



Article Holoplanktonic and Meroplanktonic Larvae in the Surface Waters of the Onnuri Vent Field in the Central Indian Ridge

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Abstract: The dispersal of organisms in an isolated environment of a hydrothermal vent remains unclear. Here, we provide direct evidence that meroplanktonic larvae may migrate thousands of meters above the ocean floor. The morphological quantitative measurements of mesozooplankton were conducted in the Onnuri Vent Field (OVF), the Solitaire Fields (SF), and the reference site (ref-site). Only one species of bivalve larva that appeared at the OVF and the ref-site (0–200 m) was similar to *Bathymodiolus* spp. Sixteen species of gastropod larvae were distinguished, among which, species 1–4, 6, and 13 had holoplanktonic features (*Atlanta, Oxygrus*, and *Limacina*), whereas species 5, 7–12, and 14–16 had meroplanktonic features. Species 5, 11, and 12 appeared only at the OVF, 9 and 10 appeared only in the SF, 14–16 appeared only at the ref-site, and species 7 and 8 appeared in all surveyed stations. The species 5, 8, 12, 14, and 15 have morphological features similar to *Vetulonia* spp., and species 7 was similar to Lepetodrilidae; species 9–11 and 16 were similar to *Phymorphynchus protoconchs*. The morphologically distinguished mollusk larvae in the upper layers of the water column (0–200 m) indicate that larvae associated with deep-sea hydrothermal vents may disperse approximately 2000 m above the vents.

Keywords: hydrothermal vent; mesozooplankton; meroplankton; mollusk larvae; bivalve larvae; gastropod larvae; dispersal; Central Indian Ridge; Onnuri Vent Field

1. Introduction

Benthic animals produce planktotrophic larvae, which spend weeks to months in the pelagic environment, feeding and developing through their free-swimming stage [1–4]. Larval dispersal is important for geographic distribution, population dynamics, and evolutionary processes of vent-endemic organisms [1,5,6]. Planktonic larval duration (PLD) is the amount of time larvae take to develop to the settlement stage [5]. PLD and dispersal strategies may differ depending on the species, climate zone, and habitat types [7]. In the near-shore ecosystems, the species living on sandy bottoms have long-distance dispersal mechanisms, whereas the rocky-shore species that depend on a narrow strip of habitat have short-distance dispersal mechanisms to reduce offshore loss of larvae [8]. Shanks (2009) reported that shallow-water and coastal species are more concentrated in complex hydrodynamic and fast-speed currents than in the deep-sea. The intertidal and shallow subtidal species are transported from inshore waters into large-scale coastal currents and then eventually return to the inshore waters of another location [9]. Deep-sea species also have complicated PLD, where larval transport distance depends on the development, behavior, and physiology of the larvae [5]. For example, veliger larvae such as limpets (e.g., Leptodrilus spp.) tend to remain near the bottom and in slower currents [10]; tubeworms (e.g., Riftia pachyptila) are buoyant and more likely to be transported above the bottom (e.g., ridge-controlled currents) [11]; and swimming larvae such as mussels (e.g., Bathymodiolus childressi) migrate up into the oceanic currents near the surface [12].



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Copyright: © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). The hydrothermal vent fields have distinct and isolated communities with chemosynthetic systems [13]. The majority of hydrothermal vent sites, particularly in the Pacific and Atlantic Oceans, have been studied [14,15]. A hydrothermal vent has either a discrete or a diffuse venting source, such as black and white smokers [16–18]. Another type of vent field is the diffused flow from porous surfaces or fissures and cracks in basalt lavas, diluted with cold seawater either from below or within the sea floor [19]. The benthic animals inhabiting the hydrothermal vent ecosystems are likely to have colonization abilities, including high rates of dispersal, growth, and reproduction [20]. The major vent fauna in the extensively studied Galapagos vents, including tubeworms (Alvinellidae), clams (e.g., *Calyptogena magnifica*), and mollusks (e.g., *B. thermophilus*), have symbiotic bacteria that obtain energy from hydrogen sulfide [21].

