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**The evolution of trophic specialisation in two lineages of corallivorous
gastropods**

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1. EXTENDED ABSTRACT

Introduction

In my PhD thesis, I deeply explored the fundamental role played by symbiotic interactions, placing a specific emphasis on the intricate dynamics of parasitism and its profound implications for ecosystem evolution. The significance of these interactions in shaping community dynamics is paramount, standing as crucial influencers alongside predation and physical disturbance. The term "symbiosis" encompasses a variety of interpretations and is often utilized to describe beneficial associations characterized by varying size disparities between the organism and its host.

Among ecosystems where symbiotic interactions play crucial roles, coral reefs have been acknowledged as exceptionally diverse environments, supporting a multitude of symbiotic interactions. The most well-known symbiosis in coral reefs is represented by the zooxanthellae, which are mutualistic dinoflagellates belonging to the order Dinophyceae. Their role is fundamental in sustaining vital physiological processes within the host. Moreover, the vulnerability of cnidarians to climate change emerges as a pressing concern, with potential cascading effects on associated fauna, underscoring the far-reaching ecological consequences. Various metazoan groups have evolved the ability to feed on corals, despite their inherent toxicity, providing intriguing models for studying the evolutionary ecology of this association. Nonetheless, our understanding of these interactions remains limited. All cnidarians feed by using the unicellular structures that characterise and give name to the entire group, the cnidocytes. Upon appropriate stimulation, typically through contact with a prey organism or potential predator, the cnidocytes either entangle the target or penetrate it, releasing venom.

Thanks to studies published in the recent past, new information about the balance of symbiotic interactions in tropical reef ecosystems has emerged. Our perception of the importance of these relationships has progressively changed, and it is now evident that molecular data provide a significant new line of evidence on the evolution of parasites. Phylogenies of parasites and of their host species, along with dated fossil occurrences, can yield estimates of divergence times based on molecular clocks. Parasitism may involve coevolutionary patterns characterised by a delicate balance of adaptations and counter-adaptations between host and parasite, as described by Van Valen (1973) in the Red Queen's hypothesis, which posits that species must constantly evolve to survive in a dynamic environment where they are in competition with ever-evolving opposing species. Alternatively, it may reflect a sequential evolution mechanism, where the evolution of the host influences the evolution of the parasite, but not vice versa. Such time-calibrated phylogenies can reveal patterns of co-evolution and host switching. Indeed, trophic specialization can drive coevolutionary processes by creating selective pressures that lead to the development of traits in adaptation to the host species. Therefore, to conduct macroevolutionary analyses, a robust phylogenetic framework, at least for the parasite, is essential. The most conventional method for understanding evolutionary relationships among taxa is Sanger sequencing, that relies on the selective incorporation of chain-terminating dideoxynucleotides by DNA polymerase during *in vitro* DNA replication. Though historically significant, it faced limitations, especially in amplifying genes for deep phylogenetic nodes. The advent of Next-Generation Sequencing (NGS) overcame these constraints, revolutionizing phylogenetic research. NGS technologies, including whole-

genome sequencing, transcriptome sequencing, and targeted enrichment, expedited marker acquisition across diverse taxa. Phylogenomics, particularly active for non-model organisms, extends beyond primary sequence information. Trees are inferred from whole-genome features, leveraging gene content, order, intron positions, and protein domain structure. Advances in NGS provide unprecedented breadth and depth in genome sequencing, covering thousands of closely related strains across various environments. Among NGS techniques, target enrichment, an RNA/DNA-based approach, stands out for phylogenomic analysis. Transcriptome-based exon capture methods within target enrichment offer significant phylogenetic potential, retrieving numerous genetic markers from genomic DNA. This cost-effective strategy finds application in high-throughput sequencing across diverse taxa, enhancing DNA for phylogenomic studies in plants, vertebrates, insects, spiders, and molluscs. In this PhD thesis, I selected the Exon-capture approach due to the high support values observed on published gastropods phylogenomic trees, as well as the availability of conserved sequence oligonucleotides derived from gastropod transcriptomes.

