Shell shape variation of the symbiotic gastropod *Phenacovolva rosea* (Ovulidae) in Vietnam

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ABSTRACT. This study investigates the shell variability of *Phenacovolva rosea*, a symbiotic gastropod inhabiting octocorals, in relation to geographical location and host coral species. We analyzed shells from 53 adult specimens collected at three locations in the north of Vietnam and one in the vicinities of Nha Trang City (southern Vietnam).

To describe the shells' outlines, elliptical Fourier descriptors were applied. Based on the shell outline data, principal component analysis was performed. Additionally, height and width of *P. rosea* shells were measured. Only the first two principal components were effective, with the first principal component accounting for 92.8% of the variation. It closely correlated with width-to-height ratio of shells. According to dispersion analysis (ANOVA), shells in Nha Trang were significantly slimmer with longer terminal processes compared to those from the three northern locations. The coral host species also impacted shell shape when considering the entire dataset. However, this difference may have stemmed from shell variations between locations, as coral composition is not independent of location. When regional samples were analyzed separately, no significant impact of the host was detected.

The factors that differed between northern locations and Nha Trang were then discussed, along with the mechanisms underlying their influence. We suggest that predation risk, influenced by water turbidity, is greater in the clearer waters of Nha Trang. This increased predator pressure may explain the presence of long terminals on *P. rosea* shells found in Nha Trang, potentially providing protection against some fish predators. Furthermore, the shorter and wider shells found in northern locations may be advantageous in waters with higher current speeds, whereas the long-terminal shells with narrow apertures observed in Nha Trang may be better suited for slower currents. The climate disparity, encompassing temperature and salinity mediated through precipitation, could also potentially influence shell morphology. However, the underlying mechanism remains unclear due to the complex nature of these interactions and the scarcity of literature data.

Isolating host-specific shell shape traits from other factors proved challenging, given the close association between host species composition and location. Laboratory experiments modeling each factor independently may provide a solution to this issue.

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Изменчивость формы раковины симбиотического брюхоного моллюска *Phenacovolva rosea* (Ovulidae) во Вьетнаме

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РЕЗЮМЕ. Данное исследование посвящено изучению изменчивости формы раковины симбиотического моллюска *Phenacovolva rosea* обитающего на восьмилучевых кораллах. Были проанализированы раковины 53 взрослых экземпляров, собранных в трех локациях на севере Вьетнама и в районе г. Ня Чанг (южный Вьетнам).

Для описания силуэта раковин были получены эллиптические дескрипторы Фурье, а затем

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к ним был применен анализ главных компонент. Кроме того были проведены измерения высоты и ширины раковин. Только первые две главные компоненты были значимы, причем первая - описывает 92.8% изменчивости формы раковины. Первая главная компонента и отношение ширины раковины к ее длине тесно связаны, согласно корреляционному анализу. Дисперсионный анализ (ANOVA) показал значимые отличия раковин, собранных в северных локациях от собранных в Ня Чанге. Они более узкие и обладают более длинными терминальными выростами, в отличие от раковин, собранных в северных локациях. Вид коралла-хозяина также значимо влиял на отношение ширины к высоте раковины при анализе всего набора данных, однако, это может быть связано с различиями видового состава хозяев между локациями. При раздельном анализе материала из Ня Чанга и северных локаций достоверных отличий формы раковины экземпляров, собранных с разных хозяев, не было выявлено. Обсуждаются факторы, по которым Ня Чанг и северные локации отличаются, а также возможные механизмы их влияния на форму раковины. Мы предполагаем, что из-за высокой прозрачности воды в Ня Чанге пресс хищников может быть выше, чем в мутной воде северных локаций. Это может объяснять развитие более длинных терминальных выростов у раковин P. rosea в Ня Чанге, которые могут обеспечивать защиту от некоторых хищных рыб. Еще один возможный фактор, определяющий форму раковины, - скорость течения. Короткие раковины, обладающие широким устьем, найденные на севере, могут быть более устойчивыми к сильным течениям, в то время как длинные выросты раковин и узкие устья в Ня Чанге могут быть неадаптивны при сильном течении. Климатические отличия между северными локациями и Ня Чангом, включающие температуру и количество осадков влияющее на соленость воды потенциально могут влиять на форму раковины. Однако конкретные механизмы влияния пока изучены плохо.

