https://doi.org/10.5194/bg-2022-177
Preprint. Discussion started: 4 October 2022
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Biogeosciences Discussions

Differential feeding habits of the shallow-water hydrothermal vent crab *Xenograpsus testudinatus* correlate with their resident vent types at a scale of meters

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Abstract. The shallow-water hydrothermal vents (SVs) located off Kueishan (KS) Islet, Taiwan, are one of the most intensively studied vent systems. Here, two distinct vent types were identified as white vents (WVs) and yellow vents (YVs), based on the color, physical and chemical characteristics of vent plumes. The endemic vent crabs (*Xenograpsus testudinatus*) are abundant in both WVs and YVs. However, most research on the vent crabs was associated with WV or unspecified vent areas. Studies on crabs dwelling in other vent types are rare. Here, we investigated the feeding habit of crabs inhabiting YV and made a comparison with WV crabs. Specifically, we examined the benthic community of WV and YV, isotopic niche width, and protein expression patterns of the crabs from the two vent types at a distance of 100 m. The coverage of sessile organisms and low-mobility fauna in WV were more abundant than in YV. The $\delta^{13}C$ and $\delta^{15}N$ values were insignificantly different between crabs from WV and YV. The niche width of crabs from WV was significantly broader than those from YV, shown as SEAc areas of 3.62 ‰^{2} vs. 0.88 ‰^{2} ($p < 0.05$). The overlap percentages in WV and YV were 23.9 % and 97.9 %, respectively. The food sources of crabs in WV were more diverse than those in YV. Based on the protein expression patterns, the vent crabs were classified into WV- and YV-dwellings. Our results revealed that the feeding habits of the endemic vent crabs (*X. testudinatus*) are adapted to their vent types at a distance of 100 m, and the trans-vent movement is uncommon.

1 Introduction

Hydrothermal vents distribute in shallow-water (SV: < 200 m) and deep-sea (DV: > 200 m), where they have unique physicochemical and geological characteristics and peculiar biological communities (Dando et al., 2000; Parson et al., 1995). The vents' plumes are rich in chemical compounds and gas, primarily reduced sulfur compounds, methane, and hydrogen gas. Based on hydrogen sulfide concentration, SVs are divided into two groups, i.e., ≧ and < 10 mmol mol^{-1} H_2S (Tarasov, 2006).

https://doi.org/10.5194/bg-2022-177
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The low H_2S concentration group was reported in SVs of Louise Harbor (8 mmol mol^{-1}, Papua New Guinea, Pichler et al., 1999a), Milos Island (4.9 mmol mol^{-1}, Greece, Dando et al., 1995), Tutum Bay (< 0.3 mmol mol^{-1}, Papua New Guinea, Pichler et al. 1999b), Punta Mita (< 0.01 mmol mol^{-1}, Mexico, Prol-Ledesma et al., 2002), and Bahía Concepción (undetected, Mexico, Forrest et al., 2005). In contrast, high H_2S concentrations were only recorded in SVs off Kueishan (KS) Islet, Taiwan (as high as 172.4 mmol mol^{-1}, Chen et al., 2016). These SVs are further distinguished according to the color of plumes, e.g., white vent (WV) and yellow vent (YV). The concentrations of H_2S in WVs and YVs were 12.94 ± 4.55 and 60.12 ± 19.57 mmol mol^{-1}, respectively (Chen et al., 2005b). WVs have a relatively low fluid temperature of 30–65 ℃ and higher pH of 1.84–6.96; YVs have temperatures of 78–116 ℃, a minimum pH of 1.52 (pH seawater scale, 25 ℃) (Chen et al., 2005b; Mei et al., 2022).

In WV, benthic organisms include bacteria, red algae, hexacoral (*Tubastraea aurea*), sea anemones (*Anthopleura* spp.), snails (*Anachis misera* and *Nassarius* sp.), chitons, serpulid polychaetes, and vent crab (*X. testudinatus*) (Chan et al., 2016; Chang, 2006; Chen et al., 2015; Jeng et al., 2004; Tang et al., 2013; Wang et al., 2014; Wang et al., 2015; Wu et al., 2021). In YV, the only macrofauna is the endemic vent crabs. Species richness of macrofauna increase with horizontal distance from the mouth regions of WV and YV to 2000 m away, indicating that the vent fluids may negatively impact several kilometers (Chan et al., 2016).

The vent crabs inhabit the pits, fissures, and crevices of sulfur chimneys and forage in vent areas during slack water (Jeng et al., 2004; Chang et al., 2018; Allen et al., 2020). They were more abundant at 5 and 35 m from the vent mouth, whereas it was less at 20 m (Tseng et al., 2020). To avoid larval contact with toxic plumes, ovigerous females migrate to the vent periphery to release their offspring and return to chimneys (Hung et al., 2019).

The detection of high proteolytic enzyme activities in the midgut gland of vent crabs indicated they are adapted to irregular food supply (Hu et al., 2012). A trophic study by $\delta^{13}C$ and $\delta^{15}N$ analysis reveals that dead zooplankton killed by sulfur plumes (as plankton-derived production) is essential to scavengers and carnivores (Chang et al., 2018; Wang et al., 2014; Wu et al., 2021). The importance of dead zooplankton to vent crabs decreases from vent center to periphery accordingly (Wang et al., 2022). Furthermore, vent crabs collected from YV had significantly more depleted $\delta^{13}C$ and $\delta^{15}N$ values than those in WV (Wu et al., 2021).

Stable isotope analysis is commonly applied in the study of animal feeding ecology. Through the processes of assimilation, consumers increase with stable isotope values of 0.0–1.3 ‰ for $\delta^{13}C$ and 1.4–5 ‰ for $\delta^{15}N$ in each trophic transfer (DeNiro and Epstein, 1978, 1981; McCutchan et al., 2003; Post, 2002). With the isotopic data, consumers' trophic position, pathways, and niche width can be calculated (Layman et al., 2011).