Most species in hydrothermal vents are benthic as adults, but they spend a portion of their lives as tiny larvae (meroplankton) in the overlying water column [5]. Previous studies on zooplankton, including meroplankton, in the water column above the hydrothermal vents were conducted in the East Pacific Rise (EPR), Guaymas Basin, Endeavour Ridge, Juan de Fuca Ridge, and Mid-Atlantic Ridge [22–26]. The larval stage (meroplankton) of macrobenthic animals living near the hydrothermal vent is an important phase of their life cycle [20,27]. The larval dispersal, especially migration behaviors of benthic organisms in hydrothermal vents has primarily been studied at EPR and Juan de Fuca Ridge [28–31]. Hydrodynamics and chemical and mass flux studies in the EPR demonstrated the transport mechanisms of vent fluids and larvae, implying eddy-driven impacts in transporting hydrothermal vent-derived heat, chemicals, and biota in a relatively low-energy environment [32].

Meroplanktonic larvae of mollusks in the cold methane seeps, including mytilid bivalve *B. childressi* and limpet gastropod *Bathynerita naticoidea*, have been collected from euphotic zones (0–100 m depth), implying that they migrated to surface waters above the ocean floor [33]. Yahagi et al. (2017) provided evidence of early life history traits and population genetics for the surface dispersal of vent species of the gastropod *Shinkailepas myojinensis* that inhabited sulfide chimneys and volcanic rocks covered by bacterial mats in diffuse venting areas. The hatched larvae swam upwards depending on temperature, and this migration was probably because of the high food source (high phytoplankton biomass) that helps in their growth and development [6].

In this study, we attempted to present the vertical distribution of the holoplanktonic and meroplanktonic larvae in the hydrothermal vents of the Central Indian Ridge. To determine the difference in distribution patterns of larvae from the deep to the sea surface in the diffuse type (Onnuri Vent Field, OVF) and chimney type vent (Solitaire Field, SF), we collected larvae using a multiple opening and closing net environmental sensing system (MOCNESS).

2. Materials and Methods

2.1. Study Area and Physicochemical Analysis

The OVF (newly discovered; $11^{\circ}23.86'$ S, $66^{\circ}24.42'$ E) and SF ($19^{\circ}33.4'$ S, $65^{\circ}50.9'$ E) were the two vent fields selected in the Central Indian Ridge (CIR) to be investigated during a cruise of the R/V ISABU in June 2018 (Figure 1A,B). The CIR is known to be slow to intermediate spreading, with spreading rates varying from <12 mm/year to 50–60 mm/year [34]. The OVF is located at the summit of the Ocean Core Complex-3-2 and vents low-temperature fluids at depths of 1990–2170 m [35]. The SF is located on the Roger plateau on the western ridge of CIR segment 15 at a depth of 2634 m [15,34]. SF is characterized by chimneys that are less than 5 m in height and with fluid emissions of high pH 4.8 and approximately 10% lower chlorine levels than the ambient seawater [15]. The reference site (ref-site, MOCNESS tow: $09^{\circ}22.4'-9^{\circ}27.7'$ S, $67^{\circ}10.8'-67^{\circ}15.8'$ E) was selected outside of the immediate influence of the hydrothermal vent fields. The ideal location was north of OVF as the direction of transport of meridional Ekman flows from north to south during the boreal summer monsoon in June [36].



Figure 1. (**A**) Map showing the selected survey stations at the Central Indian Ridge in June 2018. Surface currents indicated are the South Equatorial Current (SEC), East Africa Coastal Current (EACC), and the direction of meridional Ekman transports (Me). The major currents are cited from Hood et al. (2017). (**B**) The figure on the right shows bathymetry from the start to the end of the multiple opening and closing net environmental sensing system (MOCNESS) sampling in both study stations.

The physical properties were obtained from the conductivity (#217), temperature (#6120), and depth (#217) sensors (Sea-bird Electronics, Bellevue, WA, USA) attached to MOCNESS (Biological environmental sampling systems Inc., BESS, North Falmouth, MA, USA). PVC Niskin bottles mounted on an instrumented Rosette sampler were used to collect discrete seawater samples for chlorophyll-*a* (chl-*a*) concentration analysis. Due to limited sampling time, water samples for chl-*a* concentration analysis were not collected at the ref-site. Seawater samples (2 L) for analysis of chl-*a* concentration were collected at 5 depths, including surface and subsurface chlorophyll maximum (SCM) layers, from 0–0.5 m (surface) to 200 m at OVF and SF. Seawater samples were filtered using 47 mm GF/F glass-fiber filters (Whatman, GE Healthcare, Chicago, IL, USA) under low vacuum pressure (<125 mmHg). The filters were kept frozen in a deep freezer (-80 °C) before being extracted in 90% acetone at 4 °C in the dark for 24 h. Chl-*a* concentration was determined using Turner Designs 10-AU, which was calibrated using a chl-*a* standard solution (Turner Designs, San Jose, CA, USA) based on the method by Parsons et al. (1984) [37].

