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OPINION PAPER

Marine hydrothermal vents as templates for global change scenarios

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Abstract Subsurface marine hydrothermal vents (HVs) may provide a particular advantage to better understand evolutionary conditions of the early earth and future climate predictions for marine life. Hydrothermal vents (HV) are unique extreme environments that share several similarities with projected global and climate change scenarios in marine systems (e.g., low pH due to high carbon dioxide and sulfite compounds, high temperature and turbidity, high loads of toxic chemicals such as H_2S and trace metals). Particularly, shallow hydrothermal vents are easily accessible for short-term and long-term experiments. Research on organisms from shallow HVs may provide insights in the molecular, ecological, and evolutionary adaptations to extreme oceanic environments by comparing them with evolutionary related but less adapted biota. A shallow-water hydrothermal vent system at the northeast Taiwan coast has been intensively studied by several international research teams. These studies revealed astounding highlights at the levels of ecosystem (being fueled by photosynthesis and chemosynthesis), community (striking biodiversity changes due to mass mortality), population (retarded growth characteristics), individual (habitat attractive behavior), and molecular (adaptations to elevated concentrations of heavy metals, low pH, and elevated temperature). The present opinion paper evaluates the potential of shallow hydrothermal vents to be used as a templates for global change scenarios.

Keywords Shallow hydrothermal vent · Early earth environment · Global change template · Adaptations · Extreme habitat

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Introduction

Global change summarizes recent phenomena that cause planetary-scale changes in the earth system. The earth system consists of the oceans, land, atmosphere, poles, the planet's natural cycles, deep earth processes, biosphere, and includes the human society. In the last 250 years, global change has caused climate change, loss of critical habitats, desertification, ocean acidification, ozone depletion, pollution, widespread distribution changes and extinction of species, fish-stock collapses, and other large-scale biotic shifts (Mora et al., 2017). Global climate change is a shift in the occurrence of weather patterns over periods ranging from decades to longer time intervals. Besides, climate forcing factors such as variations in solar radiation, plate tectonics, volcanic eruptions, and biotic processes, human activities have been linked to recent climate change scenarios (Doney et al., 2009). In marine systems, hydrothermal vents are proposed to be used as templates to study global climate change in the present paper. This proposal is based on research during the past two-decades on shallow hydrothermal vents of Taiwan (Hwang & Lee, 2003; Dahms & Hwang, 2013; Chan et al., 2014; Dahms et al., 2013, 2014a, b, 2017). As such, hydrothermal vents (HVs) share several factors with global change phenomena (e.g., high temperature and CO_2, low pH and oxygen, toxic chemicals such as sulfite compounds, high trace metal loads, turbidity—see Fig. 1). Increasing levels of CO_2 and other gases are responsible for ocean acidification with a reduction of ocean water pH (Tunnicliffe et al., 2009). Research on organisms from HVs could provide insights in the behavioral, genomic, and evolutionary adaptations to an extreme environment (Campbell et al., 2009, Dahms et al., 2017) that could be compared with biota living outside the vents (Dando, 2010). Particularly, shallow HVs may provide a suitable natural laboratory for observations and experimental approaches to biotic effects and adaptations to environmental extremes and global change issues (Boatta et al., 2013). As natural habitats, HVs can be used to understand and predict global change scenarios of a future ocean and organisms living there (Kádár et al., 2007; Dahms & Hwang, 2013).

HVs are fissures in the planet's surface from which geothermally heated water provides a unique habitat of specialized, highly endemic benthic communities. Hydrothermal vents are distributed at depths ranging from a few meters to more than 5000 m throughout the world's oceans (Tarasov et al., 2005). The emitted fluids typically contain a large amount of sulfur compounds and metals that are leaching from the mineral base (Van Dover, 2000). The surrounding water chemistry is strongly influenced by these physical and chemical conditions, leading to a toxic acidified environment which is lethal to most biota from outside the HVs (Dahms & Hwang, 2013; Van Dover, 2014). Biological communities associated with shallow and deep HVs have developed behavioral, morphological, and reproductive adaptations as well as symbiotic (Adams et al., 2011; Dahms & Hwang, 2013; Dahms et al., 2013, 2014a, b, 2017), physiological and biochemical systems for sulfide detoxification (Boutet et al., 2009; Li et al., 2017), molecular responses to high temperature (Smith et al., 2013; Kim et al., 2017), and specialized sensory organs to locate hot chimneys (Gebruk et al., 2000).