The proteome is the set of expressed proteins in an organism, which varies with tissue, physiological condition, and environment where the organism lives. By proteomic tools, the difference in protein expression profiles of the studied organisms can be characterized (Lopez-Pedrouso et al., 2020). For example, the variation of protein patterns of the dove snail *A. misera* was consistent with the diffusion of local vent fluids in KS Islet (Chen et al., 2015). Proteomic studies exhibited

https://doi.org/10.5194/bg-2022-177
Preprint. Discussion started: 4 October 2022
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differential expression signatures in the Chinese mitten crab (*Eriocheir sinensis*) when treated with different feeds (Wei et al., 2018) or hyper-osmotic stress (Yang et al., 2022), in mud crab *Scylla olivacea* when exposed to heavy metals (Razali et al., 2019), and in Mediterranean crab (*Carcinus maenas*) from different harbors (Jebali et al., 2014).

Although the vent crab (*X. testudinatus*) is one of the most intensively studied species in SV systems, most research was associated with WV or unspecified vent areas. Studies on crabs dwelling in other vent types are rare. Here, we investigated the feeding habit of crabs inhabiting in YV and crabs from WV was also studied for comparative purposes. Specifically, we examined the benthic community of WV and YV, isotopic niche width, and protein expression patterns of the crabs from the two vent types.

2 Materials and Methods

2.1 Sampling sites

KS Islet is located northeast of Taiwan (Fig. 1). In the east of this Islet, there is a cluster of over 30 vents within an area of 0.5 km^2 at depths of 5 to 30 m (Chen et al., 2005a). The most common vent types are WV and YV. A summary of their environmental characteristics is in Table 1. WVs show venting temperatures of 30–65 ˚C, whereas YVs exhibit 78–116 ˚C (Chen et al., 2005b; Mei et al., 2022).

In this study, a WV (24.83404° N, 121.96172° E) and a YV (24.83553° N, 121.96361° E) were sampled, and the distance between the two vents was about 100 m. The temperature of vent plumes varied in the range of 47–59 ˚C in the WV and 100–116 ˚C in the YV (Chen et al., 2016; Hung et al., 2019). The H_2S concentration of the plumes was 18.4 ± 8.4 mmol mol^{-1} and 90.8 ± 29.1 mmol mol^{-1}, respectively (Chen et al., 2016). The gas compositions of the two vents are dominated by CO_2 (503.8 ± 78.7 and 798.4 ± 23.8 mmol mol^{-1}, respectively) and N_2 (309.9 ± 72.4 and 65.1 ± 17.0 mmol mol^{-1}, respectively) (Chen et al., 2016). The recorded environmental parameters of our sampling locations in the WV and YV included temperature, pH, and depth, i.e., 25.0 and 26.7 ℃, 7.3 and 7.8, and 17 and 7 m, respectively (Table 1).

2.2 The survey of benthic communities in the WV and YV

The WV and YV benthic communities were investigated by SCUBA diving on 4 and 24 Aug. 2010, respectively. Three quadrates (15 × 15 cm^2) were set at distances of 3, 8, and 13 m from the vent mouth in the north, east, south, and west directions. A total of twelve quadrats in WV were surveyed. While it was ten in YV due to the distance to shore was only 7 m in the north direction. We photographed the quadrats, and the number of low-mobility fauna were counted, i.e., amphipod, columbellid snail, sea anemone, calyptraeid snail, chiton, vermatid snail, polychaete, Sipuncula, and mytilid mussel. The coverage of attached organisms was scored by ImageJ, i.e., macroalgae, periphyton, and sponge. Low-mobility fauna or attached organisms were collected by hand with hammers or shovels for identification purposes. The collected samples were brought to the

https://doi.org/10.5194/bg-2022-177
Preprint. Discussion started: 4 October 2022
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laboratory and preserved in 75 % ethanol. Identifications of small crustaceans, mollusks, annelids, and other invertebrates were based on the references of Carlgren (1949), Cutler (1994), Fauchald (1977), Hooper et al. (2002), Miyake (1982), and Okutani (2000).

2.3 Preparation of vent crabs for isotope niche width and proteomic studies

Vent crabs from the WV and YV have gathered 5 m away from the vent mouths on 4 and 24 Aug. 2010, respectively. Each collected crab was covered with aluminum foil and kept in liquid nitrogen, then frozen at -80 ℃ for later use. There were nine crabs with eight males and one female from WV; 7 samples with six males and one female from YV. Crab samples were examined to eliminate debris, and epibionts, then their carapace width and wet weight were measured before dissection (Fan et al., 2016). The carapace width and wet weight range of the crabs were 19.6–27.3 cm and 3.82–12.38 g from WV, while those from YV were 17.8–24.4 cm and 2.50–7.73 g, respectively.

2.4 Determination of isotope niche width of vent crabs from the WV and YV

The leg muscle of crabs, about 0.3 g, was taken, freeze-dried, and homogenized with a mortar and pestle. For carbon and nitrogen isotope analyses, approximately 1mg of powder was weighed and encapsulated in a tin capsule. Studies using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) were performed at the stable isotope laboratory at the University of California at Davis.

During analysis, several replicates of at least two different laboratory standards, e.g., nylon (certified $\delta^{13}C$ and $\delta^{15}N$ values of -27.8 and -9.8 ‰) and USGS40, L-glutamic acid (certified $\delta^{13}C$ and $\delta^{15}N$ values of -28.9 and -4.3 ‰), were interspersed with samples. Analytical accuracy was obtained by comparing measured values for the known values of the included laboratory reference materials (e.g., acetanilide), i.e., 0.2 ‰ for $\delta^{13}C$ and 0.3 ‰ for $\delta^{15}N$. Analytical precision for both $\delta^{13}C$ and $\delta^{15}N$ based on the standard deviation of replicates of internal standards was < 0.2 ‰ (UC Davis Stable Isotope Facility). Finally, stable isotope abundances were expressed in conventional delta (δ) notation and deviations in parts per thousand (‰) relative to the analytical standards of Pee Dee Belemnite and atmospheric N_2 for carbon and nitrogen, respectively. Ratios were derived from the following equation: $\delta X\ (‰) = [(R_{sample} / R_{standard}) - 1] \times 10^3$, where X is ^{13}C or ^{15}N, and R is the corresponding ratio of ^{13}C / ^{12}C or ^{15}N / ^{14}N (Sharp, 2005).