Cnidarians serve as a valuable model for investigating host-parasite interactions, given that, despite their inherent toxicity, they serve as a food source for various organisms. Predators and parasites of stony corals, gorgonians and soft corals include, among others, bony and cartilaginous fishes, asteroids, crustaceans, polychaetes, and gastropods (prosobranchs and nudibranchs). Among prosobranchs, five families are known to feed on cnidarian: Calliostomatidae, Epitoniidae, Architectonicidae, Ovulidae, and some Muricidae, including the entire subfamily Coralliophilinae plus the Ergalataxinae species *Drupella* spp. and *Ergalatax junionae*.

The neogastropod family Muricidae Rafinesque, 1815 includes species known for preying on various invertebrates. Some, like *Drupella*, occasionally exhibit predatory behaviour, causing localized coral colony damage during population outbreaks.

Similarly, the species *Coralliophila erosa* (subfamily Coralliophilinae) occasionally undergoes shifts from parasitic to predatory behaviour, consuming extensively to the extent that the colony of *Acropora* corals fails to recover. These transitions have been demonstrated to be density-dependent, likely influenced by abiotic factors such as the reduction of fish predators that prey on molluscs. Despite these instances of occasional predation, most coralliophilines, maintain a parasitic strategy throughout their life cycle. This involves tapping into coral energy reserves without extensive movement, aiming to maximize energy exploitation while preserving the host colony and minimizing tissue damage. Their feeding strategies include suctorial feeding on photosynthetic products and proboscis introduction through the polyp's oral opening or coral epidermis. Endoparasitic genera (*Leptoconchus*, *Magilus*, and *Rapa*) excavate coral skeletons or tissues, adopting an endosymbiotic lifestyle.

Another group of corallivorous prosobranchs is the family Ovulidae J. Fleming, 1822, comprising exclusively species living as ectoparasites on sessile colonial cnidarians. The snails reside permanently on their host or in close vicinity, feeding on the polyps and their secretions. There are some species, especially those with larger size (e.g. *Ovula ovum*), which can cause damage to their host colonies. However, ovulids have consistently been observed feeding on colonial cnidarians, rather than on solitary polyps, without causing extended damage.

Another corallivorous group is Epitoniidae, a diverse family of gastropods that parasitize mostly solitary anthozoans, feeding on various genera of cnidarians.

Nudibranchs in the genus *Phestilla* (family Trinchysiidae) showcase a dynamic range in feeding behaviour on scleractinian corals. Some *Phestilla* species cause coral colony mortality, while

others, due to their small size, have a minimal impact. The size ratio between gastropods and their cnidarian targets serves as a reliable proxy for determining the likelihood of complete consumption.

Considering that the few shifts to predatory behaviour are documented in very particular situations, this PhD thesis treats all interactions between corallivorous snails, and their cnidarian hosts as parasite-host relationships.

In some cases, including members of the subclass Caenogastropoda, the gastropod-coral association relies on mechanisms that discharged the nematocysts into the stomach. Indeed, the presence of toxins in the salivary glands or in specialised venom glands is a well-documented feature of caenogastropods, which in the case of corallivorous species could have evolved through an arms race process to inactivate Cnidaria venom compounds in the snails' digestive system. Anyway, the range of host specificity of these snail lineages, which is supposed to be linked to their biochemical trophic diversification, is poorly known, especially for deep water species.

Exploring the evolution of parasitism necessitates reliable data on the associations as well as a robust phylogenetic and systematic framework of the groups involved in such associations.

Empirical data on trophic associations in invertebrates are limited due to challenges in conventional methods like behavioural observations and gut dissections, especially for small-sized organisms and difficult-to-explore habitats such as deep waters. Direct observations of feeding behaviour are rare in deep-sea environments, and physical and chemical digestion can hinder accurate morphological identification.

Genomic technologies, particularly DNA barcoding, have emerged as powerful tools for species identification in ecological research. DNA barcoding relies on a standardized genetic region acting as a "barcode," allowing for DNA-based, semi-automatic identification by comparing sequences to reference. This method has successfully identified invertebrate prey. Despite limitations, such as database reference availability and reliance on a single locus, DNA barcoding often serves as the primary method for inferring diet analysis in various circumstances.

Recent research reveals that host-mediated adaptations in marine ecosystems can impact the behaviour of small invertebrates' populations interacting with larger plant or animal hosts. These local interactions may drive parasite speciation or host-parasite coevolution. Coevolving systems, like hosts and parasites, provide valuable models for studying macroevolutionary processes affecting species groups over extended periods.

