frontiers | Frontiers in Marine Science

TYPE Perspective
PUBLISHED 24 May 2023
DOI 10.3389/fmars.2023.1167803

OPEN ACCESS

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RECEIVED 16 February 2023
ACCEPTED 12 May 2023
PUBLISHED 24 May 2023

CITATION
Hughes IV and Girguis PR (2023) A molluscan class struggle: exploring the surprisingly uneven distribution of chemosymbiosis among two major mollusk groups.
Front. Mar. Sci. 10:1167803.
doi: 10.3389/fmars.2023.1167803

A molluscan class struggle: exploring the surprisingly uneven distribution of chemosymbiosis among two major mollusk groups

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Many bivalves and gastropods from marine reducing environments such as deep ocean hydrothermal vents and seeps host chemosynthetic bacteria in a nutritional symbiosis. Despite their functional similarities, the distribution of chemosymbiosis in these two mollusk classes is surprisingly uneven: the number of bivalve species known to host chemosynthetic symbionts is more than twenty times that of gastropods, and chemosymbiotic bivalves are reported from a far greater diversity of marine habitats. Here we explore the potential drivers for this trend, including but not limited to physiological differences, habitat characteristics, and sampling bias. Sampling bias likely contributes to the magnitude of the observed discrepancy, but we posit that the phenomenon itself reveals how intrinsic (e.g. morphology) and extrinsic (e.g. organic matter availability) factors might have shaped the distribution of extant gastropod and bivalve associations. These observations also serve as an impetus for increasing investigation into gastropods and other mollusks from chemically reducing environments to better understand the evolution and ecology of chemosymbiosis among molluscan hosts.

KEYWORDS

Bivalvia, chemosynthesis, Gastropoda, Mollusca, symbiosis

1 Introduction

Chemosynthetic symbioses between eukaryotes and chemoautotrophic microbes have been reported in diverse metazoan phyla and in numerous marine environments. In nutritional chemosynthetic symbiosis, bacterial symbionts oxidize reduced chemical substrates, e.g., sulfide, to harness energy for carbon fixation. Symbionts then translocate fixed organic carbon to the host or are digested by the host (Cavanaugh et al., 2006; Dubilier et al., 2008; Sogin et al., 2020). A large portion of metazoan host diversity is represented by mollusks, specifically gastropods and bivalves. Chemosymbiotic mollusks are abundant in many chemically reducing environments, including deep sea hydrothermal vents and hydrocarbon seeps (Sasaki et al., 2010), wood and whale falls (Smith et al., 1989; Duperron, 2010), continental shelf sediments (Cary et al., 1989), and many shallow water sulfidic sedimented environments (Cavanaugh, 1983).

Notably, bivalves and gastropods have independently acquired chemosynthetic symbionts in multiple lineages. However, and unexpectedly, this adaptation appears unequally distributed between these groups, both with respect to the number of species represented and the diversity of chemosynthetic habitats where they are found. Among Bivalvia, there over 600 described species of chemosymbiotic bivalves, across at least six families (Distel, 1998; Taylor and Glover, 2010) that span a suite of marine reducing habitats, including less conventional chemosynthetic environments, like coral reef sediments (Dekker and Goud, 1994) and sewage outfalls (Burd et al., 2013). Among Gastropoda, the total number of known chemosymbioses is an order of magnitude fewer than in Bivalvia, although there are representative species in four of the six subclasses. Further, unlike their bivalve counterparts, only two potential gastropod chemosymbioses occur in shallow water environments (Smriglio and Mariottini, 2002; Judge and Haszprunar, 2014), while the rest are reported from hydrothermal vents and related deep-water environments. These observed patterns are surprising given that Gastropoda is an extraordinarily diverse clade and contains three-fold more marine species than Bivalvia (species are an incomplete proxy for diversity but provide a means of illustrating the disparities between these two classes; WoRMS Editorial Board, 2023).

Gastropods and bivalves share similarities in basic anatomy, physiology, and life history, which begs the question as to what factor(s) account for this disparity. Here we briefly summarize chemosymbiosis in bivalves, review known gastropod chemosymbioses, then consider differences between bivalves and gastropods that may account for the observed disparities in the diversity of chemosymbioses between these two molluscan classes.

