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# SNAIL SHELLS AS IMPORTANT HABITAT IN THE ACIDIC SHALLOW HYDROTHERMAL VENT ENVIRONMENT OF A VOLCANIC ISLAND: COEXISTENCE AND COMPETITION

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***ABSTRACT*** Hydrothermal vent systems are characterized by acidified and chemically extreme seawater, posing significant challenges for calcifying marine organisms. Acidification can impair calcium carbonate shell formation in molluscs and is therefore expected to constrain species distribution in such environments. The unexpected abundance of two gastropods—the mobile spiny slipper snail *Bostrycapulus gravispinosus* (Kuroda & Habe, 1950) and the sessile worm snail *Thylacodes nodosorugosus* (Lischke, 1869)—in shallow hydrothermal vents off Kueishan Island, Taiwan is described. The two species occupy distinct microhabitats within the vent field and co-occur only within a narrow sympatric zone. Observations revealed that the shells of both species served as basibionts and provided secondary substrates for a variety of epibionts, including sponges, sea anemones, algae, bryozoans, and tubular gastropods. In the sympatric zone, 32.8% of specimens found that had *T. nodosorugosus* growing on *B. gravispinosus* shells. This association resulted in reduced shell height of the basibiontic *B. gravispinosus* compared with snails without *T. nodosorugosus* growing on them, suggesting a potential negative effect on growth. These findings indicate that the interaction between the two species may involve both commensalism and exploitive competition. The attachment of *T. nodosorugosus* to available substrates, including living hosts, suggests a space-pre-emption strategy that may contribute to habitat partitioning within the vent system. This study highlights the importance of biotic interactions in structuring communities in shallow hydrothermal vent environments.

***KEY WORDS:*** *snails*, *Bostrycapulus gravispinosus*, *Thylacodes nodosorugosus*, interspecific interactions, space pre-emption, commensalism, epibiosis, hydrothermal vents

## INTRODUCTION

Taiwan is located in the Ring of Fire in the northwestern Pacific, on the edge of the Eurasian Plate, and is a region prone to frequent earthquakes (Lebrato et al. 2019). Shallow hydrothermal vents in the southern Okinawa Trough, located off the eastern coast of Kueishan Island (also known as Turtle Island or Kueishantao), Taiwan, represent a unique extreme marine environment (Song 2013). Hydrothermal emissions from seafloor fissures release sulfur-rich fluids that reduce seawater pH to highly acidic and toxic levels and lead to the formation of sulfur deposits (Chen et al. 2005, Chan et al. 2016). Vent fluids can reach temperatures of up to 116°C within vent orifices, with pH values as low as 1.52 near vent outlets (Chen et al. 2005, Chen et al. 2015). Despite these extreme conditions, the overall seawater temperature in the hydrothermal vent areas increases by less than 1°C as a result of rapid mixing with ambient seawater (Tseng et al. 2025). In contrast, acidification exerts a strong ecological effect, creating conditions that can cause near-complete mortality in zooplankton entering the vent-influenced waters (Davidson et al. 2024).

Biological studies of this hydrothermal system have primarily focused on microbial communities and benthic fauna (Girija et al. 2023, 2024), with benthic invertebrates dominating the animal assemblages (Tseng et al. 2018, 2024). Ecological interactions among benthic organisms in these shallow hydrothermal vents remain poorly understood. Previous studies have documented the presence of several molluscan species in this system (Chang 2006, Chen et al. 2015, Chan et al. 2016, Chen et al. 2018), as well as the occurrence of azooxanthellate scleractinian corals such as *Tubastraea* spp. (Chang 2006, Chan et al. 2016) and *Tubastraea aurea* (Girija et al. 2023, 2024). Acidified seawater is generally expected to affect calcifying organisms negatively by reducing calcium carbonate availability for shell and skeleton formation (Doney 2006, Machado et al. 2025), raising questions about how such taxa persist and interact in this environment.

Biological competition is a fundamental ecological process in which organisms compete for limiting resources such as space, food, mates, or light (Case & Gilpin 1974, Lockwood 1992, Luiselli 2006). Interspecific competition, in particular, can influence species distributions and community structure by disadvantaging less competitive species and potentially leading to competitive exclusion (Hardin 1960). Although several gastropod species have been reported from the Kueishan Island hydrothermal vent system, little is known about their interspecific interactions and the ecological mechanisms structuring their coexistence.

During biodiversity surveys conducted between 2013 and 2025, specimens of the mobile spiny slipper snail *Bostrycapulus gravispinosus* (Kuroda & Habe, 1950) (MolluscaBase 2025a)

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and the sessile vermetid gastropod worm snail *Thylacodes nodosorugosus* (Lischke, 1869) (MolluscaBase 2025b) were collected by SCUBA diving from shallow hydrothermal vent habitats off Kueishan Island. These two species were frequently observed in close proximity, yet occupying distinct microhabitats. The aim of the present study was to investigate their interspecific relationship. The following questions were addressed: (1) whether shell morphology reflects potential habitat competition; (2) what type of interaction occurs between these two gastropod species; and (3) how these interactions contribute to the understanding of interspecific relationships in shallow hydrothermal vent ecosystems.