We used SPSS to run the statistical analysis of multivariate analysis of variance (MANOVA) to compare the difference in isotopic values between WV and YV. Measurements of isotopic niche width, as proposed by Layman et al. (2007), were calculated for crabs obtained from WV and YV. The standard ellipse area (SEAc) was a measure of the mean score of the isotopic niche occupied by all crab individuals in each group and their potential primary food sources in the $\delta^{13}C$ and $\delta^{15}N$ space (Jackson et al., 2011). This metric corrects bias generated when sample sizes are small, represents a measure of the total amount of niche occupied in the isotopic space, and allows for robust statistical comparisons between datasets with different

https://doi.org/10.5194/bg-2022-177
Preprint. Discussion started: 4 October 2022
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sample sizes (Jackson et al., 2011, 2012). Moreover, this metric allowed us to calculate the overlap area of the standard ellipses (and respective percentages) between WV and YV habitats, which was used to measure diet similarity. Metrics including SEAc, an overlap of standard ellipses, and a Bayesian mixing model were calculated using the SIBER v2.1.6 (Stable Isotope Bayesian Ellipses in R) package in R 4.2 software (R Development Core Team, 2013).

2.5 Determination of protein expression patterns of vent crabs from the WV and YV

The protein expression profiles of vent crabs were determined by one-dimensional sodium dodecyl sulfate-polyacrylamide gel electrophoresis (1-D SDS-PAGE), followed by Chen et al. (2015) and Lin (2011). The leg muscle of crabs, about 0.1 g, were taken and homogenized with 1ml lysis buffer (7 M Urea, 2 M Thiourea, 4 % CHAPS, and protease inhibitor cocktail two tablets per 100 ml) for proteomic sample preparation. Homogenates were centrifuged at 12000 g for 30 min at 4 ˚C. The supernatant was collected, and the protein concentration was determined by Bradford assay, using bovine serum albumin as the standard. The stacking and resolving gels were prepared with percentages of 5 and 12 % (Hoefer SEM 260 system, Amersham Pharmacia). After loading 25 μg protein in each sample lane, electrophoresis was run for 30 min at 120 V and then for four h at 180 V. The gels were stained with Coomassie blue G-250 (Candiano et al., 2004). Stained gels were scanned and transformed into digitalized images using Image Scanner (Amersham Pharmacia). The Multi Gauge software v2.2 (Fujifilm) was utilized for protein quantification. The protein bands were assigned with band numbers, and their intensity levels were calculated as their relative area to the total protein area on the gel.

A cluster analysis of the Bray-Curtis similarity (BCS) indices (Primer 6.0) was employed to compare the expression of overall protein patterns among vent crabs (Clarke and Warwick, 2001). In addition, the contribution of each protein band was further examined by principal component analysis (PCA).

3 Results

3.1 Composition of the benthic community in the WV and YV

The coverage of attached organisms and the abundance of low-mobility benthos in the two vents differed. In WV, macroalgae, periphyton, and sponge coverage were 39.2 ± 6.6 %, 29.0 ± 6.4 %, and 3.6 ± 2.4 % (n = 12), respectively. YV only had periphyton of 77.0 ± 16.2 % (n = 10) (Fig. 2). Dominant low-mobility fauna in WV were sea anemones (17.7 ± 4.5 individuals per 100 cm^2), calyptraeid snail (2.7 ± 1.1 individuals per 100 cm^2), and columbellid snail (1.0 ± 0.3 individuals per 100 cm^2), respectively. The rest species were quite a few, including polychaete, chiton, sipunculid, and mytilid mussel. While, within the surveyed area of YV, no low-mobility fauna was observed. In addition, fast-moving vent crabs were always present in both WV and YV.

https://doi.org/10.5194/bg-2022-177
Preprint. Discussion started: 4 October 2022
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3.2 Isotopic niche width of vent crabs from the WV and YV

The mean values of $\delta^{13}C$ and $\delta^{15}N$ in WV were -16.59 ± 0.27 ‰ and 7.66 ± 0.43 ‰, ranging from -17.50 ‰ to -14.99 ‰ and 4.72 ‰ to 8.94 ‰, respectively (Fig. 3). While in the YV, they were -16.18 ± 0.22 ‰ and 6.98 ± 0.32 ‰, with the ranges of -17.00 ‰ – -15.22 ‰ and 5.39 ‰ – 8.00 ‰, respectively. The $\delta^{13}C$ and $\delta^{15}N$ values were insignificantly different between crabs from WV and YV (MANOVA, $p > 0.05$).

The niche width of crabs from WV was significantly broader than the ones from YV, shown as SEAc areas of 3.62 ‰^{2} vs. 0.88 ‰^{2} ($p < 0.05$), respectively (Fig. 4 and Table 2). The overlapped SEAc area between the two vents was 0.86 ‰^{2}. The overlap percentage in WV was low (23.9 %); in contrast, it was high in YV (97.9 %). This indicated that almost all the food items in YV were present in WV. The food sources of crabs in WV were more diverse.

3.3 Protein expression patterns of vent crabs from the WV and YV

Based on the protein expression results, 27 protein bands were selected for further BCS analysis (Fig. 5). Crabs from WV and YV fell into two different clusters (Fig. 6). The results further determined the contribution of each protein variable by PCA. The first to the fifth principal components accounted for 46.5, 20.4, 12.2, 9.8, and 4.2 % of the total variance, respectively. The separation was mainly contributed by the first principal component, i.e., bands 25, 10, 9, 2, and 1. Based on the cluster results, the vent crabs were categorized into WV and YV-dwellings.

4 Discussion

This was the first study to compare the feeding habits of the endemic vent crabs (*X. testudinatus*) living in different types of SVs within 100 m. The benthic community of WV and YV, food sources, and protein expression patterns of the dwelling crabs were associated with their habitats. It is supported by the crabs in YV having a narrower niche width and highly overlapped isotopic SEAc area compared to the one in WV. And based on the analysis on 27 protein bands, the crabs were clustered into two groups relating to their vent types.

