



MARINE INVERTEBRATE LARVAL DISTRIBUTION AT THE HYDROTHERMAL VENT SITE OF GUEISHANDAO

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MARINE INVERTEBRATE LARVAL DISTRIBUTION AT THE HYDROTHERMAL VENT SITE OF GUEISHANDAO

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Key words: supply-side ecology, recruitment, hydrothermal vents, vertical distribution, seasonality.

ABSTRACT

Scientists remain uncertain about numerous aspects of hydrothermal vent (HV) ecology, including the reproductive biology of their biota, as well as their recruitment and dispersal during larval stages (meroplankton) in the plankton above the HV sites. We studied the meroplankton from a shallow HV site off the northeastern coast of Taiwan, in the northwest Pacific Ocean. Our findings potentially explain how fauna endemic to HVs persist at specific HV sites. With the exception of some damaged Cnidaria and Ctenophora, the plankton net catches were in good condition and sufficient for identification.

INTRODUCTION

Other than their trophic advantage being closer to the pelagic primary producer level in the euphotic zone of the water column [1, 9, 23], drifting organisms show effective dispersal and recolonisation of areas that have been disturbed by biotic and abiotic agents [2, 29]. Stray members of epiplankton can be found here as well as their dormant stages [11, 21]. Pelagic drift makes an effective genetic exchange between geographically disjunct populations of bottom-living invertebrates feasible [8], which is specifically relevant for larvae of otherwise benthic macrofauna. It is assumed that the distribution and abundance of benthic populations are influenced by larval recruitment processes (e.g., [45]). The vast majority of these larvae, as well as other developmental instars (e.g., gametes, zygotes, juveniles, adults of invertebrates, or their vegetative parts) may colonize their prospective benthic habitats by

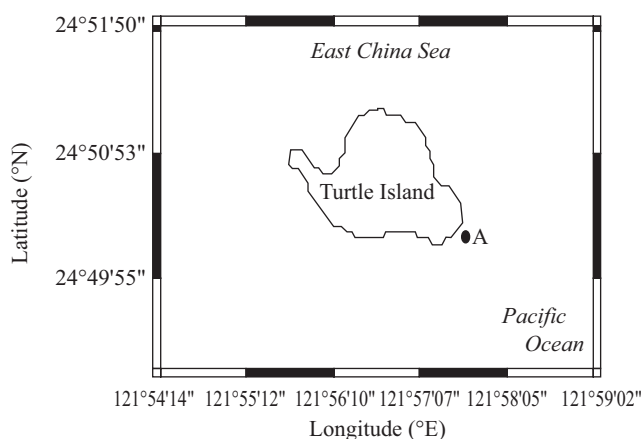


Fig. 1. HV Site A – collection site of meroplanktonic larvae throughout the water column (0 to 14 m depth) at Gueishandao.

actively swimming and/ or passively drifting in the pelagic zone as meroplankton [11, 52, 53]. Hence, determining the sources of benthic recruitment variability is partially a problem relating to zooplankton ecology [10]. Specifically, demersally drifting stages following disturbance events are critical for the provision of propagules for recruitment processes [12].

Since the discovery of deep-sea hydrothermal vents (HVs) in 1977, over 400 new species have been encountered in these environments throughout the world's oceans [18]. HVs are characterized by various extreme physicochemical conditions, such as high temperature, high sulfide and metal content, high carbon dioxide levels, low oxygen levels, and low pH [40, 44]. Biological communities associated with the vents exhibit behavioral, physiological, morphological, and reproductive adaptations [4, 6, 46, 48]. HV habitats are characterized by the spatially and temporally variable input of hydrothermal fluids [3]. Although specific vent fauna have adapted to these habitats, the extreme conditions are lethal to other organisms.