2.2. Mesozooplankton Including Larvae Sampling

The mesozooplankton samples were collected using a 1 m² MOCNESS equipped with nine nets (mesh size 200 μ m). To minimize sample contamination, net traps and bar stops were employed to restrict net bar movement when the nets were opened or closed. The system carried sensors to measure pressure, temperature, and conductivity (Sea-Bird Electronics, Bellevue, WA, USA). The MOCNESS was attached to the deep-tow winch on the R/V ISABU, and the speeds of the winch wire during pay-out and haul-in were 20-30 m min⁻¹. The speed of the vessel was between 1.5 and 2.0 knots during towing. The net angle was maintained between 35° and 55° (optimum angle: 45° ; Biological Environmental Sampling Systems Inc., BESS, North Falmouth, MA, USA) by increasing or decreasing the speed of either the ship or the winch wire. Full depth sample collection was obtained by oblique tows from 100 m above the bottom of the sea. The depth strata sampled were divided into 6–7 layers (Table 1). The volume of filtered water was calculated using a flowmeter mounted on the frame of MOCNESS (Biological Environmental Sampling Systems Inc., BESS, North Falmouth, MA, USA). Mesozooplankton samples in the codend bucket were transferred to 1 L sampling bottles. The samples were divided into two groups, one sample group was immediately fixed to a final concentration of 5% with borax-neutralized formalin for microscopic examination, and the other was fixed with ethylalcohol (99.9%) for further molecular analysis. Mesozooplankton were identified into the lowest taxonomic groups, generally species or genus, and identified and enumerated under a stereomicroscope at $10 \times -80 \times$ magnification (Discovery V8, SteREO, Zeiss, Germany) in accordance with the studies of Conway et al. (2003) [38], and Chihara and Murano (1997) [39]. The larvae of benthic invertebrates at the hydrothermal vents were identified using the photographic identification guide to larvae at hydrothermal vents by Mills et al. (2009) [27]. The gastropod larvae were distinguished and divided into holoplanktonic and meroplanktonic larvae by their morphological characteristics, which were analyzed using the photographic guide. The photographs of mollusks were taken by the stereomicroscope equipped with the camera at $25 \times$, $32 \times$, $50 \times$, $63 \times$, and $80 \times$ magnifications (AxioCam ICc 3, Zeiss, Germany). The number of individuals was converted to individuals per cubic meter (ind. 100 m⁻³). The species richness (Margalef species richness index) and diversity index (Shannon-Wiener diversity index) were calculated by using PRIMER V6.1.10 statistical package (PRIMER-E, Plymouth Marine Laboratory, Plymouth, United Kingdom).