4.1 The benthic community in the WV and YV

In this study, within the area of 15 m from the center of WV, the coverage of attached benthos was 72 %, including macroalgae, periphyton, and sponge. In YV, it only had periphyton for 77 %. Chan et al. (2016) and Wang et al. (2022) reported along a 50 m transect line from two sites near vent mouths of WV and YV, only 5 % of the substrate was covered with encrusting red algae *Hildenbrandia* spp. and three red turf algae. Wu et al. (2021) found three types of periphyton within the area of 15 m from the center of YV, while WV had two sponge species, two brown algae, two red algae, five green algae, and one type of periphyton.

https://doi.org/10.5194/bg-2022-177
Preprint. Discussion started: 4 October 2022
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Low-mobility fauna was absent in the 15 m area from the center of YV. In contrast, there were nine species in WV, including sea anemones (17.7 ± 4.5 individuals per 100 cm^2), calyptraeid snail (2.7 ± 1.1 individuals per 100 cm^2), and columbellid snail (1.0 ± 0.3 individuals per 100 cm^2). Polychaete, chiton, sipunculid, and mytilid mussels were all with density < 1 individual per 100 cm^2. In 2009 and 2010, Wu et al. (2021) didn't record any low-mobility benthic fauna in YV, while in WV, there were 14 species, including shrimp *Alpheus lobidens*, four snail species, chiton of *Ischnochiton comptus*, sea anemone of *Anthopleura* sp., coral of *T. aurea*, and four polychaete species. In 2014, Chan et al. (2016) reported along a 50 m transect line from the center of YV, sea anemone *Anthopleura* sp. occupied 5 ± 4 % of the substrate. The fauna in WV was more abundant, which included sea anemone (17.5 ± 28.9 %), immobile snails of *Bostrycapulus aculeatus* and *Dendropoma dragonella* (7–30 %), and other four snail species (1–3 individuals per 25 × 25 cm^2). Overall, the investigated results across studies were consistent with higher species diversity of benthic communities in WV than in YV.

4.2 The isotopic niche width of vent crabs from WV and YV

In this study, the $\delta^{13}C$ and $\delta^{15}N$ values of vent crabs (*X. testudinatus*) were insignificantly different between WV and YV. The values ranged from -17.50 ‰ to -14.99 ‰ ($\delta^{13}C$: -16.59 ± 0.27 ‰; n = 9) and 4.72 ‰ to 8.94 ‰ ($\delta^{15}N$: 7.66 ± 0.43 ‰; n = 9) in WV. In comparison, the values of YV-crabs were from -17.00 ‰ to -15.22 ‰ ($\delta^{13}C$: -16.18 ± 0.22 ‰; n = 7) and 5.39 ‰ to 8.00 ‰ ($\delta^{15}N$: 6.98 ± 0.32 ‰; n = 7), respectively. Wu et al. (2021) reported significantly different $\delta^{13}C$ and $\delta^{15}N$ values of vent crabs from WV and YV collected in 2009 and 2010, i.e., -16.3 ± 0.7 ‰ (n = 44) and -17.4 ± 1.1 ‰ (n = 17) for $\delta^{13}C$ and 6.7 ± 1.3 ‰ vs. 7.8 ± 1.0 ‰ for $\delta^{15}N$, respectively. Another study compared the genders of vent crabs collected in 2010 (Hung et al., 2019). They found male crabs from WV and YV differed significantly ($\delta^{13}C$: -17.2 ‰ vs. -15.8 ‰; $\delta^{15}N$: 7.1 ‰ vs. 5.0 ‰) ($p < 0.01$) but not in females (($\delta^{13}C$: -17.3 ‰ vs.17.0 ‰; $\delta^{15}N$: 7.3 ‰ vs. 7.6 ‰).

In 2014, crabs from one vent influenced by both WV and YV and three peripheral sites (150–300 m) presented a wide range of $\delta^{13}C$ (-20.5 to -14.3 ‰) and $\delta^{15}N$ (3.2 to 9.8 ‰) values (Wang et al., 2022). Insignificant differences were found in both $\delta^{13}C$ and $\delta^{15}N$ values of vent crabs among the four sites. Their means of $\delta^{13}C$ and $\delta^{15}N$ values and sample sizes were -16.9 ± 0.77 ‰ and 8.1 ± 0.94 ‰ (n = 6); -17.2 ± 1.34 ‰ and 7.5 ± 1.01 ‰ (n = 40); -16.6 ± 1.03 ‰ and 7.2 ± 1.43 ‰ (n = 156); -16.9 ± 0.66 ‰ and 8.3 ± 1.17 ‰ (n = 10), respectively. Further isotopic niche analysis demonstrated that the contribution of dead zooplankton as a food source to vent crabs living in the center and periphery varied from > 34 % to ≤ 18 %. Our results showed that the crabs' SEAc area was significantly wider in WV (3.62 $‰^2$) than those in YV (0.88 $‰^2$). This indicated that crabs in WV had more food sources than in YV. The discrepant results among studies may partly result from the differences in sampling sizes and locations. In general, the isotopic signatures of the resident vent crabs reflected their habitat heterogeneities.

In the Pechora Sea, the isotopic niche width in scavenger hermit crab *Pagurus pubescens* varied between stations because of a significant variation in macrobenthic abundance over the spatial scales (Gebruk et al., 2021b). The isotopic niche width for

https://doi.org/10.5194/bg-2022-177
Preprint. Discussion started: 4 October 2022
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the hermit crab was 0.15 ‰^{2} at 4N and 0.27 ‰^{2} at 9N, with 0.05 ‰^{2} overlapped. Differences in diet sources were correlated with local macrobenthic clams as shown at 4N, characterized by low biomass of *Astarte montagui* (32 g m^{-2}), in contrast to high biomass of *A. borealis* and *Macoma calcarea* (500 g m^{-2}) at 9N (Gebruk et al., 2021a). This result had an even lower overlapping SEAc area than our study, i.e., 0.86 ‰^{2}.