Gueishandao (Turtle Island) is located at a tectonic junction of the fault system extension of Taiwan and the southern rifting end of the Okinawa Trough [24, 49]. A cluster of more than 50 HVs at water depths ranging between 10 and 80 m off the eastern tip of Gueishandao emits hydrothermal fluids and volcanic gases such as HSO_3^- (Fig. 1). The HV discharges

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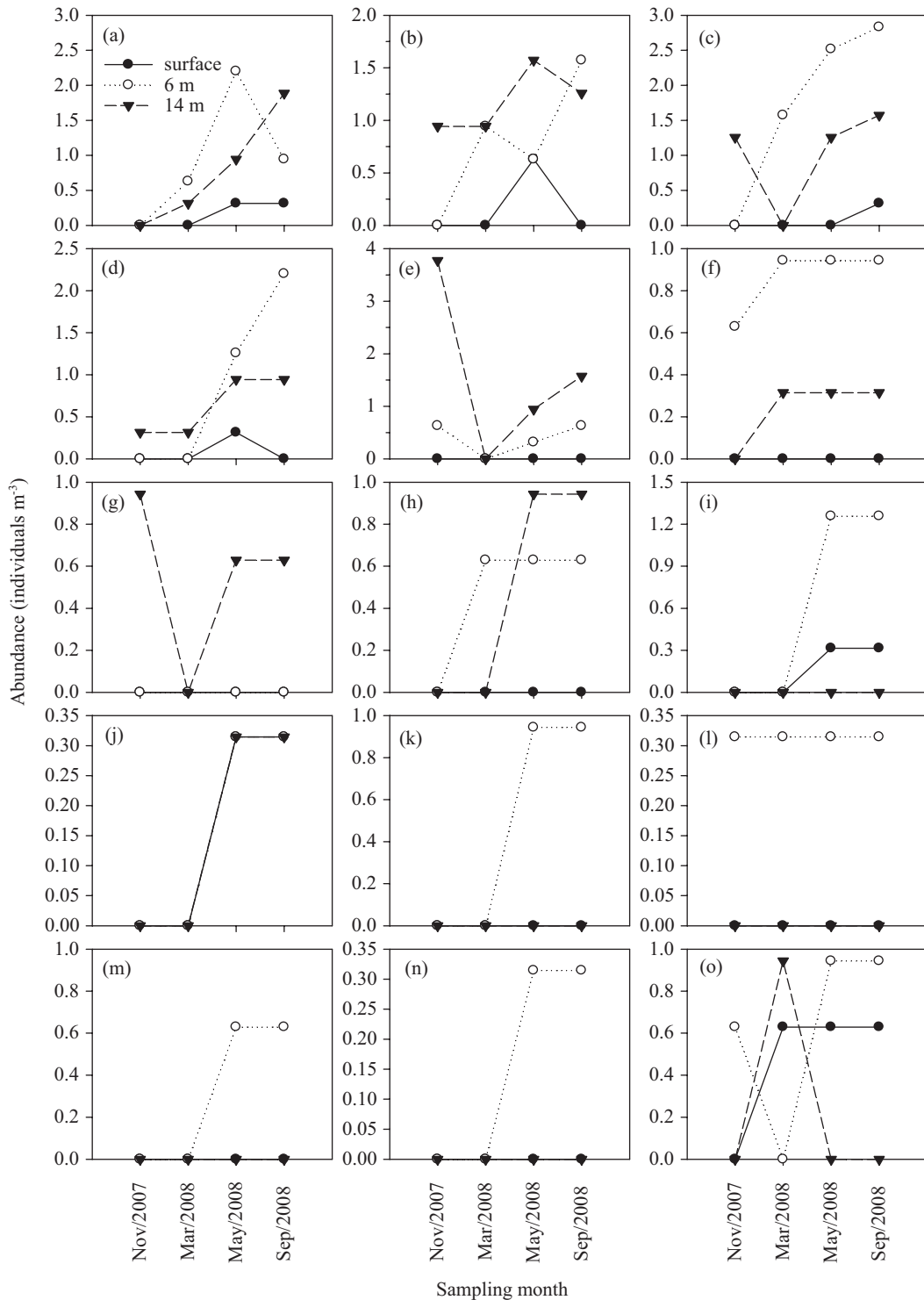


Fig. 2. Seasonal variations of meroplankton larvae in the watercolumn at Kueishantao at HV Site A at three depth layers. Crab zoea 1 (a); crab zoea 2 (b); crab zoea 3 (c); crab zoea 4 (d); Megalopa (e); Polychaeta trochophora (f); Polychaeta juvenile (g); Bivalvia veliger (h); Ctenophora cydippe (i); Echinoidea echinopluteus (j); Asteroidea bipinnaria (k); Ophiuroidea ophiopluteus (l); Bryozoa cyphonautes (m); Porifera parenchymula (n); and Anthozoa planula (o) recorded at the HV site during each sampling from November 2007 to September 2008.

are sulfur-rich and highly acidic (1.75 to 4.60 pH). They commonly have high numbers of sulfur rock formations at the chimney outlets [39] and elevated temperatures up to 116°C.