Station	Sampling Strata (m)	Temp. (°C)	Sal.	Chl- <i>a</i> (mg m ⁻³)	Total Zoopl. (ind. 100 m ⁻³)	Top Three Dominant Zoopl. (Relative Abundance)
Solitaire Field	(1) 0–200	23.7	35.2	3.1	19,522	Oithona copepodites (28%), Radiolarians (8%), Pleuromamma copepodites (6%)
	(2) 200-500	15.7	35.4	N.S.	4542	Pleuromamma copepodites (12%), Oithona copepodites (11%), ostracod sp.1 (11%)
	(3) 500–1000	7.9	34.6	N.S.	1291	Oncaea copepodites (26%), Pleuromamma copepodites (23%), Oithona copepodites (10%)
	(4) 1000–1500	4.4	34.6	N.S.	501	Radiolarians (18%), Oithona copepodites (18%), Oncaea copepodites (11%)
	(5) 1500-2000	2.7	34.7	N.S.	171	Radiolarians (27%), Oncaea copepodites (18%), Oithona fallax (18%)
	(6) 2000–2500	2.0	34.7	N.S.	60	Radiolarians (16%), Oncaea copepodites (16%), Microsetella spp. (16%)
Onnuri Vent Field	(1) 0–200	18.3	35.0	13.5	71,308	Paracalanus copepodites (16%), Pyrocystis noctiluca (11%), foraminiferans (7%)
	(2) 200-500	10.7	34.8	N.S.	4474	Radiolarians (19%), Oncaea copepodites (13%), Scolecithrix copepodites (13%)
	(3) 500–1000	6.9	34.7	N.S.	2850	Oncaea copepodites (32%), Harpacticoid copepodites (15%), Oithona copepodites (10%)
	(4) 1000-1300	4.9	34.7	N.S.	922	Oncaea copepodites (25%), Radiolarians (16%), Scolecithrix copepodites (13%)
	(5) 1300-1600	3.8	34.7	N.S.	1138	Oncaea copepodites (43%), Radiolarians (28%), Harpacticoid copepodites (8%)
	(6) 1600–1900	3.0	34.7	N.S.	19	Oncaea copepodites (42%), Harpacticoid copepodites (13%), foraminiferans (8%)
Reference site	(1) 0–200	20.9	34.8	N.S.	77,037	<i>Pyrocystis noctiluca</i> (14%), <i>Globigerina</i> spp. (7%), <i>Oncaea</i> copepodites (7%)
	(2) 200-400	11.8	34.9	N.S.	8430	Oithona copepodites (18%), Oncaea copepodites (14%), Pleuromamma copepodites (6%)
	(3) 400–1000	7.4	34.7	N.S.	11,460	Oncaea copepodites (25%), Oithona copepodites (12%), Scolecithrix copepodites (10%)
	(4) 1000–1300	5.1	34.7	N.S.	483	Oncaea copepodites (46%), Oithona copepodites (12%), Scolecithrix copepodites (6%)

Table 1. The sampling strata (depth, m), and average for temperature (temp.), and salinity (sal.), integrated chlorophyll-*a* (chl-*a*), total abundance of zooplankton (zoopl.), and top three dominant zooplankton (zoopl.) are listed for each station during the study period. N.S.: not sampled.

3. Results

3.1. Physicochemical Properties and Chlorophyll-a Concentrations

The vertical distributions of temperature and salinity in the water columns were acquired at all survey stations. The temperature observation showed that the depth of the surface mixed layer (SML) increased with an increase in latitude (°S) (avg. 79.2 m) (Figure 2). The deepest SML depth was observed in the SF (100 m; with an average temperature of 25.1 $^{\circ}$ C), and the shallowest SML depth was seen in the ref-site (63.0 m; with an average temperature of 27.2 °C). The SML depth for OVF was 74.5 m, with an average temperature of 27.0 °C. Warmer surface waters (avg. 27.2 °C) were observed in the ref-site and OVF, while relatively cooler surface water (avg. 25.1 °C) was observed in the SF. The temperature stratification in the SF and OVF was stronger from the surface to 350 m, and weakly stratified with decreasing depth. At SF and OVF, the bottom temperature was 2.7 $^{\circ}$ C (1900 m) and 4.5 $^{\circ}$ C (1300 m), respectively. The thermocline (temperature decreases rapidly from the SML) existed between 100-900 m, below which the temperature remained constant (avg. 3.2 °C) and reached 1.9 °C near the bottom (2500 m). The surface water in SF was relatively more saline (avg. 35.0) than the surface waters in OVF and ref-site (avg. 34.5). The salinity remained constant from surface to SML with increasing depth in all surveys, except between a layer of SML and 100 m. The integrated chl-a concentration within the SML was also higher in OVF (4.0 mg m⁻²) than in SF (1.8 mg m⁻²) (Figure 2).



Figure 2. The vertical profiles of temperature (°C), salinity, and chlorophyll-*a* (μ g L⁻¹) of the surveyed stations at the Central Indian Ridge during a cruise of the R/V ISABU in June 2018.

3.2. Abundance and Taxonomic Groups of Mesozooplankton

The total mesozooplankton abundance decreased with the depth, ranging from 60 to 19,522 ind. 100 m⁻³ (avg. 4348 ind. 100 m⁻³) in SF; 19 to 71,308 ind. 100 m⁻³ (avg. 13,452 ind. 100 m⁻³) in OVF; and 483 to 77,037 ind. 100 m⁻³ (avg. 24,352 ind. 100 m⁻³) in the ref-site (Figure 3). It is evident that the majority of the mesozooplankton abundance is accumulated at 0–200 m (euphotic zone) in both water columns above hydrothermal vent



fields, which may be due to higher chl-*a* concentrations in the SCM (avg. 112.5 m). The abundance at 0–200 m was approximately 11 times higher than in other layers (200–1300 m) at the ref-site.