2 Bivalve chemosymbiosis

Chemosymbiosis is well documented in many bivalve groups (see Taylor and Glover (2010) for review). The bivalve families that contain chemosymbiotic taxa are Lucinidae, Thyasiridae, Solemyidae, Vesicomyidae, Teredinidae, and Mytilidae (there is circumstantial evidence for chemosymbiosis in several members of Nucinellidae and at least one species in the bivalve family Basterotiidae, though nutritional chemoautotrophy has not yet been demonstrated; Oliver and Taylor 2012; Oliver, 2013). Most recorded bivalve chemosymbionts belong to Gammaproteobacteria (Sogin et al., 2021), however the nature of symbioses varies considerably in metabolism, transmission modes, and host-symbiont nutrient exchange.

Lucinidae is the most species rich group of chemosymbiotic bivalves, with over 400 species described worldwide (WoRMS Editorial Board, 2023). To date, all lucinids are obligately chemosymbiotic (Taylor and Glover, 2010). Although lucinids occur at hydrothermal vents and methane seeps (Sibuet and Olu, 1998; Glover et al., 2004), much of the diversity is found in shallow-water sediments rich in sulfide (Taylor and Glover, 2006).

Thyasirids are the second most species rich group of chemosymbiotic bivalves, however there are considerably fewer studies on the diversity and nature of Thyasiridae symbioses (Taylor et al., 2007). Chemosymbiosis is not obligate for all Thyasiridae (Taylor et al., 2007), and reliance on chemosynthetically fixed carbon varies substantially among the chemosymbioses (Dando and Spiro, 1993). One thyasirid species hosts endosymbionts (Fujiwara et al., 2001), whereas others appear to exclusively host extracellular symbionts on the gill surface (Southward, 1986).

Solemyidae is a unique family of bivalves with three genera (*Solemya*, *Acharax* and *Petrasma*) from diverse reducing habitats (e.g., Stanley, 1970; Neulinger et al., 2006; Coan et al., 2000). Most solemyids supplement symbiosis with heterotrophic filter feeding, though there are exceptions, such as *Solemya reidi*, that lacks the capacity to filter-feed as an adult (Felbeck, 1983; Stewart and Cavanaugh, 2006). The Nucinellidae are another bivalve family in the order Solemyida with taxa found in a range of marine habitats, including deep sea sediments (Sasaki et al., 2005) and tropical seagrass beds (Glover and Taylor, 2013). Chemosymbiosis has been inferred in this group as some nucinellids have a reduced or absent gut (Kuznetsov, 1984) and bacteriocytes are present in the gill tissue of at least two species (Oliver and Taylor, 2012). However, empirical assessments of chemoautotrophic activity in these taxa are wanting.

Vesicomyidae are another family of chemosymbiotic bivalves, primarily occurring at hydrothermal vents, hydrocarbon seeps, and whale falls (Bennett et al., 1994; von Cosel and Salas, 2001). There are over 100 described species in the family, and all members studied host chemosymbionts (Fisher, 1990; Krylova et al., 2010). Many vesicomyids have been shown to use their foot to uptake reduced sulfur compounds and transport them to symbionts in the gills (Arp et al., 1984).

Teredinidae are well known for their heterotrophic bacterial symbiosis, which aids in breaking down wood (O'Connor et al., 2014), though at least one species hosts sulfide-oxidizing symbionts in the gills. While other teredinids bore into wood, the giant shipworm, *Kuphus polythalamia*, occurs in muddy sediments and utilizes thioautotrophic symbionts in a nutritional chemosymbiosis (Distel et al., 2017).

Finally, within the family Mytilidae, the subfamily Bathymodiolinae is a group of mussels found in hydrothermal vents, methane seeps, and wood and whale falls (Duperron et al., 2009). Bathymodiolins are primarily epibenthic and are often densely packed in chemosymbiotic habitats. Although the majority of species host chemosymbionts either intracellularly or extracellularly, at least one species in the genus *Idas* is reported as a predator on other mollusks and appears asymbiotic, likely representing a secondary loss of chemosymbionts (Ockelmann and Dinesen, 2011; Rodrigues et al., 2015). Bathymodiolins host symbionts with a variety of metabolic pathways, including methane, complex hydrocarbons, sulfide, and hydrogen metabolisms (Childress et al., 1986; Duperron et al., 2005; Petersen et al., 2011; Rubin-Blum et al., 2017).