4.3 Protein expression patterns of vent crabs from WV and YV

Our proteomic results indicated that vent crabs from WV were distinguishable from those in YV and the vent crabs are adapted to their local environments. In the case of dove snails, *A. misera* inhabiting in WVs of KS Islet, their protein expression patterns were related to the diffusion of locally emitted vent fluids (Chen et al., 2015). The naturally acidified seawater in the southward sampling site had pH ranges from 7.78 to 7.82, while it was 7.31–7.83 in the east, southwest, and northwest locations. Based on the expressed protein profiles, the *Anachis* snails were classified into the south and another group. In a CO_2-SV off Vulcano Island, Sicily (Italy), sea anemones *Anemonia viridis* were collected away from a vent about 350–800 m, where the pH values were 7.6, 7.9, and 8.2, respectively (Urbarova et al., 2019). Gene expression patterns of *A. viridis* revealed two clades, i.e., low pH group (pH 7.6) vs. high pH ones (pH 7.9 and pH 8.2). Overall, mobile vent crabs, slow-moving dove snails, and sessile sea anemones all performed adaptation abilities associated with their environments.

It is known that organisms respond to environmental changes in a time-dependent manner. When the Chinese mitten crabs *E. sinensis* were transferred to high salinity (25 psu) for six days, the protein profiles of posterior gills were different from the control group (0 psu) (Yang et al., 2022). The nutrition value of linoleic acid (18:2n-6, LA) and α-linolenic acid (18:3n-3, LNA) in the Chinese mitten crabs *E. sinensis* was evaluated by feeding with LA or LNA diet for 107 days (Wei et al., 2018). Between the LA and LNA groups, 186 proteins from crabs' hepatopancreas were differentially expressed. In the Teboulba fishing harbor in Tunisia, high levels of aliphatic and aromatic hydrocarbon pollutants were in the sediments (Jebali et al., 2014). The Mediterranean crabs *C. maenas* showed differential protein expression patterns in hepatopancreas between control (day 0) and exposed groups with 15, 30, and 60 days. These proteomic-based studies exhibited the earliest responses of tested crabs to environmental changes detected at least on day 6.

4.4 Association of crabs' feeding habits with vent types

The distribution of vent crabs is related to vent systems. The compositions of vent plumes influenced all the benthic assemblage in SV ecosystems, food availability, and metabolism of vent crabs (Chen et al., 2005b; Mei et al., 2022; Hu et al., 2012; Chang et al., 2018; Wang et al., 2014; Wu et al., 2021). In previous studies, the movement of vent crabs shows different spatial scales. The daily foraging movement is in the vent area (Jeng et al., 2004; Chang et al., 2018; Allen et al., 2020). During the reproductive season, ovigerous females move to the vent periphery, release their larvae, and then return to the chimneys (Hung et al., 2019). The migratory distance was about 100–200 m horizontally from the vent mouth. It is also reported that vent crabs

https://doi.org/10.5194/bg-2022-177
Preprint. Discussion started: 4 October 2022
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were absent in the by-catch of nearby non-vent fisheries (Wang et al., 2013). The holotype and three paratype specimens of this species were collected from a 15 m deep rocky reef in the Gengxin Fish Port, Peikuan, I-Lan County, Taiwan (Ng et al., 2000). These indicate that the vent crabs can survive in non-vent environments. Through the analyses of isotopic niche width and protein expression patterns, this study extended our knowledge to realize the metabolic performance of SV endemic crabs is strongly associated with vent types, and trans-vent movement at a scale of meters is uncommon.

5 Conclusions

This was the first study to compare the benthic community, food sources, and protein expression patterns of the endemic vent crabs (*Xenograpsus testudinatus*) from different types of SVs at 100 m. The coverage of sessile organisms and low-mobility fauna in YV were fewer than in WV. It was found that narrower niche width and highly overlapped isotopic SEAc area of the crabs in YV compared to the one in WV. Moreover, based on the protein expression patterns, the crabs were clustered into two groups relating to their dwelling vent types. It is concluded that the crabs are faithful to their resident vent and the minimum movement range and timing outside the vent area are probably an adaptation to predation risk.

Author Contributions

Siou-Yan Lin and Shao-Hung Peng helped for collected samples and conducted the study; Jung-Fu Huang, Chen-Tung A. Chen, and Jia-Jang Hung were involved in the study design; Jing-Ying Wu and Li-Lian Liu designed the study, analyzed data and wrote the paper. All authors discussed the results and commented on the manuscript.

Competing interests

The authors declare that they have no conflict of interest.

Acknowledgements

We thank the Stable Isotope Facility of the University of California (Davis) for analyzing our samples. We thank Dr. Ya-Jou Chen for her assistance on experiment conduction. We also thank Mr. Jhih-hui Hung, Mr. Jeng-Ren Lia, Mr. Chih-Hsien Chang, Dr. Yalan Chou, and the SeaWatch Company for help with sample collection. This study was supported by the Asia-Pacific Ocean Research Center, National Sun Yat-sen University, and funded by the Ministry of Education, Taiwan.

https://doi.org/10.5194/bg-2022-177
Preprint. Discussion started: 4 October 2022
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Table 1. Location and environmental measurements of the study sites. (Mean ± S.E.); n: sample size.