Figure 3. The vertical distribution of total and relative abundance of the mesozooplankton community in the surveyed stations during a cruise of the R/V ISABU in June 2018 at the Central Indian Ridge.

Most of the mesozooplankton community was composed of copepods (immature and adults) for all water columns of the surveys (Figure 3, Table 1). At the SF, copepods (both immature and adults) accounted for 65–86% (avg. 74%) of the total mesozooplankton community, followed by radiolarians that accounted for 3-27% (avg. 13%) occurring throughout the water column (0–2500 m), and ostracods and chaetognaths primarily occurring in the upper layers (0–500 m). Taxonomic groups of crustacean larvae and others included amphipod larvae and unidentified eggs, which appeared in the bottom layers (2000–2500 m). At the OVF, copepods (both immature and adults) accounted for 59–83% (avg. 71%) of the total mesozooplankton community, followed by radiolarians (avg. 13%), foraminiferans (avg. 6%), and ostracods (avg. 5%), occurring in all water columns. At the ref-site, copepods (immature and adult) accounted for 61-81% (avg. 74%) of the total mesozooplankton community, followed by foraminiferans (7%), radiolarians (5%), and Pyrocystis noctiluca (4%), occurring in all water columns. P. noctiluca accounted for 11% and 14% of the total mesozooplankton community at OVF and the ref-site, respectively, occurring between 0–200 m, probably due to relatively warmer surface waters (avg. 27.2 °C) (Figure 3, Table 1).

The morphologically identified numbers in the integrated water column were 28, 45, and 52 species in 6, 6, and 8 phyla at SF, OVF and the ref-site, respectively (Figure 4). The phyla Retaria (Foraminifera), Protozoa (Dinoflagellata), Crustacea (Ostracoda, Calanoida, Cyclopoida, Poecilostomatoida, Harpacticoida, Amphipoda, Euphausiacea, Decapoda), Chaetognatha (Sagittoidae), Chordata (Thaliacea, Doliolida, Appendicularia, Ichtyoplankton), and Mollusca (Gastropoda, Bivalvia) commonly appeared at both hydrothermal vents and the ref-site, while phyla Cnidaria (Hydrozoa) and Annelida (Polychaeta) only appeared at the ref-site (Figures 3 and 4). Both the richness and diversity of the species were highest at the ref-site (richness: 4.8, diversity: 3.1) and lowest at SF (richness: 2.9, diversity: 2.6).



Figure 4. The number of mesozooplankton phyla, order, and species, and indices of species richness and diversity in the surveyed stations during a cruise of the R/V ISABU in June 2018 at the Central Indian Ridge.

Gastropod larvae were the dominant larvae at both SF (avg. 88%) and OVF (avg. 56%) (Figure 3), followed by amphipod larvae (avg. 12%) at SF and decapod larvae (avg. 17%) at OVF (Figure 3). Copepod nauplii (avg. 49%) was the most dominant larval group at the ref-site, which was followed by gastropod larvae (avg. 27%). We examined the taxonomic groups of mollusk larvae in further detail because deep-sea hydrothermal vent communities may disperse through planktotrophic modes (Figure 5) [1]. Mollusk larvae (bivalves and gastropods) can be holoplankton (spend entire life as plankton) or meroplankton (spend part of their life as plankton). We identified 18 species of mollusk larvae, including 16 unknown species of gastropod larvae, one species of bivalve larvae, and one species of pteropod larvae (*Cresis* spp.) (Figure 5).