Влияние коралла-хозяина на форму раковины обитающих на нем моллюсков сложно отделить от других факторов, поскольку видовой состав хозяев сильно зависит от локации. Только лабораторные эксперименты, моделирующие влияние каждого фактора по отдельности, помогут разрешить эту проблему.

Introduction

Phenotypic variation represents the diversity of observable traits displayed by individuals within a species under varying conditions [Vogt, 2020]. Knowledge on how different environmental contexts give rise to this diversity is crucial for gaining insights into the adaptability and survival mechanisms of organisms.

The ability of aquatic animals to develop different traits in response to their environment is welldocumented. They often exhibit distinct behaviors and noticeable physical changes in reaction to factors like water conditions, diet, and predator presence [Reznick, Travis, 1996; Tollrian, Harvell, 1999].

The mollusk shell, functioning as a recording structure, encapsulates a substantial segment of an organism's life story. As a result, shell shape has become a favored trait for studying phenotypic variations in response to environmental and biotic factors. These studies often employ geometric morphometric methods in addition to linear measurements [Trussell, 2000; Solas et al., 2013; Zdelar et al., 2018; Doyle et al., 2018; Lischenko, Jones, 2021; Nieto-Vilela et al., 2021]. Shell shape variations detected through both geometric morphometric methods and classical measurements often encompass variations in linear size, shell width-to-height ratio, shell thickness, aperture size and shape [Trussell, 2000; Bourdeau et al., 2015]. The factors most frequently indicated as influencing shell morphology include temperature, wave exposure, water current speed, predation pressure [Bourdeau et al., 2015]. Nevertheless, studies on phenotypic response to various factors have primarily focused on the well-studied intertidal species from temperate water, with limited research effort in tropical regions [Bourdeau et al., 2015].

The majority of members of the marine gastropod family Ovulidae are highly dependent on their host, the octocoral. Within this family, Phenacovolva rosea (A. Adams, 1855) stands out as a species with substantial phenotypic variability and one of the broadest known host range among Ovulidae [Lorenz, Fehse, 2009; Zvonareva et al., 2020; Zvonareva et al., 2024]. P. rosea have involute spindle-shaped shell that is smooth and glossy in the middle part, with striated terminals. It varies in size from small to large and from very narrow to inflated centrally, with different degrees of terminal processes' elongation. This remarkable shape variation, along with other characteristics such as shell and mantle coloration patterns, has even been a source of excessive species splitting [Rosenberg, 1992]. Presumably, different species have preferences for specific hosts [Lorenz, Fehse, 2009]. However, previous research has revealed that, despite this considerable variation and diverse hosts, it constitutes a single species [Zvonareva et al., 2020; Nocella et al., 2024].

Prior to this research, barcoding for the COI gene was conducted on *Phenacovolva* spp. specimens collected in Vietnam, whose species affiliation was uncertain (unpublished). Species other than *P. rosea* and divergent mitochondrial lineages were excluded. Around 30% of the specimens used in this study were subjected to COI gene barcoding. This subset comprised specimens from diverse locations and coral hosts, exhibiting various morphotypes. We deemed this subset sufficient to ensure that only specimens belonging to a single species and sharing the same



FIG. 1. Map of studied locations. A. Outline of Vietnam highlighting the two studied regions marked with black boxes. B. Detailed map showing the three northern locations: Cat Ba Island, Quan Lan Island, and Co To. C. Map depicting Nha Trang Bay and its islands.

РИС. 1. Карта мест сбора материала. А. Карта Вьетнама с двумя исследованными регионами отмеченными черными квадратами. В. Карта трех северных локаций: островов Кать Ба, Куан Лан и архипелага Ко То. С. Карта залива Ня Чанг и его островов.

mitochondrial lineage were included in the present study. Specifically, nine sequences were published in Zvonareva *et al.* [2020], while an additional eight sequences remain unpublished.

The objective of this study is to assess and analyze the variations in shell morphology of the symbiotic gastropod *P. rosea*. Our approach involves both geometric morphometric methods and classical measurements. Our primary objective is to understand which factors, cited as the most influential in other studies, may contribute to the determination of shell morphology in *P. rosea* and discuss possible mechanisms of influence in further detail.