3 Chemosymbiosis in Gastropoda

As previously mentioned, evidence for chemosymbiosis has been reported in taxa from four of the six gastropod subclasses, though relatively less work has been done on the evolution and diversity of chemosymbiotic gastropods (reviewed in Table 1). Among caenogastropods, the sister genera *Alviniconcha* and *Ifremeria* host chemosynthetic endosymbionts in the gills (Stein et al., 1988; Endow and Ohta, 1989; Windoffer and Giere, 1997). Both taxa are found at hydrothermal vents where they can form large aggregations around vent effluent (Bouchet and Warén, 1991; Desbruyères et al., 1994). *Alviniconcha* and *Ifremeria* co-occur around Pacific hydrothermal vents, but their symbionts likely rely on different chemically-reduced compounds that might alleviate niche competition (Henry et al., 2008; Waite et al., 2008; Beinart et al., 2015).

The Neomphaliones family Peltospiridae contains several chemosymbiotic taxa from hydrothermal vent sites in the Pacific, Southern and Indian oceans. Perhaps the most striking member of this family is *Chrysomallon squamiferum*, or the "scaly foot snail", so named as it secretes iron-rich sclerites on the foot (Warén et al., 2003). *C. squamiferum* and members of the peltospirid genus *Gigantopelta* host sulfur-oxidizing bacterial endosymbionts in an enlarged esophagus (Goffredi et al., 2004; Chen et al., 2017). Other peltospirids from vents, namely the *Ctenopelta* and *Hirtopelta*, have been suggested as chemosymbiotic due to a reduced digestive tract (Warén and Bouchet, 1993), and, at least in the case of *Hirtopelta*, hypertrophied gills (Fretter, 1989; McLean, 1989; Warén and Bouchet, 1993). Bacteriocytes have also been observed in the gill tissue of *H. tufari*, though the identity of these potential symbionts is unknown (Beck, 2002). Finally, another Neomphaliones gastropod suggested as chemosymbiotic is *Cyathermia naticoides*. This species is endemic to the East Pacific Rise vents and is often found in abundance on *Riftia* tubes (Warén and Bouchet, 1989). Campylobacteria have been reported extracellularly on gill tissue of this species in association with lysosomes, indicating possible endocytotic digestion (Zbinden et al., 2015).

Lepetodrilus is a Vetigastopoda genus found at a diversity of hydrothermal vent communities. Of the 16 described species, two sister taxa from the Juan de Fuca Ridge are described as chemosymbiotic: *L. fucensis* and *L. gordensis* (De Burgh and Singla, 1984; McLean 1988; Johnson et al., 2006). Both species host bacteria on the external surface of the gills, whereas other *Lepetodrilus* species appear devoid of dense gill microbes (Bates, 2006). *L. fucensis* was among the first vent gastropods to be described as chemosymbiotic, and De Burgh and Singla (1984) implicate endocytosis and lysosomal digestion of episymbionts as a type of "symbiont farming". Around hydrothermal vent effluent, *Lepetodrilus fucensis* can form aggregated stacks of individuals with a density of over 300,000 individuals m-2 (Bates et al., 2005). *L. fucensis* also filter feed and graze to supplement their nutrition (Bates, 2007a).

Bacteriocytes have also been described in the mantle of *Lepetella sierrai*, a gastropod found in the Bay of Biscay in association with empty tubes of polychaetes in the genus *Hyalinoecia* (Dantart and Luoue, 1994). It is hypothesized that these polychaete tubes provide an anoxic, sulfidic environment that supports chemosynthesis (Judge and Haszprunar, 2014). Further molecular or physiological work is needed to confirm the nature of this potential non-vent chemosymbiosis.