## MATERIALS AND METHODS

### *Field Sampling and Sample Processing*

This study is part of a long-term research program (>10 y) investigating biodiversity and interspecific interactions in the shallow hydrothermal vent system off Kueishan Island, northeastern Taiwan. Field surveys and specimen collections were conducted between 2013 and 2025 at a shallow hydrothermal vent site located southeast of Kueishan Island (latitude 24° 50′ 06″ N, longitude 121° 57′ 38″ E; Fig. 1). Gastropod specimens were collected by SCUBA diving at depths of 16–18 m. Environmental parameters were measured before biological sampling. Vent fluid temperature was recorded at five major vent outlets using a handheld thermometer. In addition, five water samples were collected from vent sites and measured onboard using a multiparameter probe (Hanna Instruments Inc., Smithfield, Rhode Island). The sampling area was characterized by large rocky substrates (up to 6 m in height) and seafloor sediments composed primarily of sand and sulfur deposits.

A total of 67 *Thylacodes nodosorugosus* and 108 *Bostrycapulus gravispinosus* individuals were collected and examined across the study period. Specimens were transported to the Chaojing Ocean Center (National Museum of Marine Science and Technology, Keelung, Taiwan) for identification and photographic documentation. All specimens were subsequently deposited in the same institution.

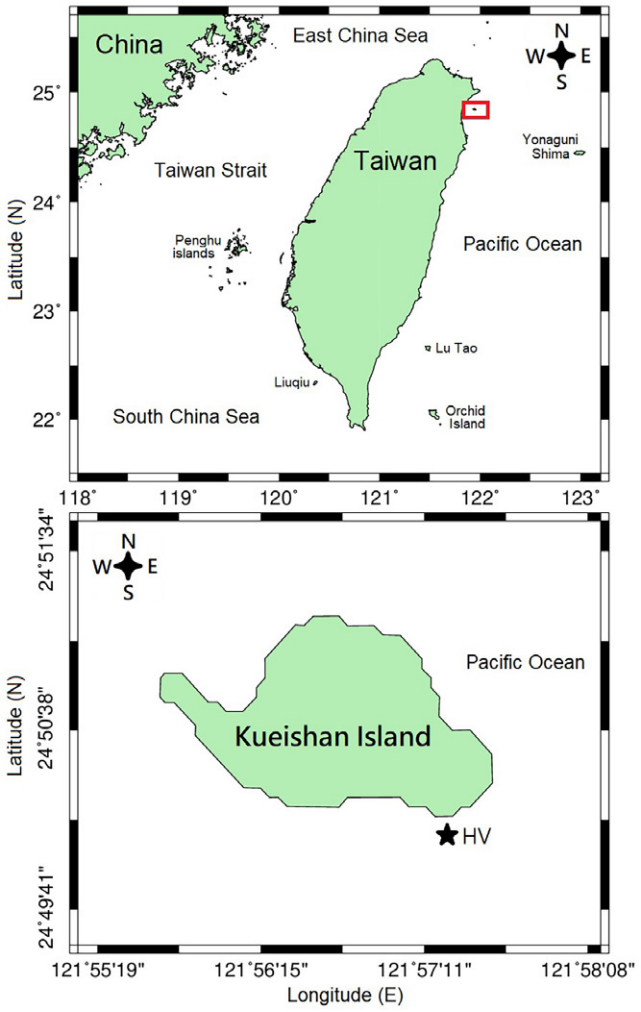


**Figure 1. Map of the study area (upper) and sampling locations (lower) around Kueishan Island. The asterisk indicates the location of HV. HV, hydrothermal vent.**

### *Shell Measurements and Statistical Analysis*

Generally, *Bostrycapulus gravispinosus* and *Thylacodes nodosorugosus* populations are distributed in different microhabitats. In sympatric zones, the two species can be found coexisting. This study found that some *T. nodosorugosus* grow on the shells of *B. gravispinosus*; because tubular shells of *T. nodosorugosus* attach to rocks, this prevents *B. gravispinosus* from moving freely. To assess whether the growth of *B. gravispinosus* is affected by the epibiont *T. nodosorugosus*, shell height (defined as the maximum distance from the umbo to the posterior margin; Fig. 2) was measured for both free-living (mobile) and basibiontic (fixed) individuals. In total, shell height was measured for 108 free-living individuals and 22 basibiontic individuals.

