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Opinion

Can Marine Hydrothermal Vents Be Used as Natural Laboratories to Study Global Change Effects on Zooplankton in a Future Ocean?

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Abstract: It is claimed that oceanic hydrothermal vents (HVs), particularly the shallow water ones, offer particular advantages to better understand the effects of future climate and other global change on oceanic biota. Marine hydrothermal vents (HVs) are extreme oceanic environments that are similar to projected climate changes of the earth system ocean (e.g., changes of circulation patterns, elevated temperature, low pH, increased turbidity, increased bioavailability of toxic compounds. Studies on hydrothermal vent organisms may fill knowledge gaps of environmental and evolutionary adaptations to this extreme oceanic environment. In the present contribution we evaluate whether hydrothermal vents can be used as natural laboratories for a better understanding of zooplankton ecology under a global change scenario.

Keywords: Hydrothermal vent; mortality; mesozooplankton; pelagic; climate change; future ocean

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1. Introduction

Zooplankton provides an important functional component of trophic webs and biogeochemical cycling [1]. Zooplankton mediates energy and matter translocation between the pelagic and benthic realm through diurnal migration and passive sinking of particulate organic matter [2]. The spatial distribution and abundance of zooplankton are affected by the transport of water masses as well as by different physical, chemical and biological effects of global change. Global change affects the earth systems including land, oceans, atmosphere, the poles, biogeochemical cycles, biosphere including human populations and society. Global changes of the last 2 centennials caused the change of climate, atmospheric ozone depletion, desertification on land, acidification of aqueous environments including the oceans, pollution in general, species extinctions and distributional range changes, and other large-scale biotic shifts (UN—Oceans, URL). In the oceans, global climate forcing factors provide changes at large spatial scale and regional hydrodynamic circulation patterns across different time scales. In addition, factors such as movement of tectonic plates, volcanic activity causing tsunamis, and biological processes including anthropogenic activities were linked to changed scenarios of the earth system [3–7].

Hydrothermal vents (HVs) caused by suboceanic volcanic activity have several characteristics in common with characteristics summarized as global change (e.g., elevated CO_2 and temperature, low oxygen and pH, elevated trace metal availability, sulfate compounds and turbidity). Ever increased levels of CO_2 and other gases forming acids in the aqueous phase provide ocean acidification with pH reductions in oceanic waters with consequences on oceanic biota [8]. Decrease pH and Eh levels characteristic for CO_2 vents increases the bioavailability and dissolution and/or desorption of metalloids and trace metals [9]. This keeps trace elements (Fe, Cd, Co, Mn, Cu, V and Cr) in solution and bioavailable.

HVs areas are characterized by turbid waters containing elevated trace metal contents. This is comparable to coastal waters with intertidal areas or coral fringe reefs that are at risk by above factors due to anthropogenic activity such as mining, industrial emissions, construction work and natural phenomena, such as heavy rain flushing, landslides which increasingly threaten the coastal waters of a future ocean.

It was suggested to use HVs as templates or natural laboratories that allow research on marine organisms in the highly adverse physicochemical conditions of HVs compared to areas without HVs. HV biota could provide insights in the evolutionary, ecological, genetic, behavioral, physiological and molecular adaptations to extreme marine environments that could be compared with their next phylogenetic relatives away from HV sites [10].

The effects of HVs on marine zooplankton were rarely studied [11]. In the few reports on zooplankton, however, oceanic venting areas have favorable effects on the composition of primary producers (phytoplankton) and the composition of zooplankton that are related to the distribution and abundances of higher trophic levels [12,13]. For their ease of access and allowing revisits, experimental approaches in a cost-saving mode, and linking chemo- and photosynthetic energy pathways, particularly shallow HVs are expected to provide suitable natural laboratories. This holds for studies of environmental extremes, biotic adaptations, and allowing the prediction of responses to a future ocean and its living and non-living resources [10].

We question here whether HVs can provide templates for a 'Future ocean scenario' for zooplankton as well. The goals of our contribution are to: (1) survey existing knowledge about zooplankton at HVs; (2) relate this to global change phenomena; (3) evaluate whether the 'HVs as natural laboratory for global change' concept is suitable for questions related to zooplankton ecology.

2. Zooplankton Research near Hydrothermal Vents

According to [14] studying the shallow HVs at Kueishan Island, Taiwan, taxon diversity and densities of mesozooplankton were increased (for abundance three times higher) at the HV side. This occurred to most zooplankton groups, among others to dinoflagellates, appendicularians, pteropods and copepods (providing the highest number of 34 species). It was reported earlier that HVs increased the assemblage composition and biomass of zooplankton especially at shallow depths in Matupi Harbor (Papua New Guinea) [15,16]. Skebo et al. [13] link the high abundance of copepods in waters adjacent to hydrothermal vents with patchy distributions caused by the avoidance of harsh environments close to the HVs and by the avoidance of jellyfish by swarming behavior. This positive effect may also be caused by hydrothermal fluids that enrich nutrients for algae and increase primary productivity [15] from chemosynthesis and photosynthesis at shallow depths [16]. Such elevated primary productivity would then support elevated densities of zooplankton in HV areas.