Shallow-water vent research has a longer history than deep-sea vent research, dating back to the 19th century (Tarasov et al., 2005). Environmental investigations on shallow-water hydrothermal vents have been conducted in many regions, including, Greece, Italy, the Kurile Islands, Baja California, Japan, Taiwan, and Papua New Guinea (Hwang & Lee, 2003, Tarasov et al., 2005). Data suggest that shallow and deep-sea vents exhibit major differences in their physical and chemical properties, resulting in dissimilar biological characteristics (Figs. 2, 3, Table 1). Shallow-water hydrothermal vents in particular contain substantially fewer biota which have an obligatory relationship with the vents than deep-water HVs (Hwang & Lee, 2003). Since shallow-water vents occur in the euphotic zone, the contribution of photosynthesis to primary production is important, whereas at deep-sea vents, organic matter is generated by chemosynthesis (Dando, 2010).

Hydrothermal vents are considered to be similar to a chemosynthetic ecosystem of an early planet. They thus provide a conceptual framework for the evolution of early life forms (Nisbet & Sleep, 2001). Adaptive processes to such a unique physical and chemical environment can further enhance our understanding of global change scenarios since the factors under discussion are comparable (e.g., temperature, pH, toxicity). We emphasize here that a gradient in hot or diffuse vent fluids that gets diluted with seawater

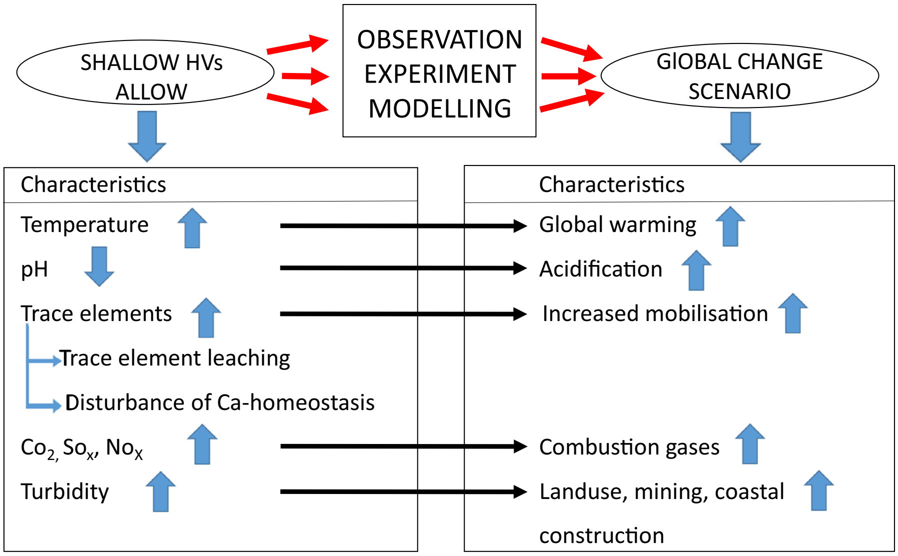

Fig. 1 Comparison of characteristics of Kueishan Island (KST), shallow hydrothermal vents with characteristics of global change biology (compiled from different literature sources)

would be more representative of a global change scenario, rather than the extreme conditions found closer to the vents.

We opt to use particularly shallow-water hydrothermal vents as proxies for a natural laboratory that would allow the study of marine organism' adaptations to highly adverse physicochemical conditions. The two major objectives of the present evaluation are (1) to compare similarities of adverse biological effects of both climate forcing and of shallow HVs, and (2) to assess the possibilities particularly of shallow HVs as templates for research on effects and adaptations of organisms to global change.