The bivalve larvae (length: 330 µm) were found at both the OVF and the ref-site between depths of 0–200 m (Figure 5). The bivalve larvae had morphological features similar to those of the planktotrophic larvae of *Bathymodiolus* spp. that were reported to be found at hydrothermal vents in the South Pacific Ocean [27,40]. Gastropod larval species of 1–4, 6, and 13 have morphological features of holoplanktonic larvae such as pelagic species of the genus *Atlanta, Oxygrus,* and *Limacina* [38]. Gastropod larval species of 5, 7–12, and 14–16 have morphological features of meroplankton but only appear at depths between the surface and 200 m (Figure 5). Gastropod larval species 5, 11, and 12 only appeared at the OVF; 9 and 10 only appeared at the SF; 14–16 appeared only at the ref-site; 7–8 appeared in all surveyed stations. Gastropod larval species 5, 8, 12, 14, and 15 have similar morphological features to macrobenthic gastropod larvae of *Vetulonia* spp. Gastropod larvae species 7 have morphological features similar to gastropod Lepetodrilidae (*Lepetodrilus* spp.). Gastropod larval species 9–11 and 16 have morphological features similar to those of *Phymorphynchus protoconchs* [27].



Figure 5. The vertical distribution of the total and relative abundance of mollusk larvae in the surveyed stations during a cruise of the R/V ISABU in June 2018 at the Central Indian Ridge. The 18 species of mollusk larvae, include 16 unknown species of gastropod larvae, one species of bivalve larvae, and one species of pteropod larvae (*Cresis* spp.). N/A represents not available.

4. Discussion

The abundance of mesozooplankton decreased with depth and was mainly accumulated in the euphotic zone (0–200 m). In this study, the near-bottom samples were approximately 0.02% and 0.3% of the total abundance in the euphotic zone of the SF and OVF, respectively. Similar results were reported in the waters of the Guaymas Basin hydrothermal vents, where the benthopelagic zooplankton biomass was about 0.02–0.08% of the surface biomass, and the biomass of zooplankton was 10 times lower in 100–200 m of the bottom than in the surface waters [22,23]. The results of the present study demonstrated that the major accumulation of mesozooplankton was at 0–200 m in the water columns above both the hydrothermal vent fields. Among them, immature copepods of Oithona (28%) and Paracalanus (16%) were dominant in SF and OVF, respectively. This may be influenced by relatively higher temperatures (>23.7 $^{\circ}$ C) at SF and higher chl-a concentrations in the SCM (avg. 112.5 m) at OVF. The plankton distribution was shown to differ significantly above the hydrothermal vents of the Mid-Atlantic Ridge depending on the productivity of the upper layers [26]. We studied the community structure of the water columns and near-bottom mesozooplankton because the research on the copepods among mesozooplankton in the near-bottom of hydrothermal vents has been limited. The near-bottom dominant copepods were poecilostomatoids at both the OVF (Oncaea and Corycaeus) and the SF (Corycaeus), and harpacticoids appeared in relatively higher abundance at near-bottom of hydrothermal vents (OVF: avg. 16%, SF: avg. 25%). Interestingly, harpacticoids did not appear at the ref-site, implying that harpacticoids may be able to feed on chemosynthetic bacteria near or above hydrothermal vents. The near-bottom copepods are able to feed on free-living chemosynthetic bacteria associated with vent effluents in areas where the effluent signature is weak, playing an important role in the transfer of vent productivity to the deep sea [41]. In addition, in chemosynthetic habitats, harpacticoids were dominant in vent epifauna and seep epifaunal communities, showing a relatively high dominance of copepods within the meiofauna communities [42]. Skebo (2004) studied copepod densities in the near-bottom water layers of the Juan de Fuca (NE Pacific) and reported densities ranging from 0.7–3.5 ind. m⁻³ over smoker vent and non-vent sites to 14.6 ind. m^{-3} over diffuse vent sites [41]. Similar results were found at the bottom plankton tows of the Guaymas Basin, in which the copepods of siphonostomes and poecilostomes (avg. 25% of the copepod population) and cyclopoids and harpacticoids were collected in all bottom plankton tows [22].

The near-bottom depth strata range at OVF (1600–1900 m) and SF (1500–2500 m) showed interesting copepod composition, distinguished from the near-bottom depth strata of hydrothermal vents. The community analysis showed that there were distinct shallow (<800 m depth) and deep (>800 m depth) faunal assemblages [24]. The distinct deep faunal assemblages at OVF included *Oncaea* copepodites (21%), foraminiferans (11%), ostracods (11%), and harpacticoid copepods (11%), and at SF, included radiolarians (22%), *Microsetella* spp. (22%), and *Oncaea* copepodites (22%). The copepods can feed directly on bacteria or dissolved organics [24]. There was a possibility of underestimation of the abundance in smaller organisms such as nauplii, copepodites, meroplanktonic larvae and copepod species of *Oncaea* and *Oithona* because of the mesh size used (200 μ m) for MOCNESS in this study. According to Gallienne and Robbins (2001), an 80 μ m net will collect 90% of the total zooplankton abundance and finer mesh nets may result in reduced estimates of larger taxa, and larger mesh (200 μ m) are likely only to catch 7% of the total zooplankters between 200 μ m in dimension [43].