Material and methods

The material for this study was collected during a series of expeditions (April-June 2018, 2019, 2020 and 2021) at four locations in the northern and southern parts of Vietnam. The northern sampling locations included Quan Lan Island in Bai Tu Long Bay, the islands of the Co To archipelago, and Cat Ba Island in Lan Ha Bay. In the southern part, samples were collected in Nha Trang Bay (Fig. 1).

Water transparency assessments were conducted by two trained divers, who provided subjective evaluations at each sampling site. Specifically, visibility at Quan Lan ranged from 0.5 to 3 meters, while the Co To and Cat Ba sites showed slightly higher visibility, falling within the range of 2 to 6 meters. In contrast, Nha Trang Bay featured notably higher visibility levels, ranging from 5 to 10 meters during the sampling period. Our assessments align with existing literature data [Huong *et al.* 2003; Latypov, Dautova, 2005], indicating that Lan Ha and Bai Tu Long bays are more turbid due to river input and anthropogenic influence.

In Bai Tu Long, the average annual temperature ranges from 22.0 to 24.0 °C, with summer monthly average temperatures rising up to 28 °C. Winter

Coral species		Total images			
	Nha Trang	Cat Ba	Со То	Quan Lan	
Astrogorgiiadae: Malacalcyonacea			<u>`</u>		
Astrogorgia sp. 1 (white)	1				1
Astrogorgia sp. 2 (red)		1	1		2
Astrogorgia sp. 3 (red&yellow)		3	3	11	17
Paramuriceidae: Malacalcyonacea					
Acanthogorgia sp.		5			5
Bebryce sp.	7				7
Echinogorgia sp. 1 (red)		2	1		3
Echinogorgia sp. 2 (yellow)	2				2
Echinomuricea sp.			2		2
Menella sp.	4				4
<i>Paraplexaura</i> sp.	4			1	5
Euplexauridae: Malacalcyonacea					
<i>Euplexaura</i> sp.	2				2
Subergorgiidae: Malacalcyonacea					
Subergorgia sp.	1				1
Ellisellidae: Scleralcyonacea					
Dichotella sp.		1			1
<i>Junceella</i> sp.		1			1
	21	13	7	12	53

Table 1. Species composition of host corals across four study locations, with the number of collected shells from each host and location.

Табл	1	Виловой	состав	KODO HIOD-VO	DORED D	HET INEY	местах	chopa	колицество	CODDATINE IN	navonuu ua	KANKHOM	vooguure
гаол	• • •	Бидовои	состав	кораллов-л	лата в	четырел	местал	coopa,	KUJIMACCIBU	сооранных	раковин на	каждом	лозлинс
V	BI	каждом ме	есте сбо	ppa.									

months experience lower temperatures, with January averaging about 17.8 °C [Giang et al., 2023]. At Cat Ba, the monthly water temperature varies from 19.0°C (January) to 32.5°C (July), [Hao et al., 2020]. In Nha Trang Bay, average sea temperatures fluctuate between 24.0 and 29.5 °C [Vo et al., 2022].

The total of 72 specimens of Phenacovolva rosea were initially collected using SCUBA diving techniques. However, to eliminate potential biases related to age-dependent shell features, only adult individuals with fully formed labrum were considered for analysis, resulting in a final count of 53 shells. Detailed information regarding the collected material is presented in Table 1.

We used dial calipers (accuracy 0.05 mm) to measure shell width and height and calculated widthto-height ratio.

The shells of P. rosea remain stable when resting on the midsection of their aperture, with both terminal processes elevated above the surface. This positioning likely mirrors their natural state on coral. To avoid potential biases arising from variations in shell positioning and projection angles due to manual handling during standard aperture-up photography, we captured each shell in its stable and natural orientation.

For each specimen, the photographs were subjected to a processing step using Photoshop CS6 "posterize" function to obtain a silhouette of the

shell. The silhouette was subjected to analysis using the SHAPE software package [Iwata, Ukai, 2002], employing Elliptic Fourier descriptors (EFD) [Kuhl, Giardina, 1982]. This approach comprehensively outlines the shell shape. Following this, the software conducts principal component analysis of EFD coefficients to condense the information within the coefficients [Rohlf, Archie, 1984]. It subsequently provides a visualization of the variation for which each principal component (PC) is responsible.

Correlation was studied between principal components and other measured shell characteristics and correlation coefficients (r) were obtained.