Effects of vent fluid temperature and chemistry

The sea bottom surrounding HVs represents a heterogeneous environment. Within this area, vent fluids and ocean waters are mixing. These two fluids have very different physical and chemical properties with steep gradients. Characteristics of the water experienced by organisms that live near the vents can change at small spatial and temporal scales. Emitted vent fluids can reach temperatures of about 116°C in shallow vents like at Kueishantao; the cooling effects of the surrounding seawater create strong thermal gradients (Girguis & Lee, 2006). The fluid emission is often unstable and sudden bursts of hot vent fluids are commonly providing vents with large thermal variability (Hwang & Lee, 2003). Vent organisms are thus subject to rapid and acute temperature changes, with temperatures fluctuating at temporal scales of seconds to minutes. Tolerance to these unstable conditions is important for vent biota (Amend et al., 2011). This might provide a limitation to our approach using HVs as templates for more gradual change during global warming which happens right now and will further increase in the coming century.

The ability of an organism to make physiological adjustments in response to temperature is important for defining an organism's thermal niche (Boutet et al., 2009). Low metabolic rate and little variation in metabolic rate may be a common adaptation within hydrothermal vents (Smith et al., 2013). The body temperature of aquatic ectotherms fluctuates over the full range of temperature in their habitat. Thus, a regulation of metabolism in response to thermal challenges is vital for these organisms (Dahms et al., 2011). Species with a high metabolic sensitivity over their environmental range have increased the long-term metabolic costs and a lower tolerance to extreme temperatures (Boutet et al., 2009; Dahms et al., 2016).

Since HV fluids have a higher water temperature and become buoyant, fluids discharged from the vents are transported upwards and are floating on the surface. The fluids discharged from the vents have a