The gases comprise a similar composition to that of low-temperature fumaroles worldwide; that is, with high CO₂ and H₂S but low SO₂ and HCl contents of a mantle source region

without significant crust contamination [3, 51]. How and to what extent HV effluents and gases affect the plankton of overlaying waters has not been investigated. [27] mentioned that the vent plumes were lethal to zooplankton, although they provided a scavenging opportunity for specific vent crabs that feed on dead zooplankton.

It is unknown how crabs become dispersed and recolonize their fluctuating habitats of newly developed HV sites, or how they persist in their generally isolated habitats. Dispersal and recruitment at HV sites remain generally popular topics for the supply-side ecology at HVs [34, 42]. Although primary dispersal stages might be pelagic larvae, adults may also have evolved recognition systems to HV signaling cues. However, these cues remain elusive because of difficulties conducting experiments at deep-water HV sites. Specifically, it has not been shown whether invertebrates from HV regions use various environmental cues to locate their vent habitat [34, 50]. The HVs at Gueishandao provide a unique opportunity for an experimental approach to the supply-side ecology of vent fauna because of their shallow water location.

The objective of this study was to evaluate specific supply-side ecology aspects of macrofauna larvae by reporting on the vertical and seasonal distribution of meroplanktonic larvae in the area of a shallow HV at Gueishandao.

II. MATERIAL AND METHODS

1. Invertebrate Meroplankton Collection, Identification, and Enumeration

We collected seasonal drift assemblages between November 16, 2007 and March 12, 2008, and again from May 27, 2008 to September 21, 2008 from surface waters (up to 1 m), midwater (6 m), and above ground (14 m) at an HV site (Site A) at Gueishandao (Turtle Island, Fig. 1). The plankton samples predominantly comprised copepods were fixed in 4% buffered formalin. We subsequently identified and counted meroplanktonic larvae in the laboratory.

2. Data Analyses

To elucidate the variations of invertebrate larvae at Site A, we employed the Paleontological Statistics software package to analyze the invertebrate larvae community of each sample [19]. Among the 12 samples taken, we applied the Bray-Curtis method to evaluate the relative similarities in composition for the 15 dominant invertebrate larvae groups. The meroplanktonic larvae characteristics of each cluster were further identified using the Indicator Value Index (IndVal) proposed by [14]. To estimate the invertebrate larvae diversity of each sample, we applied the Shannon-Wiener diversity index, Pielou's evenness index, and Margalef's richness index.