In this study, radiolarians were the dominant zooplankton throughout the water column above the hydrothermal vent sites (OVF and SF), except at the ref-site. Vereshchaka and Vinogradov (1999) investigated zooplankton aggregations at the MAR Broken Spur, finding that both gelatinous and radiolarians dominate biomass aggregation, significantly contributing to plankton biomass throughout the water column [44]. The radiolarians were dominant near the surface (60–90% of the total biomass), in the lower part of the main pycnocline (10–30% of the total biomass), and near the plume (20–30% of the total biomass) [44]. The speculation as to why radiolarians appear throughout the water column and also near the bottom is that it may be the advantageous feeding through passive absorption of particulate matter [44].

In this study, the holoplanktonic mollusk larvae made up approximately 74%, 61%, and 92% of the total abundance of mollusk larvae in the integrated water columns of SF, OVF, and the ref-site, respectively. The holoplanktonic mollusk larvae including gastropod larval species of 1–4, 6, and 13 in this study had similar morphological features with the genus *Atlanta, Oxygrus,* and *Limacina* [38]. The holoplanktonic larvae shells are relatively flat and coiled, and the swimming fins are well developed [21]. According to Lalli and Gilmer (1989) [21], the heteropods have evolved a single swimming fin, whereas pteropods

have evolved paired swimming wings, and the feeding mechanisms in open ocean differ from those in the benthic habitat due to the availability of food [21]. The holoplankton are widely distributed in the world's oceans and usually inhabit the upper ocean of generally offshore regions, where they undertake diurnal vertical migrations [21,45]. Some species of *Limacina* (ranked among the most abundant gastropods) and other abundant planktonic gastropods may have significant impacts on the epipelagic marine communities [21].

The meroplanktonic mollusk larvae including gastropod larval species of 5, 7–12, and 14–16 and bivalve larvae appeared mostly in the near-surface waters of the euphotic zone (0–200 m depth) of the study sites. Meroplankton, the planktotrophic larvae of benthic organisms, have shells with diamond shaped patterns and relatively large coils as compared with holoplanktonic larvae [27]. The planktotrophic phase is important for larval development because it allows larvae to feed during the free-swimming stage, promoting deep-sea community dispersal, colonization, and resilience [46,47]. The larvae interact with oceanic circulation, ocean ridge topography, and ridge flow and exhibit vertical migration behaviors [5,29]. Depending on the species, they spend hours to several weeks or months dispersing and drifting in the water columns by means of water currents before setting and metamorphosing on the sea floor [21].

The present study showed similar evidence that meroplanktonic mollusk larvae may disperse in the surface waters by the possibility of vertical migration. The bivalve larvae, which appeared in both the OVF and the ref-site, had morphologically similar features to planktotrophic larvae of the deep-sea hydrothermal vent species of *Bathymodiolus* spp. [27]. According to Mills et al. (2007), they collected *Bathymodiolus* species (length 400–450 μm) from near the settlements, of brownish color. B. marisindicus (avg. 31.1%) was one of the top-ranked microbenthic species at OVF [35]. However, we cannot be certain that the bivalve larvae are larvae of Bathymodiolus spp. because larvae of coastal mussels (Mytilus spp.) also have similar morphological features, thus further molecular analyses are needed to confirm the species [48,49]. The vent mussel *B. marisindicus* has been previously reported at the SF and OVF [34,35]. So, the bivalve larvae may have vertically migrated from the hydrothermal vents of the OVF to the surface waters. Arellano et al. (2014) reported cold methane seep species of mytilid bivalve B. childressi in the euphotic zone (0-100 m depth) and suggested that they had migrated to surface waters from the ocean floor [33]. The possibility of bivalve larvae being transported from the coastal, intertidal, or shallow waters maybe low because our study site is in the open ocean, approximately 1000 km away from the coasts. The dispersal of coastal, intertidal, or shallow-water bivalve larvae is through transport from inshore waters into larger scale coastal currents, and then eventually returning to the inshore waters of another location [9].