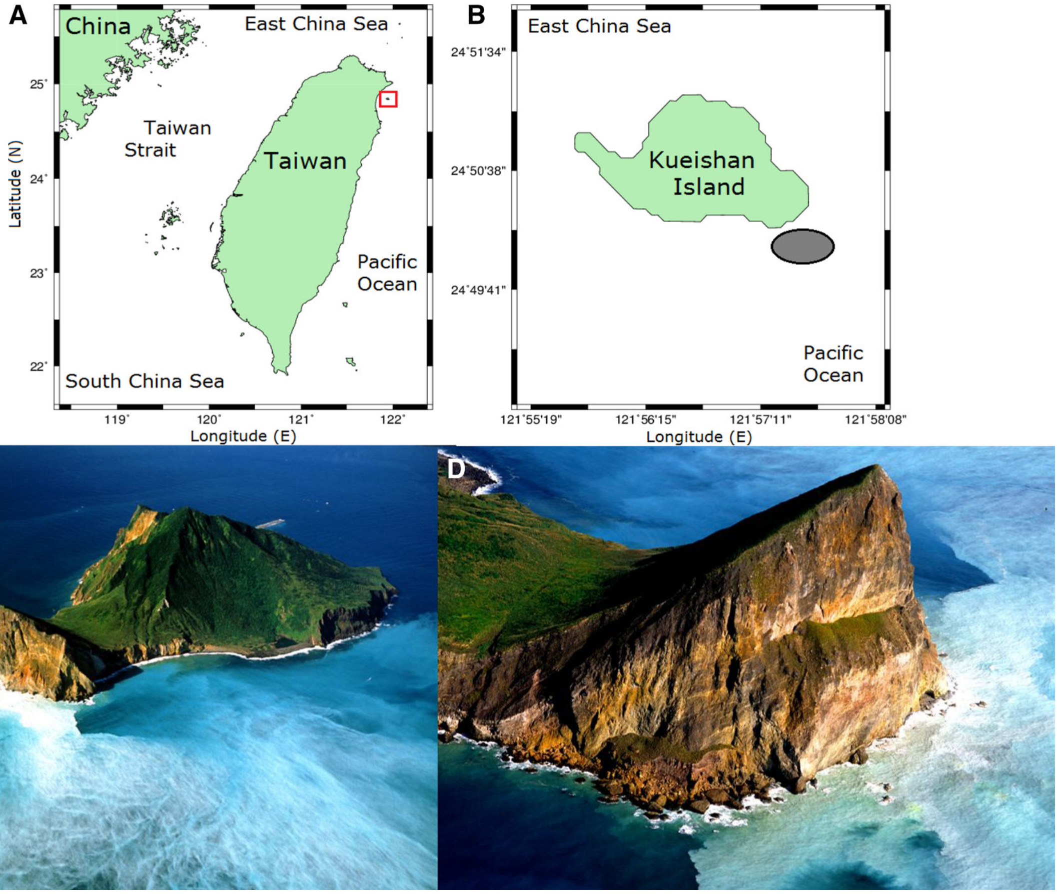

Fig. 2 Shallow hydrothermal vents at KST, off the NE coast of Taiwan are useful "natural laboratories" for the study of global change characteristics. (**A**) Location of KST at northeastern Taiwan; (**B**) depth contoures around KST; (**C**) Skyview (compiled from different literature sources)

significant impact on water chemistry and hence on the biology of organisms in the ambient environment. The surface water then appears whitish due to sulfur, sulfur bacteria, and gas bubbles, whereas the bottom layer remains transparent in many cases. Accordingly, an influence of the vent fluid on water chemistry is more pronounced in the surface layer than in the bottom layer, resulting in vertical differences in physical and chemical properties. The effects of surface water chemistry of the vent region are more similar to the fluids from the smokers than to water of the bottom layer. Accordingly, a stronger negative impact on species in surface waters can be expected than in the bottom layer. This is consistent with observations that plankton in the surface water can be killed by vent plumes and produces "marine snow" composed of sedimenting dead plankton (Jeng et al., 2004; Dahms & Hwang, 2013). Experimental cages at different depths in the HVs of Kueishan Island also indicated that copepods at the top layer had the greatest mortality (Dahms & Hwang, 2013).

Hydrological factors measured at shallow HVs reflect the environmental conditions at only one particular point in time. A previous study reported that high temporal variations in water temperature off Kueishan Island are attributable to diurnal tides (Chen et al., 2005b). It is, therefore, reasonable to expect a similar level of variation in other parameters within shallow HVs. The complex surface circulation may transport different amounts of vent effluents to particular sites in the same locality, resulting in variable patterns that are observed among the sites.

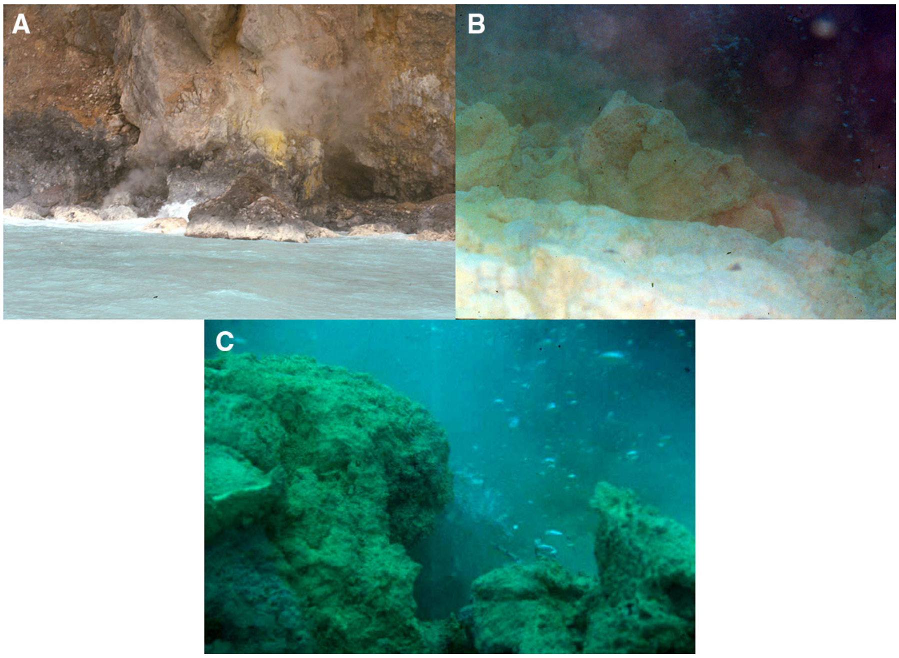

Fig. 3 KST shallow hydrothermal vents provide gas emissions above the sea surface (**A**) and from the sea bottom (**B**, **C**)