Environmental parameters	WV (White vent)	YV (Yellow vent)	Year	References
Areas of shallow-water hydrothermal vents	WVs	YVs		
The temperature of vent plume (℃)	30-65 (50.7 ± 8.2, n = 109)	78-116 (106 ± 9.16, n = 115)	Aug. 2000	Chen et al., 2005b
“	31-38	50-90	Aug. 2017	Mei et al., 2022
pH of vent plume	1.84-6.96 (3.2 ± 1.17, n = 110)	1.52-6.32 (2.49 ± 0.72, n = 116)	Aug. 2000	Chen et al., 2005b
H_2S of vent plume (mmol mol^{-1})	2.3-21.0 (12.94 ± 4.55, n = 4)	7.6-114.7 (60.12 ± 19.57, n = 6)	“	“
CO_2 of vent plume (mmol mol^{-1})	916-987 (n = 3)	976-992 (n = 2)	“	“
N_2 of vent plume (mmol mol^{-1})	0.02-0.04 (n = 3)	0.11-2.23 (n = 2)	“	“
Geographic coordinates	24.83404° N, 121.96172° E	24.83553° N, 121.96361° E		
The temperature of vent plume (℃)	55 ± 4	106 ± 6	2010-2011	Hung et al., 2019
“	47-49 (48.00 ±0 .37, n = 6)	115-116 (115.40 ± 0.22, n = 5)	2011-2014	Chen et al., 2016
pH of vent plume	5.45 ± 0.65	2.48 ± 1.06	2010-2011	Hung et al., 2019
H_2S of vent plume (mmol mol^{-1})	2.2-57.4 (18.4 ± 8.4, n = 6)	4.3-172.4 (90.8 ± 29.1, n = 6)	2011-2014	Chen et al., 2016
CO_2 of vent plume (mmol mol^{-1})	161.7-760.6 (503.8 ± 78.7, n = 8)	731-881.6 (798.4 ± 23.8, n = 6)	“	“
N_2 of vent plume (mmol mol^{-1})	109.5-633.7 (309.9 ± 72.4, n = 8)	33.4-140.9 (65.1 ± 17.0, n = 6)	“	“
Distance to vent center (m)	~ 5	~ 5	Aug. 2010	this study
Depth (m)	17	7	“	“
Temperature (℃)	25.0	26.7	“	“
pH	7.3	7.8	“	“
Deposited sulfur particles (diameter)	globules (~ 0.05–0.1 cm)	balls (> 2 cm)	“	“

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Table 2. The niche width analyses for vent crabs (*Xenograpsus testudinatus*) from different vent types. WV: white vent; YV: yellow vent; SEAc: standard ellipse area corrected. Comparisons between communities using Layman metrics were based on the posterior distribution (95 % credited intervals) of the modes ($p < 0.05$, a > b).

Metrics	WV	YV
SEAc (‰^{2}, mean)	3.62	0.88
Comparison	a	b
Overlap SEAc (‰^{2})	0.86	
Total overlap (%)	23.9	97.9

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Fig legends

Figure 1. Map of the Kueishan Islet showing sampling sites. (a) The study sites in white vent and yellow vent; (b) Photograph of the yellow vent; (c) Photograph of the white vent (scale bar: 1 kilometer on the big map and 100 meters on the enlarger map); KS Islet: Kueishan Islet; WV: white vent; YV: yellow vent.

Figure 2. The coverage and abundance of benthos in the white and yellow vents. (a) The coverage of attached organisms; (b) The abundance of low-mobility macrobenthic fauna. Mean ± S.E.M.

Figure 3. The $\delta^{13}C$ and $\delta^{15}N$ values of the vent crab *Xenograpsus testudinatus* from white and yellow vents. WV: white vent; YV: yellow vent; m: male; f: female.

Figure 4. Convex hull areas and standard ellipses areas based on $\delta^{13}C$ and $\delta^{15}N$ data of the vent crabs (*Xenograpsus testudinatus*) from white and yellow vents. Dot lines: convex hull areas; solid lines: standard ellipses areas (SEAc); WV: white vent; YV: yellow vent.

Figure 5. Gel electropherogram with molecular markers of the vent crab *Xenograpsus testudinatus* from white and yellow vents. Y2-3m: male individuals from the yellow vent; W4-6m: male individuals from the white vent; MW: molecular weight; unit: kDa; number: protein band serial number.

Figure 6. Results from the combined principal component analysis (PCA) and cluster analysis of Bray–Curtis similarity (BCS) indices using standardized overall protein expressions. WV: white vent; YV: yellow vent; m: male; f: female; 1–27: variable of protein bands.

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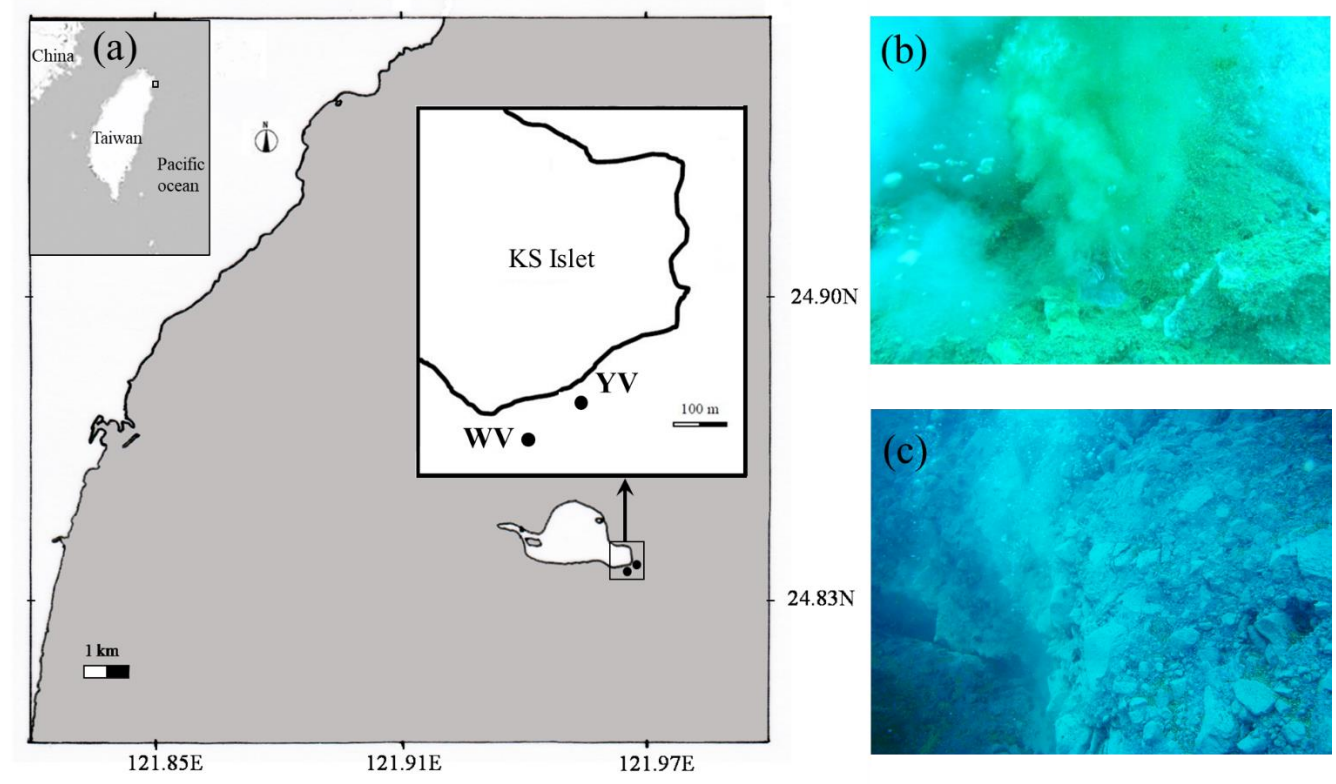