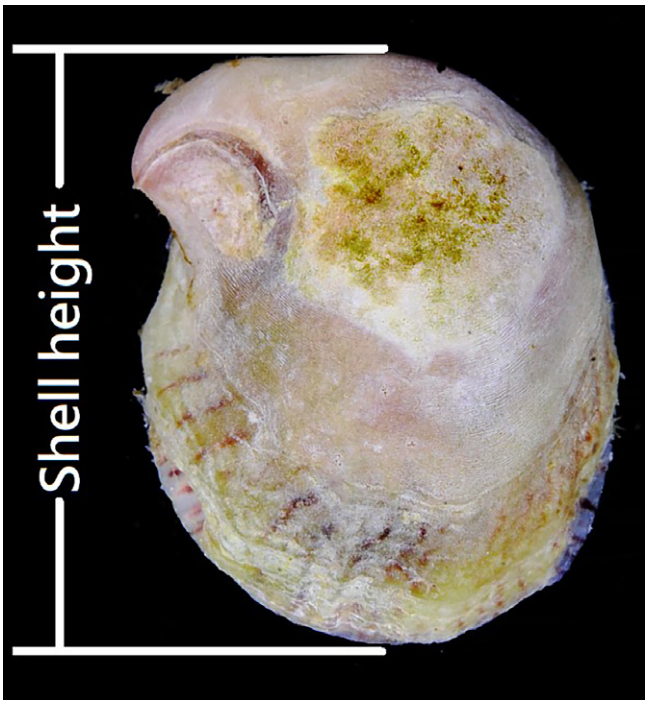


**Figure 2. Shell height of spiny slipper snail *Bostrycapulus gravispinosus*.**

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Maximum shell size was taken as the upper growth potential of individuals. To minimize potential bias introduced by juvenile specimens, all basibiontic individuals ($n$ = 22) were compared with the upper size fraction of the free-living population. Specifically, the 75$^{th}$ percentile of shell height (15.37 mm) in free-living individuals ($n$ = 29) was used as a reference for comparison. Differences between groups were tested using an independent (unpaired) Student's $t$-test (Student 1908). All statistical analyses were conducted using PAST (Paleontological Statistics) software (Hammer et al. 2001), with significance assessed at $\alpha = 0.05$.

## RESULTS

### *Investigation in Hydrothermal Vent Areas*

The hydrothermal vent water and gas discharged from crevices under rocks and the seafloor in the study area. The main vent emits gray–black plume, the pH, and temperature in the vent mouth vary in the ranges of 3.4–4.1 and 42°C–74°C, respectively. The gastropods were found on the top and side of the rock in hydrothermal vent areas. The seaweed and white furry filamentous bacteria covered the surface of this area. The patchiness distribution of sessile snail *Thylacodes nodosorugosus* (Fig. 3A) and free-living snail *B. gravispinosus* (Fig. 3B) were found in the seaweed meadow and on the bare rock surface. The edge of the seaweed meadow was a sympatric area where both snails co-occurred (Fig. 3C).

### *Shell Height Variation*

The shell height of *Bostrycapulus gravispinosus* differed between free-living and basibiontic individuals (Fig. 4). Shell height ranged from 3.82 to 18.23 mm in free-living individuals ($n$ = 108) and from 8.59 to 16.34 mm in basibiontic individuals ($n$ = 22). Mean shell height was 13.43 ± 0.28 mm for free-living individuals and 13.07 ± 0.43 mm for basibiontic individuals, with median values of 14.12 and 13.18 mm, respectively.

### *Microscopic Observations*

Laboratory observations showed that the vermetid snail *Thylacodes nodosorugosus* forms dense, intertwined aggregations (Fig. 5A). A representative cluster (approximately 34 × 55 × 25 mm: length × width × height) consisted of nine individuals forming a complex three-dimensional structure that provided substrate for a diverse epibiotic assemblage. Based on morphology and coloration, epibionts included four morphotypes of sponges, two types of sea anemones, and two types of macroalgae. In addition, portions of the shell surface were covered by amorphous sediment deposits. Together, these organisms formed a well-developed epibiotic community. In contrast, shells of the mobile gastropod *Bostrycapulus gravispinosus* supported comparatively simpler epibiotic assemblages (Fig. 5B). Examination of three representative shells (15.0–17.2 mm in height; 9–12 mm in width) revealed the presence of small molluscs, bryozoans, and green algae.

Notably, several *Thylacodes nodosorugosus* individuals were observed growing directly on the shells of *Bostrycapulus gravispinosus* (Fig. 6). These worm snails formed either intertwined or partially tubular structures anchored to the host shell.