III. RESULTS

1. Taxon Composition of Meroplankton at HV Site A

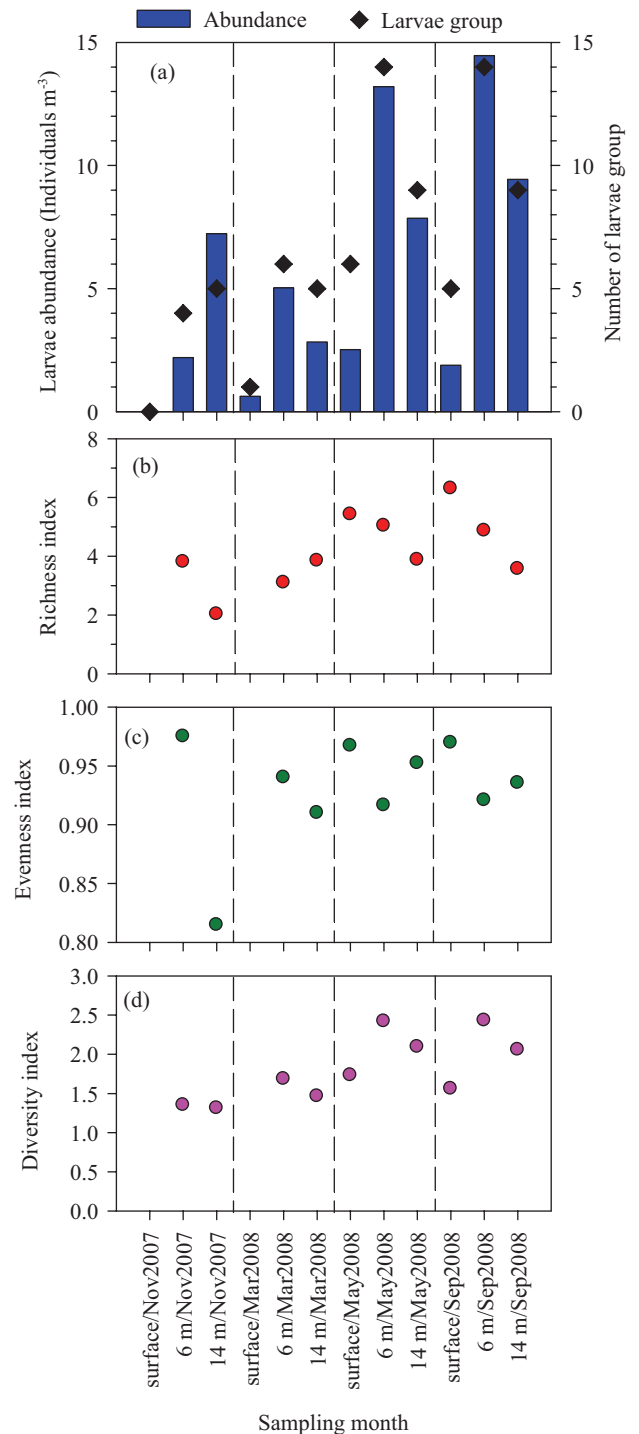


Fig. 3. Abundance of meroplankton larvae, number of meroplankton larvae group (a); indices of richness (b); evenness (c); and diversity (d) during sampling from November 2007 to September 2008.

From the 12 samples, we identified 15 meroplankton larvae in the water column at Gueishandao from 3 depths at HV Site A. The abundance of meroplankton larvae in each sample is shown in Fig. 2. The relative abundance (RA) and occurrence ratio (OR) of each meroplankton larvae group varied by the