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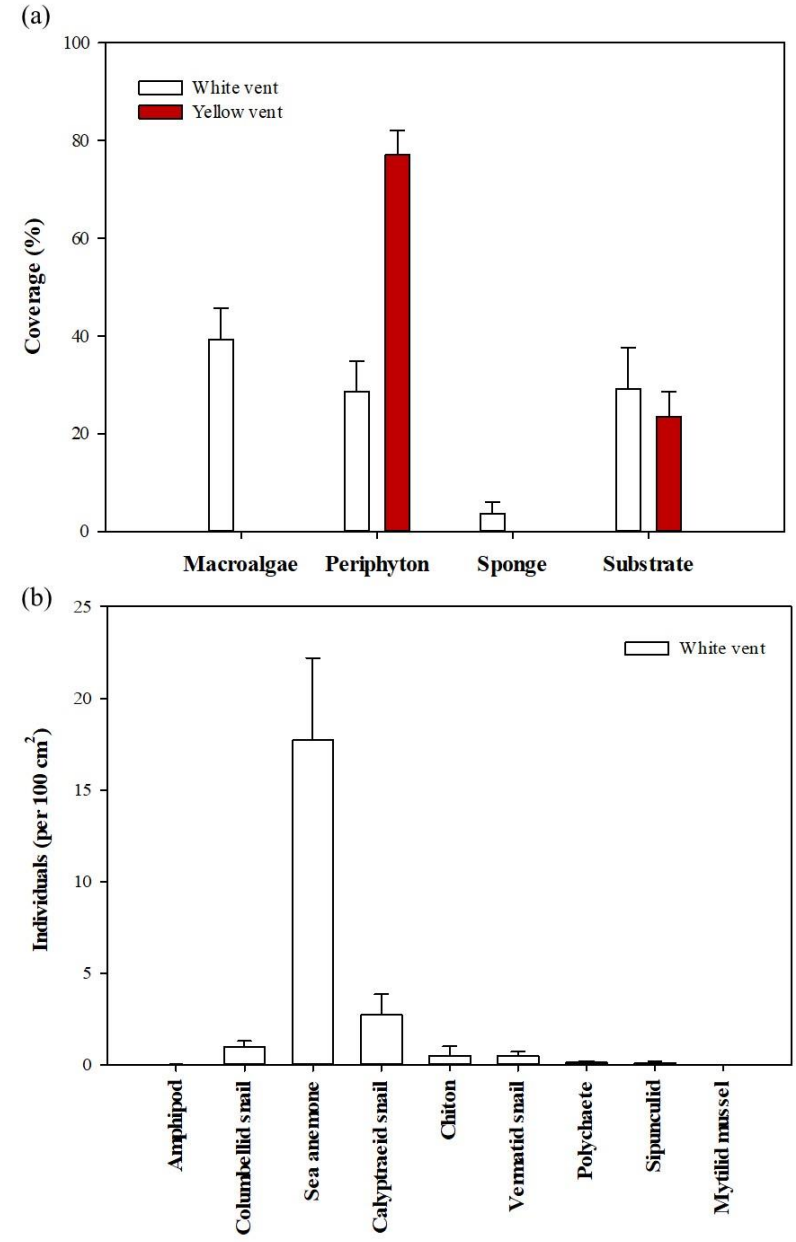

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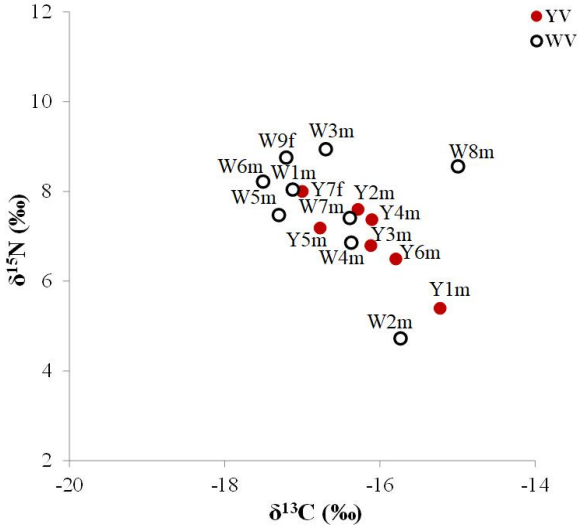