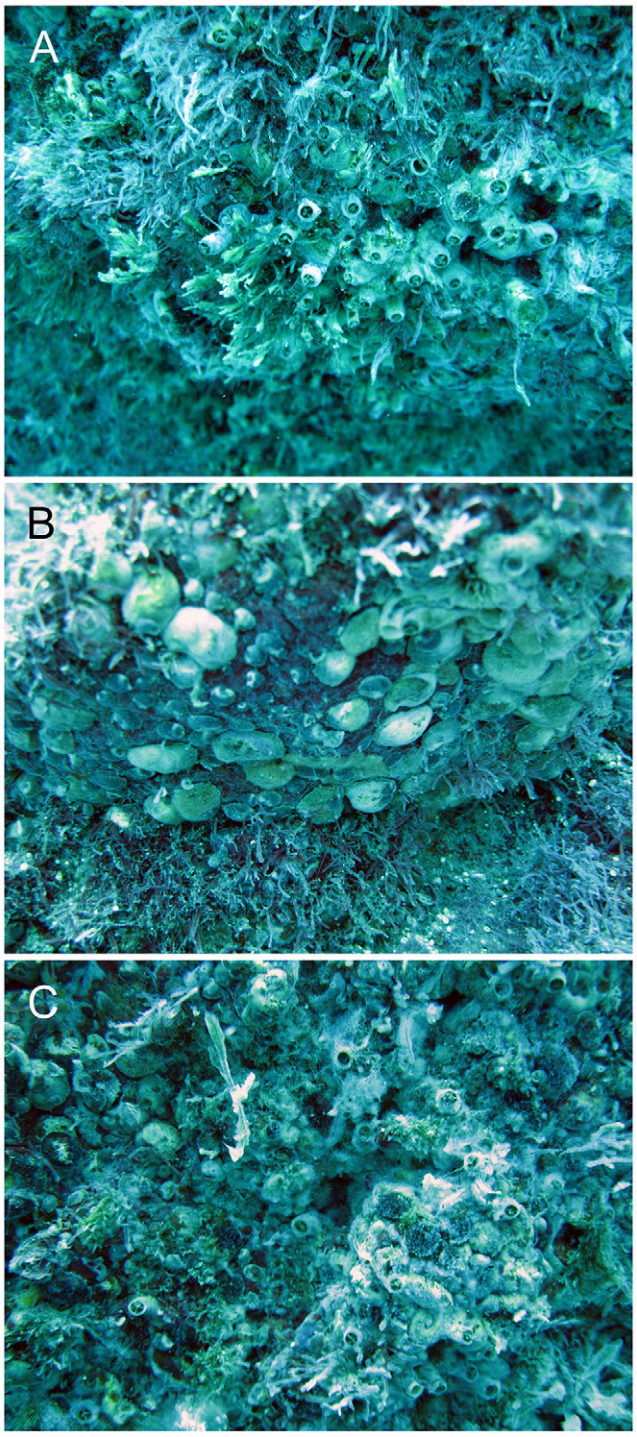


**Figure 3. Habitat of snails in the vent site. The area only occupied by *Thylacodes nodosorugosus* population (A), the area only occupied by *Bostrycapulus gravispinosus* population (B), and the sympatric area of two snail communities (C).**

Such growth appeared to restrict the mobility of *B. gravispinosus*. This association was recorded in 22 out of 67 examined *T. nodosorugosus* specimens, corresponding to an occurrence frequency of 32.83%. In host-associated cases, *T. nodosorugosus* individuals were often substantially larger than their *B. gravispinosus* hosts. For example, in one specimen (Fig. 6E),

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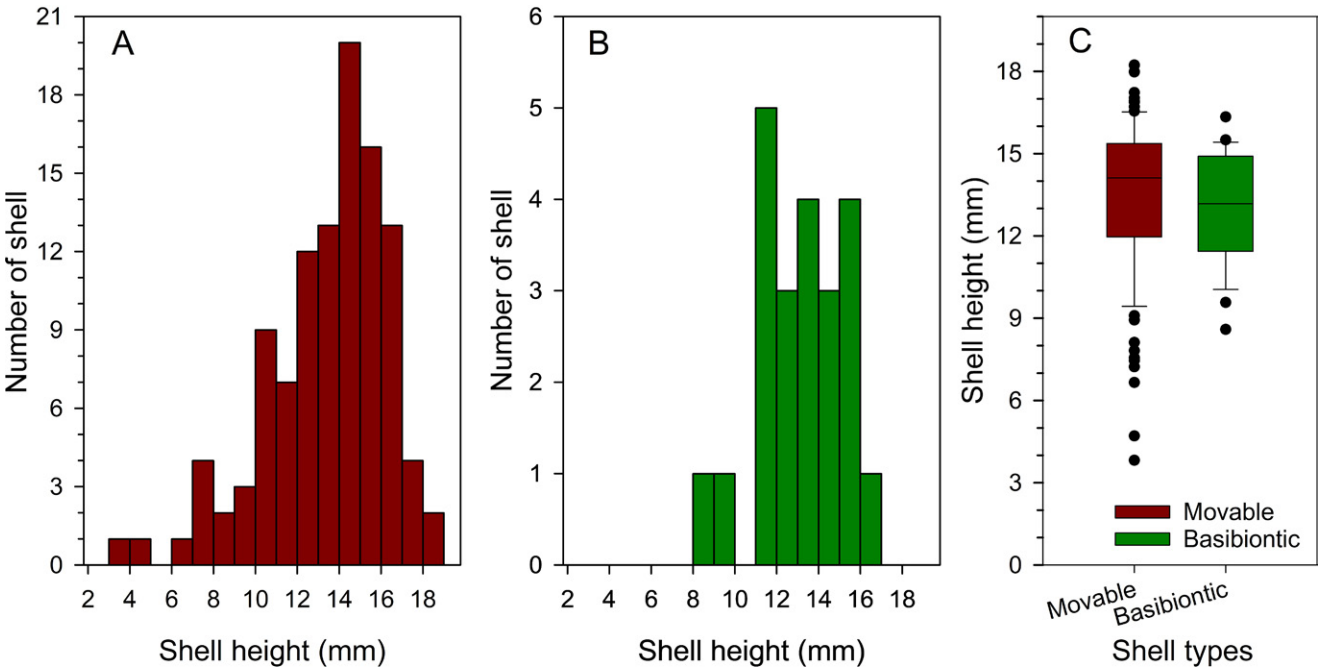