Table 1 Comparison of major physical, chemical, geological, and biological parameters at shallow-water and deep-water hydrothermal vents (compiled from different literature sources)

Parameter	Shallow-water HVs	Deep-water HVs
Light	Yes	No
Temperature		
HV fluid	Low	High
Ambient	High	Low
Hydrostatic pressure	Low	High
Hydrodynamic disturbance	High	Low
pH	Variable	Variable
Habitat stability	Low	Low
Species richness	Low	High
Endemicity	Low	High
Biomass	Low	High
Productivity	Variable	High
	Photo- and chemoautotrophic	Chemoautotrophic

Low pH as a proxy for ocean acidification

Rising atmospheric CO_2 and other gases are responsible for ongoing ocean acidification resulting in the reduction of ocean water pH and changes in the carbonate chemistry (Tunnicliffe et al., 2009). CO_2 production is primarily driven by human fossil fuel combustion and deforestation, followed by the emission of aerosols to the atmosphere. There is great concern about related biological and ecological effects, as elevated CO_2 partial pressure in seawater has direct impacts on marine calcifying organisms (Hall-Spencer et al., 2008; Fabry et al., 2008) and calcium carbonate-based systems (Silverman et al., 2009), biodiversity, trophic interactions, and other ecosystem processes (Glover et al., 2010; Chan et al., 2012).

It was shown at shallow CO_2 vents that calcification is highly impacted by reductions in seawater pH and associated changes in carbonate chemistry (Boatta et al., 2013). Shallow HVs can be taken as natural laboratories for climate change. In addition, these could explain how organisms are avoiding to be poisoned by high sulfide and heavy metal concentrations.

Sediments in fluid venting areas are generally characterized by conspicuous metal deposits of hydrothermal origin (Aldhous, 2011). This is a consequence of acid leaching from the underlying rocks, which leads to the discharge of metal-rich hydrothermal fluids (Edmond et al., 1979). Due to constant percolation of CO_2 through the sediments, a cascade of biogeochemical changes in sediments close to the vents and at the sediment–water interface can occur, affecting the precipitation of trace elements with likely harmful effects on the biota (Nuzzio et al., 2012). A substantial decrease in seawater pH and Eh observed close to submarine CO_2 vent sites may influence the solubility and bioavailability (dissolution and/or desorption) of some metals and metalloids. This probably contributes to keeping Fe and other elements (Mn, Co, Cd, Cu, Cr, and V) in dissolved form, leading to low enrichment in sediments. For example, the geochemistry of Fe plays a prominent role in the transfer of trace elements at the water–sediment interface (Hsiao & Fang, 2013). A decrease from pH 8.1–7.4 is responsible for a 40% elevation of Fe solubility in the water column. In addition, the redox potential provides another decisive factor in Fe chemistry. Aiuppa et al. (2000) showed that reducing environments are contributing to increasing Fe solubility. In contrast, the simultaneous rise in pH and Eh can cause the precipitation of dissolved Fe into solid compounds with increasing distance from a vent site. In addition to the synergistic effects of declining pH and perturbation of carbonate chemistry, ocean acidification may have an indirect effect by increasing the availability of contaminants (Vizzini et al., 2013).

HV systems commonly also show a very high turbidity and heavy metal content, similar to many coastlines where coral reefs or intertidal zones are threatened by turbidity and due to factors like road construction, flushing, typhoon, heavy rain, etc. Therefore, effects on organisms affected by HV turbidity and heavy metal content are expected to have similar outcomes for the environmental conditions of a future ocean.