Then, we conducted dispersion analysis for categories with a minimum of 3 data points (one-way ANOVA) for the location (53 specimens) and hostspecies predictors on whole dataset (43 specimens) and separately for northern locations (26 specimens) and Nha Trang (15 specimens).

In instances where the ANOVA indicated significant effects, we employed Tukey's unequal-N post hoc tests to perform pairwise comparisons of means among the different host coral species and locations. All statistical analyses were carried out using Statistica 12 software (StatSoft, Inc. 1984-2014).

Results

In the collected specimens, shell height ranged from 16.8 to 42.5 mm, with a width variation between



- FIG. 2. Shell shape variation in *P. rosea*. Left. Visualization of shape variations accounted for by each principal component using the PrinPrint program in the SHAPE software package. Right. Contrasting shell shape variants. All six shells are shown in the standard aperture-up position, with two of them also resting on their aperture as examples of the images used in the outline analysis. A. Location – Nha Trang, host – *Echinogorgia* sp. 2. B. Co To, *Astrogorgia* sp. 2. C. Quan Lan *Astrogorgia* sp. 3. D. Nha Trang, *Menella* sp. E. Nha Trang, *Bebryce* sp. F. Nha Trang, *Paraplexaura* sp.
- РИС. 2. Изменчивость формы раковины *P. rosea*. Слева. Визуализация изменчивости формы раковины для каждой главной компоненты по отдельности, выполнена в программе PrinPrint пакета SHAPE. Справа. Контрастные варианты формы раковины. Все шесть раковин приведены в стандартной позиции устьем вверх, для двух из них приведены фото с дорзальной стороны, как пример изображений использованных в анализе силуэтов. А. Локация Ня Чанг, хозяин *Echinogorgia* sp. 2. В. Ко То, *Astrogorgia* sp. 2. С. Куан Лан, *Astrogorgia* sp. 3. D. Ня Чанг, *Menella* sp. Е. Ня Чанг, *Bebryce* sp. F. Ня Чанг, *Paraplexaura* sp.

4.3 and 10.3 mm. The width-to-height ratio spanned from 0.15 to 0.36.

Only the first two principal components were effective, collectively explaining 96% of the variation in shell shape. The first component (Fig. 2) accounted for 92.8% of the total shell shape variation. Shells with negative eigenvalues are slenderer than the consensus shape and have longer terminal processes. PC1 aligns well with the width-to-height ratio, exhibiting a correlation coefficient between these measures of r = 0.99 (p < 0.001). Therefore, we provide graphs only for the width-to-height ratio later in the text, as the graphs for PC1 are almost identical. PC2 accounted for 3.2% of the variation. It is related to the curvature of the shell, with negative eigenvalues responsible for apparent bending of the shell to the left from the symmetry axis, while posi-

tive eigenvalues characterize symmetrical shells and shells with slight bending to the right. However, the shell shape characteristics represented by PC2 are less apparent due to a narrower variation, especially compared to PC1 (Fig. 2).

The results from the ANOVA indicate significant influences of the collection location on PC1 (p<0.001) and width-to-height ratio (p<0.001). However, there were no significant differences observed in height, PC2, and width. A notable distinction is evident in Nha Trang compared to the three northern locations (p<0.001 in all three cases), characterized by lower PC1 and a lower width-to-height ratio in Nha Trang (Fig. 3A). This is visually represented as slender shells in Nha Trang and inflated shells in the northern locations (Fig. 2).

In the analysis of the dataset containing all six



FIG. 3. ANOVA tests of the width-to-height ratio of shells of *P. rosea*, vertical bars denote 0,95 confidence intervals A. Across four studied locations (current effect: F(3, 49)=32,260, p=,00000). B. Across six coral host species, irrespective of collection location (current effect: F(5, 35)=12,866, p=,00000).

РИС. 3. ANOVA для отношения ширины раковины к высоте у *P. rosea*, «усы» обозначют доверительный интервал 0,95. А. В четырех локациях (F(3, 49)=32,260, p=,00000). В. На шести видах корплов-хозяев независимо от места сбора (F(5, 35)=12,866, p=,00000).



FIG. 4. ANOVA tests of width-to-height ratio of *P. rosea* shells across different host species, vertical bars denote 0,95 confidence intervals. A. In three northern locations (current effect: F(2, 23)=,09015, p=,91411). B. In Nha Trang (F(2, 12)=1,4096, p=,281).