**Figure 4. Shell height distribution of movable (*n* = 108) *Bostrycapulus gravispinosus* (A), basibiontic (fixed) by *Thylacodes nodosorugosus* (*n* = 22) (B), and comparison of the shell height between movable and basibiontic individuals (C).**

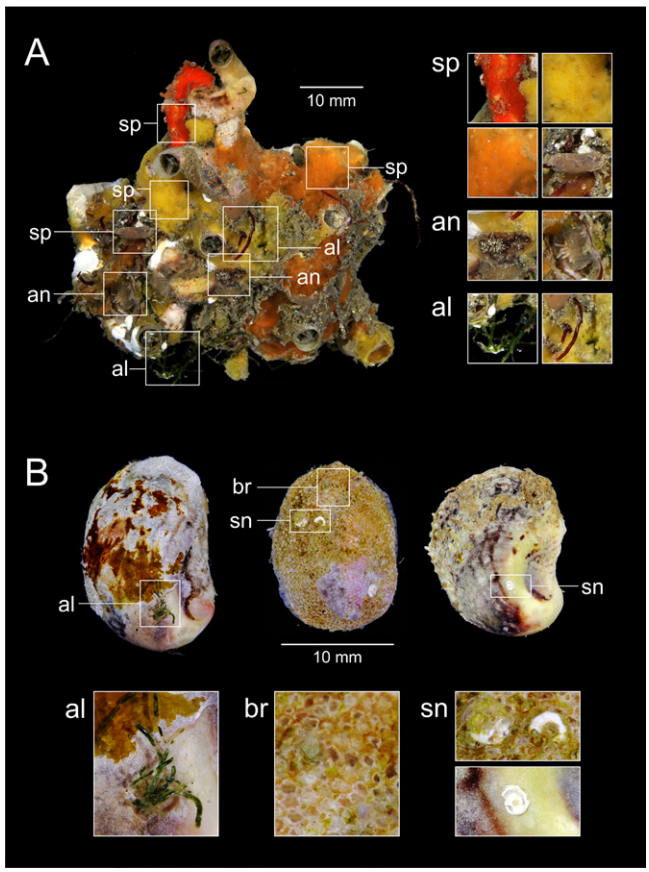


**Figure 5. The morphological records of the sea snail from the toxic shallow hydrothermal vent area off Kueishan Island. Dorsal views of worm snail *Thylacodes nodosorugosus* (A) and spiny slipper snail *Bostrycapulus gravispinosus* (B). al = algae, an = anemone, br = bryozoa, sn = snail, and sp = sponge.**

the host shell measured 11.33 mm in length, whereas the epibiotic *T. nodosorugosus* tube extended to approximately 100.39 mm. This highlights the pronounced size disparity between the two species in this association.

### *Statistical Analysis*

Comparison of upper size shell height between free-living and basibiontic *Bostrycapulus gravispinosus* revealed a significant difference (Table 1). The upper size fraction of the free-living group had a mean shell height of 16.42 ± 0.86 mm (75$^{th}$ percentile subset, $n$ = 29), whereas basibiontic individuals had a mean shell height of 13.07 ± 2.00 mm ($n$ = 22). This indicates that the basibiontic group not only showed a shorter shell height but also showed substantial interindividual variability, with a high degree of data dispersion. Shell height in basibiontic individuals was significantly lower than in free-living individuals ($t$ = 8.09, df = 49, $P$ < 0.0001, independent samples Student's $t$-test). In addition, basibiontic individuals exhibited greater variability in shell size. In essence, this morphological difference certainly reflects the specific selective or adaptive influence of the two habitat types (movable or host attached) on the shell height characteristic of *B. gravispinosus*.