Two heterobranch gastropods have also been suggested as chemosymbiotic. The first, *Parvaplustrum wareni*, occurs at hydrothermal vents in the Bering Sea in densities of up to 31,000 individuals/m-2 (Chaban et al., 2022). Evidence for chemosymbiosis in this taxon comes from the dense aggregates of bacteria that occur externally on gill filaments. *Lurifax vitreus* is an orbitestellid gastropod originally described from hydrothermal vents on the Mid Atlantic Ridge (Warén and Bouchet, 2001). Bacteriocytes have been identified in the mantle of this gastropod based on TEM microscopy (Hawe et al., 2014). Individuals of *L. vitreus* have also been described from non-vent environments in Mediterranean Sea (Smriglio and Mariottini, 2002; Giuste and Sbrana, 2012), though these identifications were made from shells collected by dredges, and soft parts were not examined.

4 The uneven distribution of chemosymbiosis among molluscs

As described above, to our knowledge there are at least 600 likely and confirmed bivalve chemosymbioses that span a wide array of chemically reducing environments. In contrast, to our knowledge there are approximately 19 likely and confirmed gastropod chemosymbioses that are found in far fewer chemically reducing environments, namely select hydrothermal vents and, putatively, Polychaetae tubes and Mediterranean sediments (Smriglio and Mariottini, 2002; Judge and Haszprunar, 2014). It is highly likely that sampling bias towards bivalves has a marked influence on the realized disparity. That said, even in chemosynthetic environments where both bivalves and gastropods are present and well-studied (e.g., seagrass beds and hydrothermal vents), chemosymbiotic bivalves are far more diverse. We thus raise the question of what other factors may have collectively resulted in this phenomenon. In the paragraphs below we consider the roles of environmental medium (including sulfide toxicity), physiology, habitat productivity, motility, and our biases in the definition of chemosymbioses.

4.1 Environmental medium

Chemosymbiosis often occurs at the interface between oxic and anoxic environs (Stewart et al., 2005). At hydrothermal vents, chemically reduced substrates are replete in the vent fluids that often emanate from cracks in the basaltic crust (or emerge from polymetallic sulfide deposits). At mud flats, seagrass sediments, and many other habitats that harbor chemosymbioses, chemically

TABLE 1 Summary of known gastropod chemosymbioses.

Taxonomy			Environment		Morphology				Behavior		Refs
Subclass	Family	Genus and Species	Chemosynthetic Environment	Geographical Distribution	Hypertrophied Gills	Digestive System Adaptations	Symbiont Location	Symbiont Classification(s)	Aggregation	Supplementary Grazing	
Caenogastropoda	Paskentanidae*	*Alviniconcha adamantis*	Hydrothermal Vents	Mariana Basin	Y	Y	Gills	Gammaproteobacteria	Y	Suggested	Johnson et al., 2015; Breusing et al., 2022
		Alviniconcha boucheti	Hydrothermal Vents	Manus, Fiji, and Lau Back-arc Basins	Y	Y	Gills	Camplylobacteria	Y	Suggested	Suzuki et al., 2006a; Beinart et al., 2012; Johnson et al., 2015
		Alviniconcha hessleri	Hydrothermal Vents	Marina Back-Arc Basin	Y	Y (Stomach 1/100 volume of Provanna spp.)	Gills	Gammaproteobacteria	Y	Suggested	Okutani and Ohta, 1988; Stein et al., 1988; Johnson et al., 2015
		Alviniconcha kojimai	Hydrothermal Vents	Manus, Fiji, and Lau Back-arc Basins	Y	Y	Gills	Gammaproteobacteria, Camplylobacteria	Y	Suggested	Urakawa et al., 2005; Johnson et al., 2015
		Alviniconcha marsindica	Hydrothermal Vents	Central Indian Ridge	Y	Y	Gills	Camplylobacteria	Y	Suggested	Suzuki et al., 2005; Johnson et al., 2015
		Alviniconcha strummeri	Hydrothermal Vents	Southern Lau basin	Y	Y	Gills	Gammaproteobacteria, Camplylobacteria	Y	Suggested	Suzuki et al., 2006b; Beinart et al., 2014; Johnson et al., 2015
		Ifremeria nautilei	Hydrothermal Vents	Southwest Pacific	Y	Y (Stomach 1/100 volume of Provanna spp.)	Gills	Gammaproteobacteria	Y	Suggested	Bouchet and Warén, 1991; Windoffer and Giere, 1997; Borowski et al., 2002
Neomphaliones	Peltospiridae	*Chrysomallon squamiferum*	Hydrothermal Vents	Central Indian Ridge	Y	Y (Stomach 1/10th size of typical gastropod deposit feeder)	Oesophagus	Gammaproteobacteria	Y	Unlikely	Warén et al., 2003; Goffredi et al., 2004; Chen et al., 2015a
		Ctenopelta porifera	Hydrothermal Vents	East Pacific Rise	Y	None reported	Gills	Unknown	Y	Unknown	Warén and Bouchet, 1993
		Gigantopelta ageis	Hydrothermal Vents	Southwest Indian Ridge	Not reported	None reported	Oesophagus	Gammaproteobacteria	Y	Unknown (may be similar to *G. chessoia*)	Chen et al., 2015b; Lan et al., 2021
		Gigantopelta chessoia	Hydrothermal Vents	East Scotia Ridge	Not reported	Y (Small single-loop digestive system)	Oesophagus	Gammaproteobacteria (others present)	Y	Grazing in early life stages only	Chen et al., 2015b; Chen et al., 2017
		Hirtopelta hirta	Hydrothermal Vents	East Pacific Rise	Y	Y	Gills	Unknown	N	Unlikely	McLean, 1989