РИС. 4. ANOVA для отношения ширины раковины к высоте у *P. rosea*, «усы» обозначют доверительный интервал 0,95. **А.** В трех северных локациях (F(2, 23)=,09015, p=,91411). **В.** В Ня Чанге (F(2, 12)=1,4096, p=,281).

coral species from both Nha Trang and northern locations, each hosting at least three specimens of *P. rosea*, host coral significantly influenced PC1 and width-to-height ratio (p<0.001) (Fig. 3B). *Menella* sp., *Paraplexaura* sp. and *Bebryce* sp. differed from *Astrogorgia* sp. 3 and *Acanthogorgia* sp.; *Menella* sp. and *Paraplexaura* sp. differed from *Echinogorgia* sp. 1 (all p<0.05). However, no significant impact was observed on width, height, and PC2.

The composition of host species varies among locations, with no host species shared across all four locations. This distinction is particularly pronounced between Nha Trang and the northern locations. Only *Paraplexaura* sp. is shared between these two regions, present in Nha Trang and one specimen in Quan Lan. Furthermore, the northern locations exhibit differences among each other, with *Astrogorgia* sp. 3 being the only host species shared among all three of them. It is notable that the significant difference observed in the analysis of six host species may primarily stem from influence of location, indicating differences in host species composition across various study locations.

Therefore, to mitigate the influence of varying coral compositions, we conducted separate analyses of host influence for three northern locations. The results revealed no significant effects on any of the shell shape parameters (Fig. 4A).

Similarly, when analyzed separately in Nha Trang, no significant influence of the host coral on any of the parameters was detected (Fig. 4B).

Discussion

PC1 closely aligns with the characteristics of the width-to-height ratio. Notably, we observed a significant difference between Nha Trang and the three northern sites, characterized by slender shells in Nha Trang and inflated shells in the northern locations.

It is crucial to emphasize the remarkable range of variation in the shell of *Phenacovolva rosea*, which is readily apparent to the naked eye. This distinction sets it apart from other studied gastropod species in which shell shape variation is less conspicuous, often requiring measurements and morphometric methods for detection [Urabe, 1998; Trussell, 2000; Cotton *et al.*, 2004; Avaca *et al.*, 2013; Solas *et al.*, 2013].

The structure of our data makes it difficult to fully isolate the impact of host coral on shell morphology from the regional differences in shape, given the variability in coral species composition across locations. Nevertheless, by conducting a dispersion analysis on shape variables, we can lay the basis for further exploration of the potential mechanisms of influence of various factors, including those identified as the most significant in previous studies on shell shape formation.

Temperature

Researchers have frequently explored latitudinal variations in shell shapes, often linking these differences to gradual changes in water temperature. The impact of water temperature on various traits of calcium carbonate-based shells is substantial. This is attributed to the decrease in the availability of CaCO₃ as the water temperature decreases, coupled with an increase in its solubility [Clarke, 1983]. Consequently, the deposition and maintenance of shells become more challenging in colder water environments [Graus, 1974; Vermeij, 1978]. In support of this, tropical mollusks exhibit higher calcification indices than their temperate counterparts [Graus, 1974].

Studies examining the influence of temperature regimes have revealed their effects on growth rate, shell thickness, shell shape, and callosities formation [Trussell, 2000; Doyle *et al.*, 2010; Melatunan *et al.*, 2013; Bourdeau *et al.*, 2015; Irie, Marimoto, 2016]. However, these studies have sometimes yielded conflicting results, underscoring disparities in shell characteristics between laboratory-grown specimens and those found in natural environments. This suggests that temperature alone may have a limited or indirect impact on shell shape under natural conditions [Doyle *et al.*, 2010; Bourdeau *et al.*, 2015].

The regions being investigated showcase notable climatic disparities, as evidenced by climatic classification maps [Beck *et al.*, 2018]. In the north, there is a considerably broader spectrum of air and water temperatures, accompanied by colder winters. While extensive research has been conducted on the impact of temperature on shell morphology, there remains a lack of information regarding how natural temperature fluctuations throughout the seasons affect shell characteristics. The effects of temperature described in existing literature do not fully align with our findings, where shell shape variation is notably more pronounced. While variations in calcification rates or growth seasonality may contribute to shell shape, the precise mechanisms of temperature influence remain unknown.

