., 2020; Barrat et al., 2022a,b), seawater (SW; Alibo and Nozaki, 2000) and sediment from the Haima seeps (Wang et al., 2020) are shown for comparison.

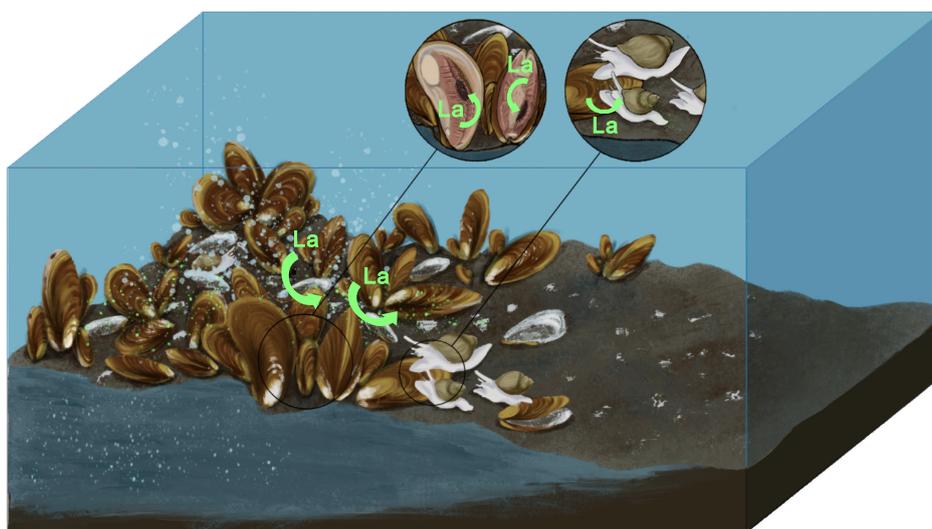


Figure 3 Conceptual diagram of predator-prey interactions within seep ecosystems. La = lanthanum.

Conclusions and Perspectives

Rare earth element (REE) analyses of four invertebrate taxa from the Haima seeps of the South China Sea, the thiotrophy-dependent vesicomyid clam *Archivesica marissinica*, the aerobic methanotrophy-dependent bathymodiolin mussel *Gigantidas haimaensis*, the turrid gastropod *Phymorhynchus buccinoides*, and the scale worm *Branchiopolynoe pettiboneae*, revealed that REE compositions faithfully record predation on bathymodiolin mussels by the gastropod and the scale worm. By using a Bayesian mixing model, we have developed a new approach for evaluating the trophic transfer within the food chain at seeps based on REE abundances. Our results suggest that approximately 50 % of the food consumed by the gastropod is sourced from the mussels, whereas mussels could represent up to 90 % to

the diet of the scale worm. The novel REE geochemistry approach presented here provides a promising tool for studying the community structure and predator-prey interactions in seep dwelling organisms.

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Additional Information

Supplementary Information accompanies this letter at <https://www.geochemicalperspectivesletters.org/article2420>.



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