## DISCUSSION

### *Molluscs in Shallow Hydrothermal Vent Environments*

The occurrence of molluscs in hydrothermal vent environments is notable given that the acidified seawater can impair calcium carbonate formation. Early surveys at Kueishan Island reported *Nassarius* sp. and an unidentified chiton species from vent-influenced areas, although the precise proximity to vent orifices was not clearly specified (Chang 2006). Subsequent studies recorded additional species, including

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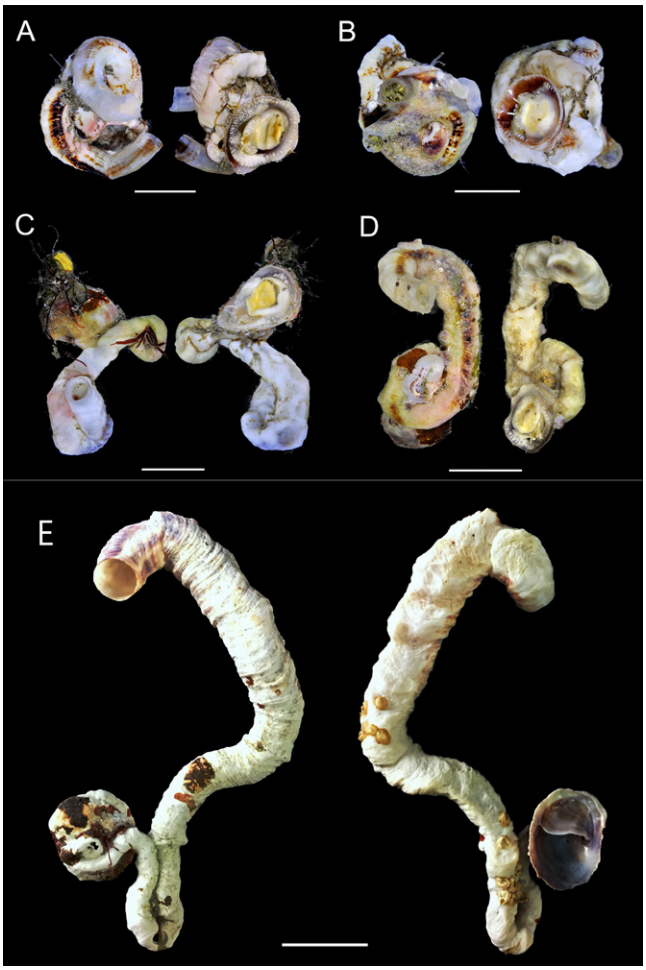


**Figure 6. The specimens show *Thylacodes nodosorugosus* growing on the shell of *Bostrycapulus gravispinosus* (left: dorsal view and right: ventral view). Scale bar represents 10 mm.**

the dove snail *Anachis misera* (Chen et al. 2015), and later expanded the species list to include multiple gastropods and chitons inhabiting shallow vent habitats. As survey coverage and frequency increased, six molluscan species (*Bostrycapulus aculeatus*, worm snail *Dendropoma dragonella*, *A. misera*, *Ergalatax contractus*, and one chiton *Chiton komaina*) were recorded in hydrothermal vent areas (Chan et al. 2016). The six new species records were miter snail *Strigatella scutulata*, dwarf hairy triton *Monoplex vespaceus*, tortoise dove shell *Pardalinops testudinaria*, telescoped dove shell *Pyrene punctata*, *Pollia mollis*, and muricate cone *Conus muriculatus* (Chen et al. 2018). By 2018, at least 13 molluscan species had been documented, primarily at depths shallower than 20 m. Later, the worm snail was identified as *Thylacodes adamsii* (Wang et al. 2023). Among these, *Thylacodes nodosorugosus* and *Bostrycapulus gravispinosus* are consistently reported and appear to be well adapted to the highly acidic and sulfur-rich conditions (Chan et al. 2016, Chen et al. 2018). Previous research in this system has largely emphasized biodiversity patterns, with comparatively limited attention to ecological interactions or physiological adaptations (Chen et al. 2015, 2018, Wang et al. 2023).

**TABLE 1.**

**Statistical results of Student's *t*-test in comparison of *Bostrycapulus gravispinosus* shell height between movable (75th percentile shell heights, $n = 29$) and basibiontic (fixed; $n = 22$) groups**

| | Movable | Basibiontic | Student's *t*-test |
|---|---|---|---|
| Shell height (mm) | 16.42 ± 0.86 | 13.07 ± 2.00 | $t = 8.09$, df = 49, $P < 0.0001$* |

df = degree of freedom.
*Significant at the $P < 0.001$ level (two-tailed).

Although studies of hydrothermal vent fauna have often focused on the vent crab *Xenograpsus testudinatus* and its adaptations to toxic environments (Chen et al. 2023, Chou et al. 2023, Chan et al. 2024, Tseng et al. 2025), molluscs exhibit higher species diversity in this system (Chan et al. 2016, Chen et al. 2018); however, their physiological mechanisms for coping with acidified seawater remain poorly understood. Given that molluscan shells are primarily composed of calcium carbonate, which is highly susceptible to dissolution under low pH conditions (Gazeau et al. 2013, Li et al. 2025), this raises important questions regarding their persistence. Various reports indicate that numerous molluscan species are affected by ocean acidification, and evident that molluscs are the biological group most vulnerable to future ocean acidification (Jiao et al. 2025, Shimizu et al. 2025). Shallow hydrothermal vents at Kueishan Island are often considered natural analogs of future ocean conditions characterized by warming, acidification, and pollution (Dahms et al. 2018, 2023). Understanding how molluscs survive and maintain shell integrity in these environments may therefore provide important insights into species resilience under future ocean change scenarios.