Salinity

In contrast to temperature studies, research on the role of salinity in shell shape variation is less common. Limited data is available on this topic, primarily focusing on its impact on the shell morphology of bivalves [Valladares *et al.*, 2010; Márquez, Van Der Molen, 2011; Telesca *et al.*, 2018].

The climatic differences observed among the study locations cannot be solely attributed to temperature disparities; variations in precipitation also play a significant role, impacting salinity levels. This is particularly notable in the northern regions, where annual precipitation exceeds that of Nha Trang [Beck et al., 2018]. Additionally, Nha Trang is situated in an upwelling zone, receiving high-salinity water [Barthel et al., 2009]. Furthermore, Cat Ba, located in the Red River delta, and Quan Lan and Co To, positioned slightly northeastward, may experience less influence from river water then Cat Ba. Observations suggest that shells collected from Cat Ba are the sturdiest, whereas those from Nha Trang, which lacks major rivers and undergoes lower annual precipitation, display slender shells of P. rosea. Therefore, salinity may also play a role in shaping the shells of P. rosea. However, due to the limited understanding of this aspect, it is challenging to propose an exact mechanism of influence.

Predation risk

The risk of predation is a frequently debated factor influencing shell shape diversity. Numerous studies have investigated predator-induced alterations in gastropod shell characteristics, primarily focusing on interactions with crabs [Kitching *et al.*, 1966; Trussel, 2000; Delgado *et al.*, 2003; Doyle *et al.*, 2010; Moody, Aronson, 2012; Sepúlveda *et al.*, 2012]. In the case of *P. rosea*, fish are the primary predators, as the host coral employs structural and chemical defenses to protect itself and its symbiont [Sammarco, Coll, 1992; Lucas *et al.*, 2014], deterring unspecialized animals like crabs and other mollusks from climbing on the coral [Rosenberg, 1992; Burkepile, Hay, 2007].

As suggested by Palmer [1979], one of the main defenses against fish predation is spination. However, in the case of *P. rosea*, the spination differs from Palmer's notion of an effective stout spinose sculpture strategically positioned to withstand fish attacks and redirect their force, thereby increasing effective size. *P. rosea* typically possesses only two 'spines' (i.e. the terminal processes) oriented in opposite directions.

Shell-crushing fish exhibit two distinct jaw morphologies for shell crushing, utilizing either oral jaws or pharyngeal jaws. Although the 'spines' of *P. rosea* might not effectively protect against oral jaw crushers, for pharyngeal jaw crushers, long terminals could potentially increase the effective size of the mollusk, making it challenging for the fish to manipulate the shell within its mouth.

Differences in predation pressure may indeed exist between the three northern locations and Nha Trang. This biotic factor is likely influenced by local hydrology, particularly water turbidity. Clearer waters in Nha Trang facilitate visual predators in locating mollusks on their hosts, whereas the higher turbidity in the northern locations hampers fish vision, allowing mollusks to remain undetected [Ortega *et al.*, 2020]. Consequently, conditions in Nha Trang may promote the development of long terminals as a defense against certain predators.

Current power

Another frequently discussed factor influencing the shell shape is wave exposure [Johannesson et al., 1993]. Gastropods exposed to wave action tend to have more globular shells, featuring a larger rounded aperture and a larger foot, which enhances their ability to secure a stronger attachment to substrata. In contrast, at sheltered sites, shells take on a more elongated form with a smaller aperture and foot [Kitching et al., 1966; Crothers, 1981; Rolán et al., 2004]. Nevertheless, it is consistently acknowledged that distinguishing between the influence of waves and predation pressure is challenging, given the interconnected nature of these two factors in the cases of most studied intertidal gastropod species and crabs [Sánchez et al., 2011; Sepúlveda, Ibáñez, 2012; Sepúlveda et al., 2012].

While wave action may not directly apply to our study due to the occurrence of mollusks deeper and in sheltered areas, similar features associated with strong currents, such as a globular shape and larger aperture, have been reported in the literature for mollusks exposed to currents [Murty, Rao, 1978; Crothers, 1981; Lam, Calow, 1988].