Given this background, some evolutionary issues have arisen about the evolution of trophic ecology in corallivorous gastropods:

Did the adaptation to the cnidarian host affect the macroevolutionary patterns of corallivorous snails?

Can this adaptation be explained as a coevolutionary process?

To answer these and other questions, corallivory in marine snails has been investigated from an evolutionary perspective. The overarching aim of this project is to elucidate the levels of specificity of parasite-host relationship and the macroevolutionary patterns of snails feeding on corals, in two different caenogastropod lineages: the family Ovulidae and the muricid subfamily Coralliophilinae, that independently evolved corallivory.

Ovulidae Fleming, 1828, also known as egg-cowrie, comprise a group of specialised parasitic caenogastropods that feed by browsing primarily on anthozoans. They currently comprise 292 accepted species (WoRMS 2023). Egg-cowries are predominantly tropical, with only few species inhabiting temperate areas. Most species live in shallow waters, between 10 and 50 metres, but some are collected as deep as 1100 m. Their shells can be pyriform, ovate, cylindrical or lanceolate with a slit-shaped aperture; in living specimens of most species the shell is almost entirely covered by the mantle, that camouflages the gastropod on its coral host, and a few species have aposematic colorations. Egg-cowries reside permanently on their cnidarian host or in its close vicinity, feeding on polyps and their secretions. Certain species seem to favour a single cnidarian host while others are reported to have a more varied diet including hosts of different genera, and even families of Anthozoa.

The muricid subfamily Coralliophilinae Chenu, 1859, is a highly diverse lineage of gastropods, currently comprising 268 extant species (WoRMS 2023). Coralliophilinae are distributed worldwide, mostly in warm temperate and tropical oceans. All species for which their ecology is known exhibit symbiotic relationships (ecto or endobiotic) with anthozoans, including sea-anemones, soft corals, and scleractinians, on which they feed. While some snail species feed on solitary polyps, others are associated with colonial anthozoans, with exceptional cases of species able to swap between solitary and colonial hexacorals. For some coralliophiline species, significant impact of their trophic habits on coral reef communities has been demonstrated. While common in shallow waters, Coralliophilinae are better represented in the deep-water ecosystems, particularly in the mesophotic zone, but also in bathyal and abyssal habitats.

Methodology

The main objective of this project has been pursued through three tiers:

- 1 Improving the molecular phylogenies of the two gastropod lineages that were incomplete and mostly restricted to shallow water species.
- 2 Building an extensive dataset of gastropod-cnidarian associations, merging literature and new original data, obtained through a variety of methods including an ecological DNA-Barcoding approach through DNA amplification of gastropod stomach content and/or coral tissues.
- 3 Reconstructing the evolution of trophic ecology in corallivorous gastropods by identifying the ancestral coral hosts of major lineages.

For the first tier, I employed Sanger sequencing and Exon Capture strategy to construct robust phylogenies of the target families and conducted integrative taxonomy analyses to identify gastropod species.

For the second tier, I investigated gastropod/coral associations by integrating data available in the literature with new information obtained through morphological and/or molecular identification. Regarding the morphological aspect, the examination of polyp arrangement and distribution, as well as the calcareous skeleton when present, was employed. In the molecular part, coral tissue was amplified directly from the polyp or, in the absence of preserved host specimens, when the

entire body of the snail was available, the stomach and foregut were dissected and processed for the amplification of cnidarian DNA directly from the snail's digestive system using cnidarian primer sets.

For the third tier, various bioinformatic tools have been employed to reconstruct the evolution of host/parasite associations, highlighting shifts in snail/coral relationships over time.

The thesis is divided in three chapters.

In the **first chapter** I generated an extensive molecular dataset comprising sequences (Sanger methodology) of two mitochondrial (*cox1* and *16S* rDNA) and one nuclear gene (*28S* rDNA) from 524 ovulid specimens collected worldwide. Gastropod species were delimited employing an integrative taxonomy approach, combining expert morphological identification, molecular data thanks to the utilisation of the *cox1* dataset, and ecological data of association with cnidarians. Integrative taxonomy is defined as the science that aims to delimit the units of life's diversity from multiple and complementary perspectives (phylogeography, comparative morphology, population genetics, ecology, development, behaviour, etc.). The cytochrome c oxidase subunit I (*cox1*) gene is the main mitochondrial molecular marker playing a pivotal role in species delimitation research and is a crucial barcode sequence. Due to its robustness and reliability, this molecular marker has been accepted as the standard taxon barcode for most animals, including gastropods.