Cage experiments resulted in high mortality (>95%) of planktonic copepods that were translocated to HVs at depths of 1–13 m above the seafloor next to HVs of KST island [17]. The mortality value was three times higher than that at distant control sites which were not affected by HV plumes (with 20–30% mortality). There are several reports on the trophic position of HV zooplankton. Hung et al. [18] explained the relatively low C/N ratios of the precipitating particulate organic matter from the HV field of Kueishan Island with a high zooplankton contribution. A food web study by Wu et al. [19] applying $\delta^{13}C$ and $\delta^{15}N$ analysis revealed that the water-column-derived fraction of dead zooplankton provides important energy supplements to carnivores and scavengers like the HV crab *Xenograpsus testudinatus*. Further isotopic niche analysis through this study demonstrated that the contribution of 200 dead zooplankter as a food source to vent crabs living in the center and periphery varied from >34% to $\leq$18%. The results of Chang et al. [2] based on isotope analyses showed that photosynthetic and chemosynthetic producers contributed nearly equally to carbon fixation that is fueling the HV system at Kueishantao. In their study, the authors found both zooplankton and HV crabs acted as important trophic mediators between water column and sea bottom. The results of another isotope study by Wang et al. [20] partially contradicted the above findings in that trophic provisions at the shallow-water HVs of Kueishan Island were mainly provided by phototrophic production (microalgal contribution: 26–54%), then by zooplankton (19–34%) and to a minor extend by chemosynthetic production (14–26%).

3. Variable Hydrographic Effects of HV Effluent Temperature, pH and Chemistry Affecting Zooplankton

The sea floor of HV fields provides a rather heterogeneous environment. HV fluids can reach temperatures of about 116 °C in shallow vents like at Kueishan Island [21] with demarcated thermoclines. Vent fluids and surrounding waters with contrasting chemical and physical characteristics often show strong gradients. HV effluents affect the chemistry to a larger extent at the surface than at the bottom, providing differences of physical and chemical characteristics along the water column axis. Observations that zooplankter at the surface are killed by HV effluents and produce "marine snow" composed of sedimenting plankton carcasses and diverse microbiota including HV bacteria [22].

HV fluid emissions are often unstable and sudden outbreaks of HVs vent fluids are commonly providing vents with large hydrological variability [23]. It is expected that HV biota developed adaptations to tolerate such fluctuating environmental conditions, particularly if they are zooplankter drifting in the water column above HVs. This might provide a limitation to our expectation to use HVs as examples for the more gradual alterations during global changes for decades to come. Variations of other environmentally effective parameters within HV systems are expected as well.

4. Conclusions

We conclude that HVs are particularly useful as "natural laboratories" to approach consequences of global change and global climate change for resident biota that had sufficient time to evolutionary and individually adapt to such extreme environments. However, there is no evidence for an endemic zooplankton assemblage as yet, also not from the better investigated shallow water HV situations. The scarce information available indicates that zooplankton is transported to HV areas and is negatively affected by toxic HV plumes and may die there after such an abrupt environmental transition. This way they provide a high input of allochthonous biomass to the respective HV system. There is a substantial knowledge gap about many issues regarding the fate of zooplankton in HVs as outlined below.

Rather generally, the effects of multiple stressors are difficult to disentangle. This holds for examples for basic phenomena related to simultaneously acidified and warming oceans. The interaction of just these two stressors may differ with taxon, populations, gender and ontogenetic stages. Organisms associated with HVs were shown to have adaptations regarding their reproduction, morphology and behavior. HV biota were also shown to have evolved molecular adaptations to an extreme environment and specialized receptors to find or avoid HVs and their effluents in order to aggregate there or to avoid the HV environment altogether. Such adaptations need to be studied also with zooplankton at HVs since there is a particular knowledge gap here.

The ease of access to shallow-water HV systems -offers scientists the rare opportunity to design meaningful in situ and laboratory experiments. Hydrographic regime changes of the physical and chemical background of zooplankton can instantly be monitored. Fast responses are more difficult to capture in HVs of the deep sea.

The following issues among others related to zooplankton in HV areas are of particular interest: (1) Are there any endemic zooplankton assemblages in HVs? (2) Is zooplankton aggregating or trapped in a toxic environment? (3) Are there taxon-specific differences within patchy distributions? (4) Are the measured higher zooplankton densities near vents caused by dead zooplankton that settles at HV sites? (5) How are the ratios of dead versus alive zooplankton? (5) What are the ultimate mechanisms of toxicity causing mortality among zooplankton at HVs? (6) What are particular mechanisms or adaptations to avoid toxicity effects? (7) To what extent are dead versus alive zooplankter vertically segregated in the water column or are they advectively transported?

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