(Continued)

10.3389/fmars.2023.1167803

TABLE 1 Continued

Taxonomy			Environment		Morphology				Behavior		Refs
Subclass	Family	Genus and Species	Chemosynthetic Environment	Geographical Distribution	Hypertrophied Gills	Digestive System Adaptations	Symbiont Location	Symbiont Classification(s)	Aggregation	Supplementary Grazing	
		Hirtopelta tufari	Hydrothermal Vents	East Pacific Rise	Y	Y	Gills	Unknown	N	Unlikely	Beck, 2002
	Neomphalidae	*Cyathermia naticoides*	Hydrothermal Vents	East Pacific Rise	Y	None reported	Gills**	Camplylobacteria	Y	Suggested	Zbinden et al., 2015
Vetigastropoda	Lepetellidae	*Lepetella sierrai*	Polycheate tubes (genus *Hyalinoecia*)	Bay of Biscay	Not reported	Y (Stomach absent, complex multi-lobed midgut)	Mantle	Unknown	N	Suggested	Judge and Haszprunar, 2014
	Lepetodrilidae	*Lepetodrilus fucensis*	Hydrothermal Vents	Juan de Fuca Ridge	Y	Y (Stomach 1/2 size of non-symbiotic cogeners)	Gills**	Gammaproteobacteria	Y	Observed	De Burgh and Singla, 1984; Bates, 2007a; Bates, 2007b
		Lepetodrilus gordensis	Hydrothermal Vents	Gorda Ridge (NE Pacific)	Y	Y (Stomach 1/2 size non-symbiotic cogeners)	Gills**	Unknown	Y	Suggested	De Burgh and Singla, 1984
Heterobranchia	Orbitstellidae	*Lurifax vitreus*	Hydrothermal Vents, Hydrocarbon Seeps, "Bathyal Sludge"	Mid Atlantic Ridge, Mediterranean Sea, South Pacific	Not reported	None reported	Mantle	Unknown	N	Unknown	Warén and Bouchet, 2001; Smriglio and Mariottini, 2002; Hawe et al., 2014
	Parvaplustridae	*Parvaplustrum wareni*	Hydrothermal Vents	Bering Sea	Y	None reported	Gills**	Unknown	Y	Suggested	Chaban et al., 2022

*Members previously assigned to Provannidae.