The coral hosts of the ovulid species have been identified by supplementing literature data with new records, employing morphological identification and/or molecular markers (the mitochondrial *16S* rDNA and *mtMSH*, and the nuclear *ITS2*).

Phylogenetic reconstruction, incorporating nine fossil calibration points, elucidated the evolutionary relationships among the gastropods. Once provided a robust species phylogeny, the evolutionary patterns across lineages were the next topic of my studies: diversification analysis across time and clades were conducted. The final step involved an ancestral state reconstruction analysis, by inferring the historical associations of ovulid lineages with cnidarian families or subclasses.

In **the second chapter**, an extensive molecular dataset of sequences (Sanger methodology) of 586 specimens of Coralliophilinae, was generated. These specimens, gathered globally from tropical, subtropical, and temperate regions, have been identified employing an integrative taxonomy approach. Molecular work involved DNA extraction, amplification, and sequencing of two mitochondrial (*cox1*, *16S*) and one nuclear (*ITS2*) markers. Cnidarian hosts were identified through an integrative approach, combining literature data with new records, employing morphological and/or molecular markers (the mitochondrial *16S* rDNA and the nuclear *ITS2*), and incorporating data from DNA barcoding of the snail stomach content. All the obtained cnidarian sequences were matched with sequences available in Genbank with the NCBI BLAST web interface. The study incorporated four fossil calibration points to estimate node ages on the phylogeny and diversification dynamics through time and clades. The final step involved an ancestral state reconstruction analysis, which inferred the coralliophiline phylogeny with depth range and the associated cnidarian families or orders.

In **chapter three** the hypotheses that arose in chapter one on possible new molecular based ovulids classifications, were validated, by applying an exon-capture strategy to target thousands of loci with Next-Generation Sequencing techniques. Samples were carefully selected to encompass genus-level diversity among lineages of egg-cowries based on integrative taxonomy results obtained in chapter one. Target exons were designed in the framework of a collaboration with the malacological research team of the Muséum National d'Histoire Naturelle, Paris (MNHN), aimed at reconstructing the phylogeny of the Neogastropoda by a large exon-capture dataset. Identification of the targeted exon involved using the chromosome-level and annotated genome of *Conus ventricosus* Gmelin, 1791 along with 15 transcriptomes from the GenBank and other MNHN team projects. Filtering and alignments yielded a final dataset of 1,125 exons represented by 9,429 sequences. Tree reconstruction resulted in the production of two datasets (NT, Nucleotide and AA, Amino acids) analysed in non-partitioned and partitioned (by codon position) approaches, yielding a total of four well supported phylogenetic trees.

Discussion

In this thesis I have investigated several aspects of the evolution of the trophic ecology of two target caenogastropod corallivorous lineages. Within marine invertebrates, these corallivorous gastropods provide exceptional tools to perform these studies, since their dietary specialisation and interactions with coral reefs offer a window into the complex dynamics of trophic relationships in marine ecosystems.

The **first chapter** uncovers fascinating insights into egg-cowries evolution. In this research the taxonomic coverage has been significantly broadened with respect to previous phylogenetic works. This study has revealed an unusual need for taxonomic lumping in ovulid diversity, at variance from the norm in gastropods. In particular, my findings have underscored the high variability in shell morphology in this group, severely weakening the usefulness of shell characters alone for the distinction of closely related species and even of some genera. Furthermore, the mantle colour patterns in Ovulidae exhibit high interspecific variability, primarily linked to coral associations rather than phylogenetic relationships. Out of the 36 nominal extant genera represented in our dataset (92% of the total recognised), eight (*Pedicularia*, *Ovula*, *Dentiovula*, *Diminovula*, *Margovula*, *Procalpurnus*, *Crenavolva*, and *Simnia*) were not monophyletic as traditionally conceived. Notably, three type genera of subfamilies (*Pedicularia*, *Ovula*, and *Simnia*) are unveiled as non-monophyletic, prompting a call for revisiting existing classifications, but not affecting the subfamily nomenclature. The seven lineages recognised as potentially worthy of subfamilial rank, demand a redefinition of the familial classification. Robust molecular evidence indicates that the Ovulidae originated and early diversification between 47 and 63 mya, according to fossil record data. The analysis of diversification rates shows a decrease early in the ovulid history persisting steadily until the present day. It is likely that during the earliest stages of the ovulid evolution, a higher diversification rate was due to the exploitation by the ovulids of cnidarians as a novel trophic resource; subsequently, the rate gradually declined in both lineages as time progressed. The associations between ovulids and cnidarians reveal a specialised parasite