The effects of multiple stressors: warmer temperature and lower pH

As ocean waters are becoming warmer and more acidic at the same time, both environmental stressors cannot be studied in isolation. Organisms face warmer and more acidic waters and the interaction of these physical variables may be different with species and developmental stages (Wood et al., 2010). To provide two examples here, Arnold et al. (2013) showed the interactive effects of ocean acidification and global warming on the growth and dimethylsulfate synthesis of the coccolipthore microalgae *Emiliania huxley*. Ericson et al. (2012) demonstrated the interactive effects of these two stressors which reduce fertilization rate and the growth of early developmental stages of the sea urchin *Sterechinus neumayeri* from the Antarctic.

Shallow HVs off Kueishantao as natural laboratories: a case study

Shallow HVs are ideal habitats to study the interactive effects of these two variables in marine organisms since the surrounding waters and sediments are naturally warmer and more acidic (Hwang & Lee, 2003; Ka & Hwang, 2011). Gradients of pH and temperature may be stable or fluctuating depending on the geophysical stability of the HVs (Hall-Spencer et al., 2008). The capacity and the associated energetic costs of HV biota to withstand fluctuations of pH and temperature can be compared with phylogenetically related non-HV biota. Since HVs share several characteristics with global change phenomena, they may provide suitable templates for experimental approaches to biotic effects and adaptations to environmental extremes and global change factors (Hwang & Lee, 2003; Zielinski et al., 2011). Particularly, in situ studies and the retrieval of organisms would be much facilitated when studying HVs in shallow waters. This was done before not only at several shallow-water HV sites worldwide (see Morri et al., 1999; Tarasov et al., 1999; Karlen et al., 2010; Bianchi et al., 2012) but also at the NE coast of Taiwan (Hwang & Lee, 2003; Hwang et al., 2007).

Shallow HVs off Kueishantao, an island close to the northeastern Taiwan coast, 60 miles from HVs of the Okinawa Trough (Zeng et al., 2013) are located at a tectonic junction of the fault system extension of

Taiwan and the southern rifting end of the Okinawa Trough (Wang et al., 2000). The Kueishantao hydrothermal vent field (121°55′E, 24°50′N, about 0.5 km^2) is situated in shallow waters southeast of Kueishantao (Zeng et al., 2013). The area surrounding the field is characterized by a seafloor with lava and pyroclastic sediments. The last major eruption occurred about 7000 years ago (Zeng et al., 2007) off northeastern Taiwan, near the southern Okinawa Trough. There are several hydrothermal vents in shallower waters (15–300 m depth) with the lowest recorded vent water pH worldwide (Chen et al., 2005a). Gases produced here at the vent sites are mainly composed of carbon dioxide and a small amount of hydrogen sulfide (Tang et al., 2013). The vents can be divided into "yellow spring" and "white spring" types. The temperature of the yellow-spring fluids is between 78 and 116°C, and the temperature of the white-spring fluids is between 30 and 65°C (Kuo et al., 2001). Yellow-spring effluents have a very low pH (as low as 1.52) and a wide range of chemical compositions. White-spring effluents are characterized by relatively low concentrations of copper, iron, and methane (Chen et al., 2005a). The hydrothermal fluids reach their highest temperatures about 3.5 h after each high tide. The effluents from the vents emerge to the sea surface and are then transported and mixed by tidal movements (Chen et al., 2005b). Gases produced here at the vent sites are mainly composed of carbon dioxide and a small amount of hydrogen sulfide (Tang et al., 2013). The hydrothermal mineralization products at the Kueishantao vent field are mostly sulfur-forming chimneys, mounds, and sedimentary balls (Hwang & Lee, 2003; Zeng et al., 2011). Metagenomic characterization of the bacterial communities at the vent smokers and the surface waters of Kueishantao has revealed a high abundance of chemosynthetic bacteria (Tang et al., 2013; Wang et al., 2015). Like in most shallow-water vent ecosystems, energy is supplied here by both photosynthesis and chemosynthesis (Jeng et al., 2004). The macrofauna at Kueishantao is characterized by vent crabs, sea anemones, gobies, sessile algae, mollusks, and sea snakes (Hwang & Lee, 2003). These organisms are commonly seen in the surroundings of the vents in low abundances and their life histories are highly affected by vent eruptions (Peng et al., 2011; Dahms et al., 2013, 2014a, b). In shallow-water HVs, species richness is commonly positively correlated with distance from the HVs (Zeppilli & Danovaro, 2009). The influence of the vent decreases with increasing horizontal distance because of the dilution and lower concentration of toxicants by sea water (Melwani & Kim, 2008). However, previous studies at shallow-water HVs commonly considered only small spatial scales around the vents and are limited in reflecting the range influenced by HVs (Tarasov et al., 1999).