**Episymbionts.

reduced substrates are abundant in the anoxic sediments, resulting from anaerobic microbial processes such as sulfate reduction (Preisler et al., 2007). At such localities, chemosymbiotic hosts must bridge the redox gradient through behavioral and morphological adaptations. Here, bivalves may have an advantage as many are infaunal and use their siphon to access oxygenated surface water while using a highly adapted foot to tap into sulfide-rich sediment porewaters to support their symbionts (Dando and Southward, 1986; Zanzerl and Dufour, 2017). Indeed, much of the diversity of chemosymbiotic bivalves is represented by infaunal, or semi-infaunal groups including the majority of lucinids, thyasirids and solemyids (Taylor and Glover, 2010). The acquisition of chemosynthetic symbionts in infaunal bivalve groups may have facilitated widespread diversification of species and habitats, contributing to the bivalve/gastropod disparity (Seilacher, 1990). However, there are also many gastropod groups that are infaunal and occur in chemosynthetic sediments. For example, burrowing members of Strombidae and Cerithiidae are found in sediments alongside lucinid clams (Ibrahim et al., 2015; Lima et al., 2017), yet chemosymbiosis has not been reported in either gastropod group. Perhaps bivalves are advantaged in this scenario, as they may be better suited to supplement symbiont-derived nutrition with heterotrophic filter feeding when symbionts alone cannot support host metabolism, as the case for the majority of molluscan chemosymbioses (Duplessis et al., 2004; van der Geest et al., 2014).

4.2 Physiology and morphology

Chemosymbiotic organisms are faced with the challenges of accessing both oxidants (typically oxygen) and reductants such as sulfide, methane, and hydrogen (Childress and Girguis, 2011). Sulfide is fundamental to many chemosymbioses, however it is toxic to metazoans and presents a major challenge for chemosymbiotic hosts writ large (Powell and Somero, 1986; Grieshaber and Völkel, 1998; Tobler et al., 2016). The bivalve/gastropod disparity begs the question as to whether gastropods face greater physiological or morphological challenges in hosting chemoautotrophic symbionts. One hypothesis is that some gastropods, such as those without an operculum, may be more vulnerable to sulfide toxicity than bivalves and thus are less likely to host intracellular chemosymbionts. However, there are many species of gastropods that lack intracellular symbionts (e.g., Vermeij, 1973; Warén and Bouchet, 2009) and live in environments with elevated sulfide (where sulfide concentrations are comparable to those of hydrothermal vents; Jorgensen and Revsbech, 1983; Gartman et al., 2011). Given the abundance and diversity of gastropods in sulfidic environments, both with and without endosymbionts, it is unlikely that sulfide sensitivity alone is driving this observed trend in chemosymbiotic diversity.

There are also morphological differences that may contribute to the observed gastropod/bivalve disparity. As mentioned, many chemosymbiotic mollusks host symbionts on or within the ctenidia (Table 1). Although gill structure varies considerably within classes (Owen, 1978), many bivalves have large demibranch gills, compared to the relatively smaller gills of many gastropods, which are located beneath the shell. Large gills may be advantageous for bivalve chemosymbioses, as it may provide larger surface area for symbiont colonization. There are a number of extant chemosymbiotic gastropods, however, that successfully host symbionts in hypertrophied gills, and several others that host symbionts in the esophagus (e.g. *Gigantopelta chessoia;* Chen et al., 2017) or mantle (e.g. *Lurifax vitreus*; Hawe et al., 2014), indicating that gill morphology does not inherently preclude chemosymbiosis in gastropods.

4.3 Habitat productivity and motility

Many shallow water chemosynthetic environments also harbor a robust photosynthetic community (e.g., mangroves and seagrass beds), which plays a role in driving chemosynthesis *via* the decay of organic plant material by sulfate-reducing bacteria (Jørgensen, 1977). In these environments, both bivalves and gastropods could take advantage of photosynthetic and chemosynthetic food sources. Motile gastropods have the potential to graze both surface photosynthetic and subsurface chemosynthetic bacteria, without having to expend the extra energy and oxygen required for hosting intracellular symbionts (Childress and Girguis, 2011). Though filter and deposit feeding are both used by many chemosymbiotic bivalves (Allen, 1958; Duplessis et al., 2004; Zanzerl et al., 2019), hosting intracellular chemoautotrophic symbionts can be an efficient way to take advantage of carbon fixed *via* chemosynthesis for less motile groups. In shallow reducing environments, both bivalves and gastropods exploit carbon fixed by different pathways, but motility in gastropods may allow more efficient heterotrophy without the physiological impacts and costs of hosting chemosynthetic symbionts.