behaviour, wherein, in the majority of cases, individuals of the same ovulid species feed on cnidarians belonging to the same family. My analysis results in a diversified framework at the subfamily level: while certain subfamilies display a clear pattern of specialisation (with usually a single family of cnidarian hosts), others exhibit a higher degree of dietary variance. The reconstruction of the ancestral associations and dietary shifts unveiled the dynamic evolutionary history of these gastropods. Two distinct hypotheses have emerged from my research: the ancestral coral hosts were the hydrocorals Hydroidolina (family Stylasteridae) or the scleractinians Hexacorallia. Further information about the coral host of genera with an ancient history (e.g. *Pseudocypraea*) is required for testing these hypotheses, both plausible, although we would favour an ancestral exploitation of shallow water hexacorals by the first egg-cowries that could have subsequently colonised deeper habitats following an onshore-offshore trend widely documented in marine fauna. In any case, it seems evident that the diversification of the Ovulidae has not been strictly coupled with cnidarian evolution (no pervasive co-evolutionary pattern). Indeed, all families within Octocorallia, Hexacorallia, and Hydroidolina originated significantly earlier than Ovulidae, with the most recent emergence occurring approximately 100 mya.

In the **second chapter** the coralliophiline taxonomic coverage has been increased to 46% of the accepted species and 77% of the accepted genera. Integrating morphospecies identification and genetic analysis, the study identified 123 molecular species among the samples initially ascribed to 111 morphospecies. Taxonomic analyses of Coralliophilinae revealed a contrasting trend compared to Ovulidae, as the majority of cases of morphological-molecular incongruence suggest an underestimation of actual species diversity, leading to the splitting of ten nominal species. I am inclined towards considering coralliophiline shell morphology as highly plastic probably in response to adaptive pressures, and therefore not suitable as an uncritical source of diagnostic features for supraspecific taxonomy, a pattern not unusual in gastropods. This molecular insight prompts a reevaluation of nominal species and hints at the prevalence of cryptic species complexes in molluscs. Moreover, phylogenetic results address issues concerning the polyphyly of accepted genera within the dataset. Six out of ten accepted genera are not monophyletic as traditionally conceived, raising questions about the existing coralliophiline systematics. The time-calibrated phylogeny shed light on the evolutionary history of Coralliophilinae, pinpointing the origin around 41-43 million years ago. Diversification rates showed an initial burst of diversification followed by a steady decline, echoing patterns observed in other corallivorous gastropod lineages. Similarly to Ovulidae (chapter one), this study proposes a link between the initial burst of diversification and the exploitation of cnidarians as a novel trophic resource. My research supports the hypothesis of multiple shifts from shallow to deep habitats, while the exploration of Coralliophilinae's association with cnidarians reveals a predominantly specialised parasitic behaviour. Coralliophilinae exhibit a feeding behaviour on various cnidarian families that belong to five orders within the subclasses Hexacorallia and Octocorallia. In the majority of cases, individuals of the same coralliophiline species feed on cnidarians belonging to a single family, with a few documented exceptions where a single gastropod species feeds on corals of two or more different families. The ancestral state reconstruction identified the scleractinian family Pocilloporidae as the most probable ancestral host, persisting nowadays in the *Galeropsis monodontus* complex. The

association with Scleractinia, started between 23-42 mya, remains stable until present day, with few major shifts, suggesting that ecological factors play a significant role in host selection. It emerged that the ancestral lineages of Coralliophilinae have evolved by feeding on shallow water Scleractinia, and then, repeated colonisations of deep water habitats occurred in several lineages. The evolutionary trajectories of Coralliophilinae, like those of Ovulidae, suggest adaptation to contingent ecological circumstances rather than strict phylogenetic coevolution. As the diversification of cnidarian orders predates that of Coralliophilinae, this study challenges the concept of strict co-evolution. Instead, it proposes a pattern of sequential evolution, aligning with the findings observed for Ovulidae in chapter one.