### *Feeding Ecology and Growth Constraints*

The suspension feeder *Thylacodes nodosorugosus* captures particulate organic matter and zooplankton (Gotshall 1994). Snails of the genus *Bostrycapulus* are globally widespread in tropical and temperate oceans (Collin & Rolán 2010), species of the genus *Bostrycapulus*, including *Bostrycapulus gravispinosus*, are suspension feeders that rely on water flow rather than mucous entrapment (Chan et al. 2016, Wang et al. 2023). Hydrothermal vent conditions at Kueishan Island are known to cause high mortality in zooplankton (Davidson et al. 2024), potentially increasing the availability of detrital organic matter. This may represent an important food resource for both species. Stable isotope evidence further indicates that these two gastropods use different food sources within the vent ecosystem (Wang et al. 2023), suggesting resource partitioning. When *B. gravispinosus* becomes immobilized due to the attachment of *T. nodosorugosus*, its ability to exploit spatially heterogeneous food resources is likely reduced. Despite evidence of dietary flexibility in both species (Wang et al. 2023), restricted mobility may limit feeding efficiency in *B. gravispinosus*, thereby constraining growth. This interpretation is consistent with studies in other bivalves and gastropods, where reduced food availability leads to diminished somatic growth (e.g., Silina 2023, Rennie et al. 2025).

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***Epibiosis and Microhabitat Complexity***

Epibiosis refers to the spatial association between a substrate organism (basibiont) and an attached organism (epibiont) without direct trophic dependence (Wahl 1989). In this study, both *Thylacodes nodosorugosus* and *Bostrycapulus gravispinosus* supported diverse epibiotic assemblages, including sponges, algae, bryozoans, and other invertebrates, representing typical epibiotic communities. Marine gastropod shells commonly serve as substrates for a wide range of organisms (Wilson 2021, Pereira et al. 2022, de Guzman et al. 2023). Past studies have identified various organisms growing on molluscan shells, including known taxa such as: algae (Avaca et al. 2021, Pereira et al. 2022), crustose algae (Pereira et al. 2022, Cho et al. 2022), foraminifera (Barnet 2025), sponges (Volkmer-Ribeiro et al. 2019), bryozoans (Linneman et al. 2014, López-Gappa & Zelaya 2021), hydrozoans (Brooks & Mariscal 1986, Namikawa 2022, Namikawa et al. 2023), barnacles (de Almeida Alves-Júnior 2022), and polychaetes (Pyecroft 2022, Rawson 2025). Epibionts are generally nonspecific and can colonize natural and artificial substrates (McGowan & Iyengar 2017, Ambrose & Munroe 2025, Rong et al. 2025). Attachment to living hosts can provide ecological advantages, including enhanced access to food and improved hydrodynamic conditions (Wahl 2008, 2020). In this study, epibionts did not appear to cause direct physical damage to host shells, suggesting a predominantly nonparasitic interaction. Compared with open natural marine environments, even small limpets have been found with 86 taxa of epibionts on their shells (Pereira et al. 2022), the Kueishan Island hydrothermal vent area provided fewer epibiont species compared with the records of open ocean environments. Epibiotic diversity in the Kueishan vent system appears lower, likely reflecting environmental constraints such as acidity, temperature, and sulfur toxicity (Davidson et al. 2024). Nevertheless, the presence of epibiotic assemblages indicates that even extreme environments can support structurally complex microhabitats.

The surface characteristics of organisms are of crucial importance in the context of the majority of biological interactions (Kasemo 2002). In this regard, epibiosis has been shown to act as an ecological lever, with the capacity to amplify or buffer biotic and abiotic stress (Wahl 2008); however, epibiosis can have both positive and negative effects on hosts. Therefore, the relationship between epibionts and their hosts is complex (Harder 2008, Fernandez-Leborans 2010). For example, algae can cover shell surfaces, sometimes providing camouflage to enhance concealment and help hosts to evade predators (Aguilar-Estrada et al. 2022). An example are barnacles growing on the shells of mussels, helping to defend against predators and thereby reducing the mortality rate of the host (Downes et al. 2023); however, when barnacles grow on the shells of other organisms, they increase resistance to movement of the host, adding weight load and raise energy expenditure for movement of the host (Wahl 1996, Farren & Donovan 2007). Sponges often cover host shells (Farren & Donovan 2007), and some species (e.g., clionid sponges) may even burrow through the shell, potentially causing death (Leidy 1889, Carroll & Reitsma 2025). Bryozoans growing on shells not only increase shell weight but can also protect the host shell from chemical erosion (Linneman et al. 2014). The organisms observed on gastropod shells in this study did not cause invasive damage to their hosts, nor were any fatalities being observed. This symbiotic relationship suggests that microhabitats within hydrothermal vent communities facilitate the coexistence and growth of diverse species.