The gastropod larvae (species 7) that appeared mostly in the euphotic zone (0-200 m) at OVF and SF had morphological similarities to gastropod larvae Lepetodrilidae (Lepetodrilus spp.), which inhabit the hydrothermal vent sites of Juan de Fuca Ridge and EPR [27,44]. The abundance of vent gastropod larvae (Lepetodrilus sp. and two peltospirid species) is significantly higher in the plume than away from it (mean abundance = 21.0 ind. 1000 m^{-3}) [50]. Gastropod larval species 5, 8, 12, 14, and 15 have similar morphological features to macrobenthic gastropod larvae of Vetulonia spp. that were found in the hydrothermal vents and hydrothermal seeps at the North Fiji Basin [51]. Gastropod larval species 9–11 and 16 have morphological features similar to those of *Phymorphynchus protoconchs* [27]. The vent mollusk fauna in SF includes B. marisindicus (Mitilidae), Lepetodrilus sp. (Lepetodridae), Eulepetopsis sp. (Neolepetopsidae), Scaly-foot gastropod (Peltospiridae), Shinkailepas spp. (Phenacolepadidae), Alviniconcha spp., Desbruyeresia spp. (Provannidae), and Phymorhynchus spp. (Turridae) [34]. The vent mollusk fauna in OVF includes B. marisindicus, B. sp.1, Gigantidas n. spp., Alvinocaris markensis, Paralepetopsis ferrugivora, and Lepetodrilus spp. [35]. Larval dispersal in the planktonic larval stage is an important component of the life cycle of species, particularly in isolated habitats such as hydrothermal vents [28]. Adams et al. (2012) studied and reviewed the reproductive patterns and larval durations, behaviors and vertical distributions, and the coupling of vent topography and hydrodynamics that affect dispersal [5]. Yahagi et al. (2017) provided evidence of early

life history traits and population genetics for the surface dispersal of gastropod vent species *Shinkailepas myojinensis* that inhabited sulfide chimneys and volcanic rocks covered by bacterial mats in diffuse venting areas [6]. The hatched larvae swam upwards at 16.6–44.42 mm/min depending on temperature, and were likely to migrate to surface water because of the high food source (high phytoplankton biomass) that helps in their growth and development [6]. Therefore, in this study, the gastropod larvae in the surface waters may have dispersed or vertically migrated from the deep-sea hydrothermal vent sites (OVF and SF).

5. Conclusions

The quantitative measurements of mesozooplankton including holoplankton and meroplankton were conducted in the OVF, SF, and ref-site. The integrated abundance of mesozooplankton over the water column was relatively higher in the ref-site $(77,037 \text{ ind. } 100 \text{ m}^{-3})$ than in the vent sites (avg. 53,398 ind. 100 m^{-3}). It is evident that most of the mesozooplankton was accumulated in the euphotic zone (0–200 m). Mollusk larvae (gastropods and bivalves) appeared at all stations. Only one species of bivalve larva that appeared at the OVF and ref-site (0–200 m) was morphologically similar to *Bathymodiolus* spp. that inhabits the hydrothermal vents. The gastropod larvae were morphologically identified as holoplanktonic and meroplanktonic. Sixteen species of gastropod larvae were distinguished morphologically. Gastropod larvae species 1–4, 6, and 13 had holoplanktonic features (Atlanta, Oxygrus, and Limacina), while gastropod species 5, 7–12, and 14–16 had meroplanktonic features. Gastropod larvae species 5, 11, and 12 only appeared at OVF, 9 and 10 only appeared at SF, 4–16 appeared only at ref-site, and gastropod larvae species 7-8 appeared in all surveyed stations. Gastropod larvae species 5, 8, 12, 14, and 15 have similar morphological features to the macrobenthic gastropod larvae of Vetulonia spp. Gastropod larvae species 7 have morphological features similar to gastropods Lepetodrilidae, and species 9-11 and 16 have morphological features similar to *Phymorphynchus protoconchs.* The morphologically identified mollusk larvae of gastropods and bivalves in the upper layers of the water column (0-200 m) indicate that larvae associated with the hydrothermal vents may disperse approximately 2000 m above the vents.

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