When comparing deep sea and shallow-water sites, there are inherent environmental stress differences between the two environments (Table 1). Hydrostatic pressure is one of the most important parameter that was distinguishing deep sea from shallower waters (Siebenaller, 2000) and HVs accordingly. Shallow-water organisms have to cope with more hydrodynamic stress than organisms from deeper water (Nielsen et al., 2017) and their HVs.

Chan et al. (2014) investigated the response of metal accumulation in the coral *Tubastraea coccinea* from several environments such as from the Kueishantao HVs. Metal accumulation was found substantially higher in the tissues than in the skeletons. The metals yielded differential amounts between skeletons and tissues indicating that such coral had a distinct selectivity for assimilating metals from seawater. The above study indicates that metal accumulation in skeletons and tissues represents a suitable instrument for monitoring long-term effects of corals in various polluted environments. However, tissues were more sensitive than skeletons. We may conclude that shallow HVs can be used as "natural laboratories" to assess the effects of climate change.

Conclusions

Easily accessible shallow HVs pose important advantages for experimental possibilities to researchers using genomic methods since it is feasible to perform short-term and long-term experiments regarding the genomic effects of low pH and temperature in organisms from HVs. They can be used as natural laboratories to assess the effects of global climate change. Time of collection to preservation is minimized in shallow HVs and high-quality DNA/RNA, a prerequisite for genomic studies, can be routinely extracted from the organisms. Caution should be used when relating biological changes along pH gradients to the direct effect of pH, as interactions with multiple stressors, including trace element enrichments, may be present at the same time. The combination of stressful physical and chemical factors and elevated element concentrations in sediments and seawater may create a harmful environment for most marine biota. HVs may be considered as analogues for low pH environments with non-negligible trace element contamination, which in a scenario of continuous anthropogenic impact, may become a common global change issue.

In situ studies are of particular importance and interest in the era of genomics and next-generation sequencing (NGS) methods. NGS techniques require high-quality DNA and RNA templates and this is technically difficult and expensive with deep HV animals since substantial time passes from the collection of animals to the flash-freezing of tissues. During this time, the quality of DNA and particularly RNA may degrade significantly, rendering RNA-seq or other transcriptomic studies of limited use. Gene expression (RNA-seq), proteomics, metabolomics-based experiments require an instant cessation of all cellular activities in order to provide an accurate profile of the gene expression, as well as proteomic and metabolic activities. Access to a shallow-water HV system provides researchers with the opportunity of designing robust genome-based experiments with no compromise on the tissue quality. The reduction of cost and accessibility of shallow HVs also allows long-term monitoring experiments with frequent observations. Sudden changes in chemistry and/or geology can quickly be monitored and opportunistic experiments with the resident fauna can be conducted. Such quick responses are next to impossible in deep HVs. Of particular interest are the following OMICs-based questions regarding HV animals and microorganisms: (1) comparison of transcriptomic profiles between resident and non-resident biota but phylogenetically related fauna to test for genes related to habitat adaptations; (2) comparison of transcriptomic profiles of resident fauna at different distances from the vents to test the amount of variability of gene expression in different combinations of pH and temperature; (3) metagenomic studies of benthic and water column bacterial communities inhabiting the HVs to compare the microbial diversity of HVs compared to those at different distances from the vents; (4) community transcriptomics which may reveal universal patterns of protein sequence conservation in natural HV microbial communities versus those found further away from the vents; (5) community proteomics and metabolomics.

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