***Interspecific Interactions and Space Competition***

Competition among organisms can be broadly categorized into exploitation competition (indirect competition for shared resources, such as food, space, and light; Paine 1984), and interference competition (direct negative interactions that prevent another organism from obtaining resources) (Case & Gilpin 1974, Lockwood 1992, Amarasekare 2002). In benthic marine systems, space is often a limiting resource, particularly for sessile organisms. The present study provides evidence that *Thylacodes nodosorugosus* utilizes *Bostrycapulus gravispinosus* shells as settlement substrates, representing a form of space pre-emption. Such strategies are widely observed in sessile marine organisms, including barnacles and mussels, where early colonization of substrate confers competitive advantage (Paine 1984, Spiecker & Menge 2024). The outcomes of exploitation competition determine resource allocations (Schmitt 1996, Alcaraz et al. 2020). Competition among sessile organisms is a major process on coral reefs (Chadwick & Morrow 2011). Exploitative competition was demonstrated in several aquatic snails (Skilleter & Underwood 1993). Interspecific competition among gastropods in algal beds limits both species richness and species abundance evenness within communities (Béguinot 2021). In the intertidal zone, it also influences the distribution and abundance of herbivorous gastropods in areas of resource overlap (Putnam & Peckol 2018). The latter study observed different small size organisms (sea anemones, sponges, and algae) growing on *T. nodosorugosus* shells, likely competing for these small habitats. Even small animals compete for space, such as two cnidarians—hydroids and sea anemones competing for attachment space on gastropod shells (Brooks & Mariscal 1986). Much research remains to be done on the interactions among different benthic organisms within hydrothermal vent ecosystems. Such survival strategy is commonly observed in habitat competition among barnacles (Senthilnathan 2023) or mussels (Murashko 2023), and dominant algal growth inhibits barnacles and mussels from utilizing the same substrates (Paine 1984, Spiecker & Menge 2024).

At the habitat scale, the coexistence of *Bostrycapulus gravispinosus* and *Thylacodes nodosorugosus* merits particular attention. Both *T. nodosorugosus* and *B. gravispinosus* snails anchor themselves to rock surfaces, preventing the other species from attaching to that space. Both species were observed occupying distinct zones within the vent environment, suggesting spatial partitioning. Consequently, some zones are entirely occupied by *T. nodosorugosus* and other zones are entirely occupied by *B. gravispinosus* in hydrothermal vent areas; however, in areas where substrate is limited, *T. nodosorugosus* may settle on living hosts. This interaction can be interpreted as classical commensalism (Van Beneden 1876) from the perspective of *T. nodosorugosus*, which gains a substrate for attachment. In contrast, *B. gravispinosus* experiences reduced growth, likely due to impaired mobility and restricted access to food resources. Previous studies found that the shell shape and force of attachment of snails could influence the challenges of its habitat (Alcaraz et al. 2024), and grazer commensalism for food can influence species incidence and spatial segregation (Ibáñez et al. 2021). This dual outcome suggests that the interaction encompasses elements of both commensalism and exploitation

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competition. Similar patterns have been reported in other benthic systems, where competition for space and food resources influences growth, survival, and spatial distribution (Byers 2000, Cross & Benke 2002, Ibáñez et al. 2021). Given that both species are filter-feeding molluscs (Wang et al. 2023), the present study inferred that the impaired body growth of *B. gravispinosus* was caused by restricted feeding behavior and access to planktonic food.

## CONCLUSION

Shallow hydrothermal vent systems at Kueishan Island support a diverse assemblage of benthic organisms beyond the well-studied vent crab *Xenograpsus testudinatus* (Tseng et al. 2024). Species inhabiting these environments demonstrate tolerance to acidified and chemically extreme conditions, providing a valuable insight into potential biological responses to future ocean change. This study highlights the importance of interspecific interactions, particularly space competition and epibiosis, in structuring benthic communities in hydrothermal vent ecosystems. The ability of organisms such as *Thylacodes nodosorugosus* to use alternative substrates, including living hosts, underscores the role of habitat limitation in shaping species interactions. Observations of macroalgal growth on rocky substrates near vent outlets further suggest that primary production may play an important role in supporting local food webs. Future research should focus on the trophic dynamics, physiological adaptations, and long-term ecological processes that enable species persistence in these extreme environments.

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## CONFLICT OF INTEREST

The authors declare no competing financial interests or conflict of interest.

## ETHICAL APPROVAL

This work did not require ethical approval from a human subject or animal welfare committee.

## LITERATURE CITED

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