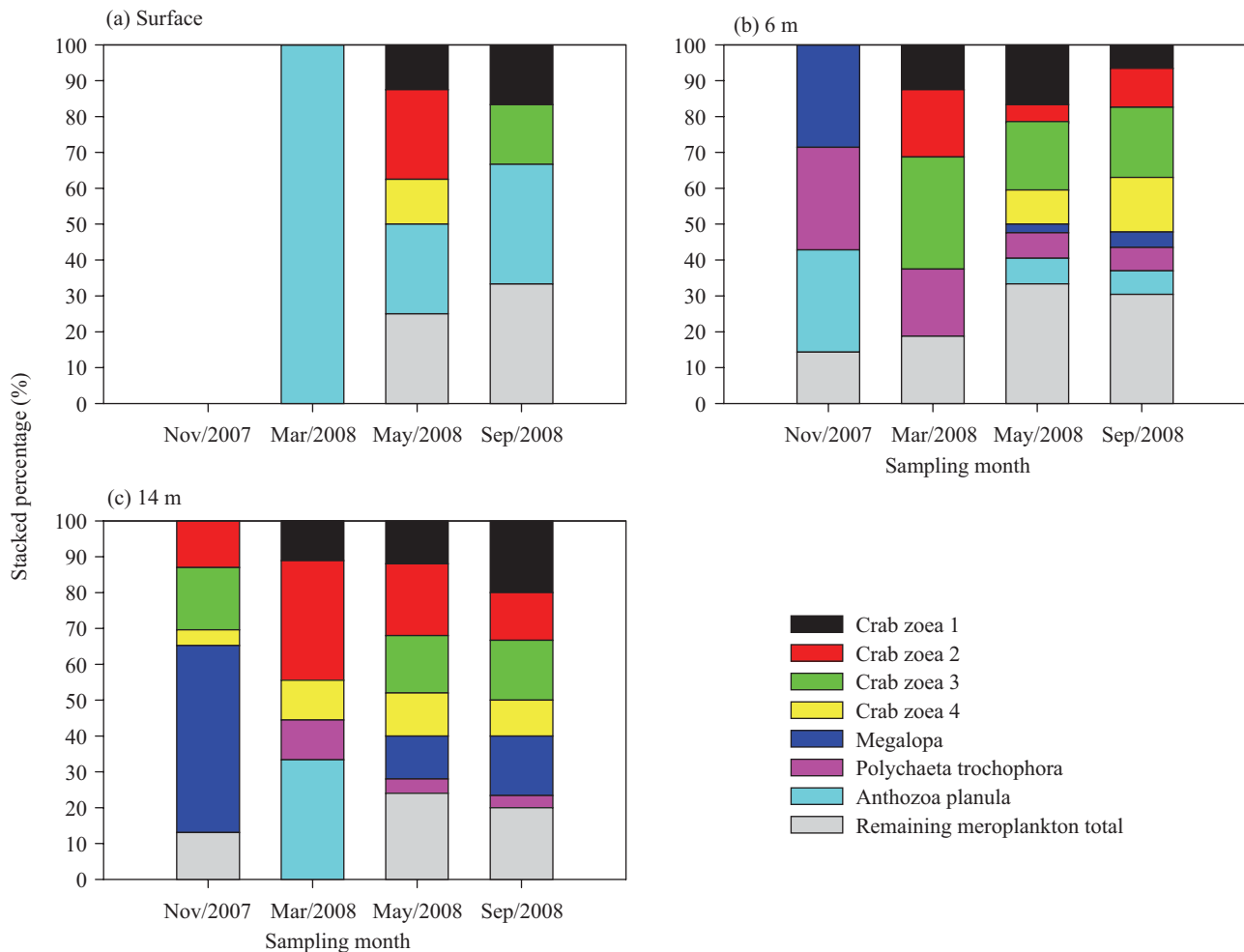


Fig. 4. Percentages of seven highly abundant meroplankton larvae groups (RA > 5%) which were identified at each sample of the sampling cruise from November 2007 to September 2008.

month the samples were obtained. The results show that among all samples, the RA of crab zoea 3 was highest (16.82%), followed by crab zoea 2 (12.62%), megalopa (11.68%), crab zoea 1 (11.21%), and crab zoea 4 (9.35%). The highest OR of meroplankton larvae was crab zoea 1 and crab zoea 2 (66.67%), followed by crab zoea 3, crab zoea 4, polychaeta trochophora, and anthozoa planula (58.33%).

Fig. 4 shows the seasonal variations of meroplankton larvae abundance, number of groups, and the richness, evenness, and diversity indices over the sampling period. The varied abundance and group composition of meroplankton larvae among all samples are shown in Fig. 3(a). Only the surface water sample collected in November 2007 did not contain any meroplankton larva. Among the remaining 11 samples, the abundance of meroplankton larvae ranged from 0.63 (surface sample – March 2008) to 14.46 individuals m^{-3} (midwater sample – September 2008). The number of the meroplankton larvae group in each sample ranged between 1 (surface sample – Mar/2008) and 14 station $^{-1}$ (midwater sample – May 2008 and September 2008). The indices of richness, evenness, and di-

versity showed high variation between samples. Because the record of the identified meroplankton larvae group was less than 2 for the March 2008 surface sample, the richness, evenness, and diversity indices could not be calculated. Among the remaining 10 samples, the richness index ranged from 2.02 (aboveground sample – November 2007) to 6.3 (surface sample – September 2008) (Fig. 3(b)). The evenness index of each sample ranged between 0.81 (aboveground sample – November 2007) and 0.98 (midwater sample – November 2007) (Fig. 3(c)). The Shannon-Wiener diversity index ranged from 1.31 (aboveground sample – November 2007) to 2.43 (midwater sample – September 2008) (Fig. 3(d)).