In our specific case, shells from northern locations appear more globular and feature wider apertures, which may be better suited to strong currents, while the elongated terminal processes observed in shells from Nha Trang could potentially impede the snail's ability to withstand strong currents. These elongated processes might function similarly to a sail, while the narrow aperture could limit the development of a substantial foot, thereby reducing attachment strength. However, we did not directly measure current strength at the collection sites, and thus lack definitive confirmation that currents in northern locations are stronger. Nonetheless, this speculation gains credibility considering that northern bays, being shallower compared to Nha Trang, suggest the possibility of stronger tidal flows that could indeed influence shell shape.

Host species

Various host species exhibit different structural characteristics, such as branch thickness, presence of calyces and others. Therefore, it is reasonable to hypothesize that corals may influence the shell shape of symbionts. For example, slender corals might require slimmer shells to effectively mitigate predation risk and secure their symbiont unnoticed by predators, while thicker corals may accommodate wider shells. Our study partially supports this idea.

Although the difference was not significant when considering the mean values, *Astrogorgia* sp. 3 and *Acanthogorgia* sp., which have tall calyces and nonretractile polyps resulting in wider branch diameters, tend to host mollusks with more inflated shells. Conversely, *Menella* sp. and *Paraplexaura* sp., with fully retractile polyps and low calyces, tend to host mollusks with slenderer shells when considering the mean values of the width-to-height ratio.

Additionally, *Bebryce* sp. exhibits non-significant differences from other corals in Nha Trang, but mean values suggest that shells on this coral are the most inflated in Nha Trang, possibly due to its tall calyces resulting in larger branch diameter. However, this pattern is not observed for *Echinogorgia* sp. 1, which hosts inflated shells despite its slender branches with fully retractile polyps and low calyces.

Another less apparent mechanism we can speculate about involves the diverse chemical defenses of coral species [Coll *et al.*, 1982]. Mollusks must contend with and neutralize these defenses through metabolism [Coll *et al.*, 1983]. This process may demand varying amounts of energy and resources, consequently affecting shell production.

However, since the differences in shell shape within the same region are not significant, we lean towards suggesting that the host species may be a less influential factor compared to the location itself.

Zvonareva et al. [2024] conducted a study on mantle camouflage of P. rosea, partially using the same material as the current study. A divergent mitochondrial lineage was later discovered in that dataset (unpublished), which were excluded from the dataset of the present study. However, their findings revealed that the coloration of the mollusk depended on the coloration of the host coral, with darker mollusks found on darker corals and lighter mollusks on lighter corals. Additionally, they observed that camouflage efficiency was also a host-dependent trait, while the collection location did not have a significant effect. In contrast, the current study found the opposite pattern: the shells significantly differed between locations, and there was no difference depending on the host when the difference in coral composition between locations was eliminated. This highlights that different organismal traits behave differently in response to the same factors.

Conclusion

We discovered that the shells of *Phenacovolva rosea* collected in Nha Trang were significantly slimmer and exhibited more pronounced terminal processes compared to those from three northern locations.

We explored various factors that could differ between Nha Trang and northern locations, which previous studies have identified as highly influential on the shells of other molluscs. We suggest that predation risk, influenced by water turbidity, is greater in the clearer waters of Nha Trang. This increased predator pressure may explain the presence of long terminals in P. rosea shells found in Nha Trang, which could potentially provide protection against some fish predators. Furthermore, the shorter and wider shells found in northern locations may be advantageous in higher water current speeds, whereas the long-terminal shells with narrow apertures observed in Nha Trang may be better suited for slower currents. The climate disparity, encompassing temperature and salinity mediated through precipitation, could potentially influence shell morphology. However, the underlying mechanism remains unclear due to the complex nature of these interactions and the scarcity of literature data. Host-specific shell shape traits were challenging to isolate from other factors, as the host species composition was closely linked with location.

Studying mollusks within their natural populations makes it difficult to ascertain definitively which factors are driving shell morphology, particularly when these factors are not independent of each other. One potential approach to addressing this challenge could involve expanding the dataset to include a broader range of host species shared across different locations. However, this may prove challenging given that the location not only influences the environmental conditions for mollusks but also determines the available coral species. For instance, certain corals are restricted to specific conditions such as turbidity levels, water currents, sediment types, and depths [Fabricius, Alderslade, 2001].

Therefore, laboratory experiments that isolate each factor independently could provide a more robust method for elucidating these relationships and shedding light on the fundamental biological question: to what extent plasticity and local adaptation contribute to the variability of particular species.

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