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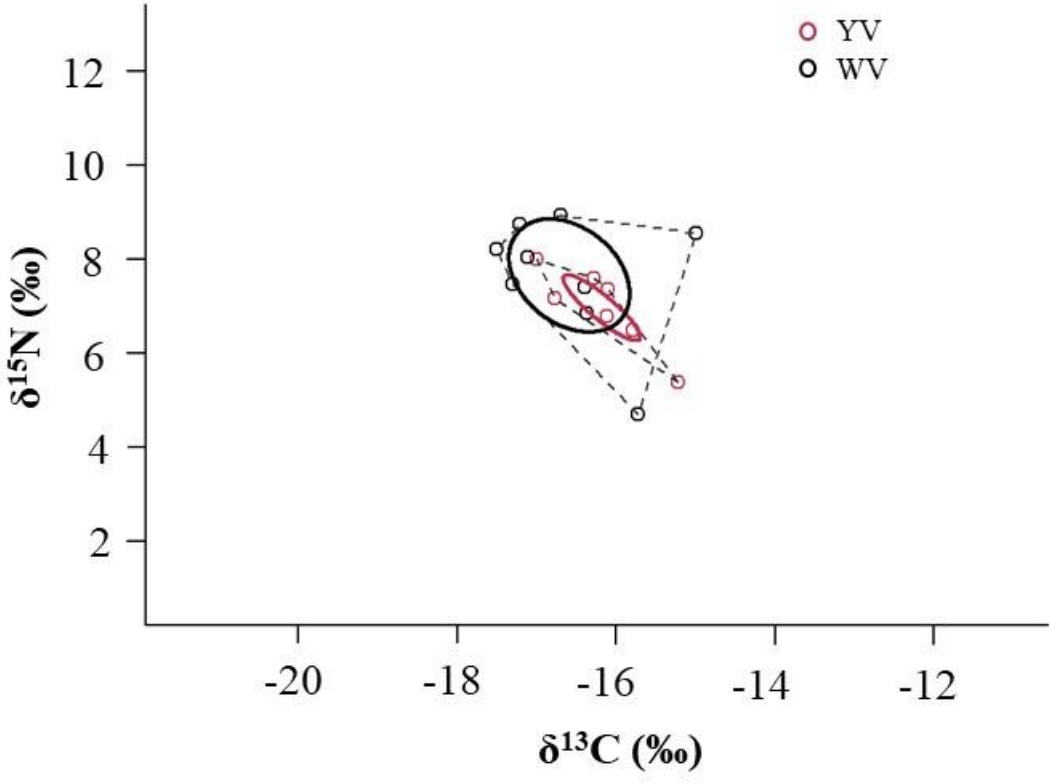

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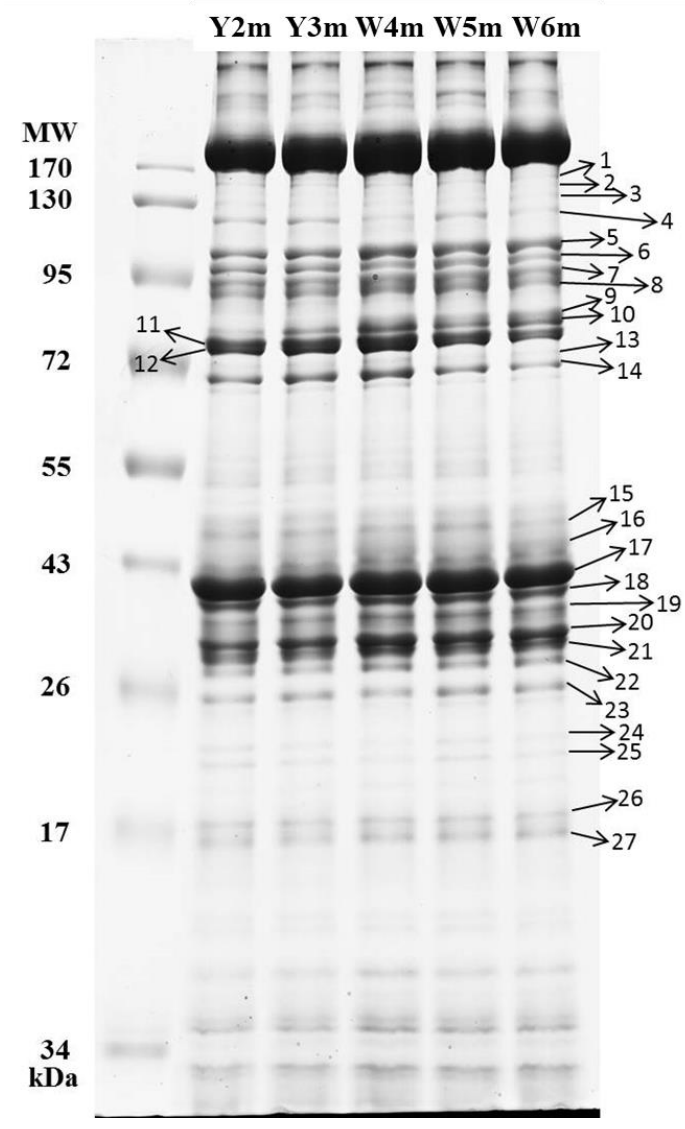

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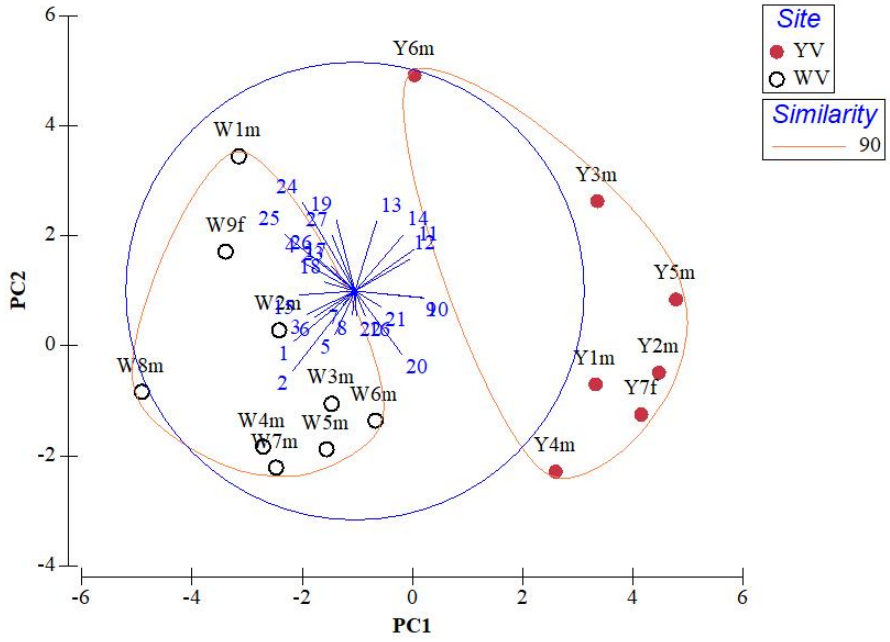

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