2. Seasonality Succession, Distribution and Composition at Three Depths

The seasonal succession patterns of meroplankton compositions recorded at the 3 depth layers are clear. Fig. 4 shows the proportions of dominance, meroplankton larvae composition and distribution for each sample. This figure also provides the dynamic composition of meroplankton for

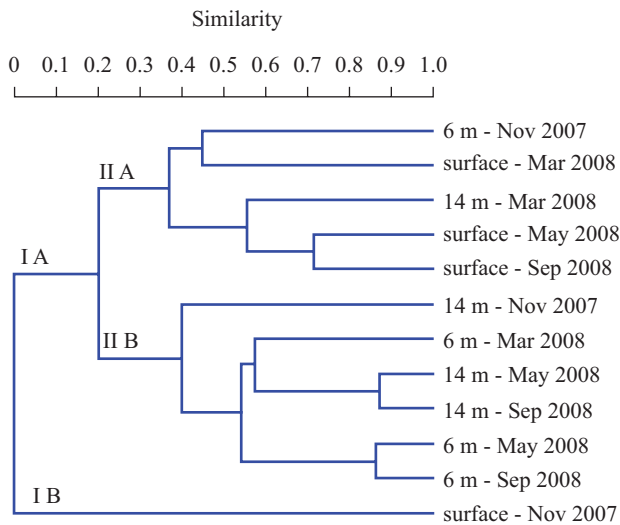


Fig. 5. Dendrogram showing the similarities between stations measured using the Bray-Curtis distance measurement for meroplankton larvae composition. Recorded during sampling from November 2007 to September 2008.

RA values greater than 5% of the total abundance. The RA data indicate that Gueishandao endemic crab larvae (*Xenograpsus testudinatus*; i.e., zoea 1, zoea 2, zoea 3, zoea 4, and megalopa) comprise the dominant organism in the waters at this HV site. Furthermore, the crab larvae were distributed widely over the 3 depths.

Among the 3 discussed depths strata, anthozoa planula and crab larvae were dominant in surface samples (Fig. 4(a)). In the sample obtained in March 2008, only the surface sample contained anthozoa planulae. In addition, high proportions of megalopa (Fig. 4(b)) and polychaeta trochophora (Fig. 4(c)) occurred in the midwater and aboveground samples, respectively.

3. Meroplankton Larvae Community Structures

The Bray-Curtis analysis of meroplankton larval assemblages shows various larval community structures (Fig. 5). Table 1 demonstrates zooplankton meroplankton larvae with index values (IndVal) greater than 5% for each group. At the highest level, a single sample (surface – Nov/2007) without any identified meroplankton larvae was allocated into Group I-B (Fig. 5). The remaining 11 samples were separated into Group I-A. The second hierarchical level distinguished samples by abundance. The samples comprising Group-II A contains 5 samples characterized by low abundance (0.67 ± 0.90 individuals m^{-3} , mean \pm SD). The dominant meroplankton in Group II-A are crab zoea 1 (5.63%), crab zoea 1 (6.25%), and anthozoa planula (34.38%), indicating that the majority of surface samples had a low abundance. Group II-B comprised 6 samples with high abundance (3.81 ± 9.02 individuals m^{-3}), and was dominated by the following 7 meroplankton larvae: crab zoea 1 (9.62%), crab zoea 2 (12.09%), crab zoea 3 (19.23%), crab zoea 4 (8.24%), megalopa (10.53%), poly-

Table 1. Indicator meroplankton larvae and index values (%) for each cluster identified using the Bray-Curtis cluster analysis method (Fig. 5).

Merozooplankton	Group	
	II A	II B
crab zoea 1	5.63	9.62
crab zoea 2	6.25	12.09
crab zoea 3		19.23
crab zoea 4		8.24
Megalopa		10.53
Polychaeta trochophora		5.04
Bivalvia veliger		5.49
Anthozoa planula	34.38	
Cumulative contribution (%)	46.25	70.24

chaeta trochophora (5.04%), and Bivalvia veliger (5.49%) (Table 1).