Although most hydrothermal vent ecosystems lack extensive photosynthetic inputs, they can be comparable in productivity to shallow water ecosystems and support microbial mats at high densities (Gaill et al., 1997). Many vent gastropods are motile grazers (Gaudron et al., 2015), but perhaps there are unique attributes of hydrothermal vents that account for the high concentration of gastropod chemosymbioses. Vent flows are highly dynamic, with fluid flow regimes changing over many time scales (from minutes to days; Johnson et al., 1988). This environment may provide highly motile gastropods with a competitive advantage for access to sufficient reductants and oxidants for their symbionts. In western Pacific vents, *Alviniconcha* and *Ifremeria* form large aggregations around vent effluent, moving around to access reduced and oxidized substrates as needed (Desbruyères et al., 1994). Chemosymbiotic gastropods also have the ability, to some extent, to move out of environments when they become less suitable (e.g. higher temperatures or lower oxygen or sulfide concentrations). These attributes of vents may contribute to the prominence of motile gastropods in some vent communities, but do not preclude the overall success of bivalves in hydrothermal ecosystems.

4.4 Sampling

We must, of course, consider the impact of sampling bias. The discovery of chemosymbiotic metazoan taxa was relatively recent and the number of documented chemosymbiotic taxa has grown sporadically, particularly among mollusks. For example, the first members of Lucinidae were described by Linnaeus (1758), however it wasn't until the 1980s that lucinids were found to host chemosynthetic bacteria (Cavanaugh, 1983; Fisher and Hand, 1984). As such, it may be easy to attribute much of gastropod/bivalve disparity to sampling bias in favor of the bivalves. That being said, existing evidence from well-studied sites such as the Eastern Pacific Rise reminds us that this observed disparity may be a biological reality. Nevertheless, despite over four decades of research on chemosynthetic symbioses, some new chemosymbiotic gastropods have been described recently, including two species of *Gigantopelta* (Chen et al., 2015b), *Chrysomallon squamiferum* (Chen et al., 2015a), and *Parvaplustrum wareni* (Chaban et al., 2022). Further, much of the evidence for chemosymbiosis in previously described gastropods has also been reported in the last decade (Hawe et al., 2014; Judge and Haszprunar, 2014; Zbinden et al., 2015).

Finally, we acknowledge the challenges of how we define chemosymbiosis. There is a vibrant discussion in the community about what constitutes a symbiosis (Martin and Schwab, 2013), and to date there is no one simple "litmus test" for determining if an organism is chemosymbiotic. Even among widely accepted chemosymbioses, there is considerable variation in the nature of host/symbiont dynamics. Further investigation into gastropod holobionts from both deep and shallow-water chemosynthetic environments may reveal previously unknown chemosymbiotic relationships.

5 Conclusions

Chemosymbiosis has evolved multiple times in diverse lineages of bivalve and gastropod mollusks. Despite physiological and functional similarities between these two groups, bivalves have a far higher diversity of chemosymbiotic taxa, both in terms of species richness, and the breadth of marine reducing habitats occupied. This observed trend presents and interesting framework for investigating the evolution and diversification of chemosymbiotic metazoan hosts. If this trend is robust, this disparity reflects evolutionary, ecological, and/or physiological differences between these two lineages that favors chemosymbiosis in extant bivalves. That said, these observations underscore the need for continued sampling to reveal the undiscovered diversity of gastropod hosts, as well as the need to continue to refine our notions of what constitutes a chemosymbiosis.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author/s.

Author contributions

IH and PG conceptualized this study. IH drafted the manuscript, with edits and comments from PG. All authors have read and approve the final manuscript.

Funding

This work was supported by a grant to PG from the Gordon and Betty Moore Foundation (grant #9208). This work was also supported by the department of Organismic and Evolutionary Biology at Harvard University.

Acknowledgments

We thank Stephane Hourdez and members of the Girguis laboratory for helpful discussions and comments. We would also like to thank our reviewer and editor Sébastien Duperron for helpful feedback which improved the manuscript.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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