IV. DISCUSSION

Previous studies emphasized the ecological role of pelagic larvae for bottom-living invertebrates [43], and assumed an inverse correlation between planktotrophic larvae and depth as well as toward the polar regions – whereas there is enhanced direct development and brood care along these gradients. Numerous subsequent studies (e.g., [16, 36–38]) amended this assumption. Lecithotrophic larvae, as well as other ontogenetic stages with direct development, have been shown to potentially occur as meroplankton in the water column [17, 31]. Effective dispersal may enhance the recolonization potential of disturbed bottom-living areas, which generally influences succession speed and direction, as well as benthic community attributes. Therefore, restricted dispersal capabilities should become a key factor for evolution and zoogeographic distribution patterns. Dispersal and recruitment remain an eminent topic of investigation, particularly for invertebrates from HV sites considering their fragmented and otherwise isolated occurrence [34, 41].

Few macrofauna species have been identified at the Gueishandao HV site discussed in this study – among them, *X. testudinatus* Ng, Huang & Ho, 2000 (Crustacea: Decapoda: Brachyura: Grapsidae) described by [35] in a volume edited by [25]. Megalopa stages were identified and juvenile crabs in the fissures and crevices of 3 sulfur aggregates that weighed 38.27 kg. HV studies have resulted in the discovery of numerous new species of crabs [33]. In a review of HV decapods, [32] listed 125 species belonging to 33 families. We studied *X. testudinatus* that was discovered by Takeda and Kurata in 1977 as the third species of the genus *Xenograpsus* (Bythograeidae) from shallow water HVs off the east coast of Taiwan.

Low abundances of the crabs at the discussed HV sites of Gueishandao during winter may indicate that individuals

translocate into deeper waters and return to shallower sites during summer. Reproduction is interrupted only during winter for approximately 4 months (unpubl. data). In laboratory studies, we successfully reared the megalopa larvae through metamorphosis and several juvenile stages [22]. Laboratory observations of the behavior of pelagic larval zoea and benthic megalopa stages of *X. testudinatus* indicate that they tend to stay near the bottom, even when swimming. The field distribution of larvae clearly indicates that zoea and megalopa stages are distributed throughout the water column (Fig. 2). Furthermore, there is a positive correlation between abundance and depth, with the highest densities recorded at the sea bottom. When juvenile or adult vent crabs collected from the HV outlet of a shallow water HV site off Gueishan-dao were released approximately 10 m from the gas bubble-and flume-emitting outlet, they returned immediately to the outlet, indicating an attraction to currently unknown HV site conditions (unpubl. observations).

Previous research on the behavior of megalopa stages indicated that these larvae swim actively over a range of temperatures (2 to 25°C) near the vents. It is unknown whether these crabs exhibit migratory behavior caused by factors other than the attraction of food [26].

Previous studies have examined the reproductive biology [47] and behavior of larval stage crabs [47] at several HV sites. In addition, [22] reported that HV chimneys provide structurally complex habitats for larval and juvenile *X. testudinatus* crabs. These microhabitats comprise cavities that have at least partially been created by the juvenile crabs themselves. Settlement of larvae to habitats with adequate protection, food, and temperature is critical for the survival of individual crabs during early development stages. Settlement on unprotected sea bottom exposes young crabs to predation and dislocation caused by ocean currents. The spatial heterogeneity of sulfur aggregates may, therefore, provide a crucial habitat.

Effective dispersal becomes particularly critical when the sea bottom is disturbed, devastated, or even defaunated, providing the recruitment for the recovery of bottom communities. The particular disturbance could be biotic (e.g., predation or bioturbation) or abiotic (e.g., HV effluents, sediment suspension, translocation caused by storms, currents, or tides, as well as anoxia, salinity, or temperature change). Regarding other plankton above HVs, it remains unclear to what extent meroplankton is affected by toxic HV effluents [7, 13], which also applies to invertebrate larvae that provide meroplankton at HV sites [5, 20, 28]. Major holoplankton taxa were represented by the coelenterates hydrozoa and scyphozoa, and further unidentified taxa were observed irregularly during sample collection. When considering recolonization processes that are also caused by various disturbances, scales of time and space where disturbance events occur are crucial. Water-column drift, however, is restricted to the reproductive periods and larval release of relevant macrofauna [30].

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