Chapter three aimed to test the phylogenetic hypotheses presented in chapter one, impacting the subfamily systematics of the Ovulidae family. The results enabled a comprehensive exploration of the taxonomic implications arising from an exhaustive phylogenetic analysis. By utilizing exon-capture data, the study not only challenged the current taxonomic classification by revealing non-monophyly in four genera (as indicated in chapter one results) but also uncovered conflicts with existing taxonomic arrangements. The evaluation of key hypotheses led to proposed substantial revisions, including the redefinition of subfamilies and the incorporation of genera within them. In particular, I have found no major evidence in support of the proposal recent classification to classify Pedicularia and allied in a distinct family Pediculariidae. Moreover, the results suggested that Ovulidae comprises five subfamily-level lineages characterized by tropical and subtropical distribution and a wide depth range. Additionally, it became evident that five species (*Ovula isibashii*, *Naviculavova kurziana*, *Hiatavolva depressa*, *Contrasimnia xantochila*, and *C. formosana*) require a new subfamilial reclassification within the subfamily Prionovolvinæ.

Utilising the exon capture strategy to augment the volume of molecular data, represents a notable enhancement in refining the phylogenetic analysis of Ovulidae. Almost all the deepest nodes in the trees are strongly supported. This outcome conclusively highlighted that ovulid shell and mantle inadequately serve as reliable for systematics. Consequently, any hypotheses regarding the group's evolution should be formulated and validated within a robust molecular phylogenetic framework.

Conclusion

The research presents a complex perspective on the phylogenetic patterns within two gastropod lineages, challenging established morphology-based taxonomy and prompting a reconsideration of the reliability of molecular phylogenetic approaches. With my research I have confirmed the crucial role of an integrative taxonomy approach in evolutionary studies, especially when morphological diagnostic characters identified until now are, for several reasons, not reliable. This is demonstrated by the primary challenge in this work, which was the identification of species, bearing on both molluscs and corals. Indeed, the study reveals a more diverse landscape within the Ovulidae and Coralliophilinae than was previously recognized, regarding not only species delimitation but also the classification of genera and subfamilies. Moreover, results about the coral-gastropod associations underlined how much our knowledge about host-parasite associations in marine environments are limited and stressed the power of molecular tools in

trophic ecology analyses. From trophic ecology aspects, the study showcases the remarkable adaptability and specialization of gastropod species over time, particularly in exploiting diverse ecological niches. Contrary to expectations, our findings do not support the existence of widespread co-evolutionary processes between two lineages of corallivorous gastropods and their cnidarian hosts. Instead, the results reveal a pattern characterized by multiple unrelated switches from one cnidarian family to another, resembling an association by colonization, where a parasite evolves with one host species and then transitions to another. The exploited evolution of all the families of Octocorallia, Hexacorallia, and Hydroidolina predate Ovulidae and Coralliophilinae significantly. Consequently, the origin and diversification of Ovulidae and Coralliophilinae appear unrelated to cnidarian evolution, indicating an absence of a pervasive host-parasite co-evolutionary pattern. The evolutionary trajectories of both gastropod lineages align more with a pattern of sequential evolution, where the host's evolution influences the parasite, as seen in certain associations of phytophagous insects. The exploitation of coral niches represents an ecological opportunity that might have driven the evolution and diversification of corallivorous snails without significantly impacting cnidarian evolution. This intricate interplay between ancestral associations and modern diversification underscores the complexity of gastropod evolution and host interactions. While patterns of co-evolutionary processes within specific lineages are not ruled out, their detection would necessitate denser sampling and finer taxonomic identification of cnidarian hosts, potentially at the genus or species level. In conclusion, the comprehensive methodological approach employed in this thesis, spanning specimen collection, molecular techniques, taxonomic validation, and macroevolutionary analyses, establishes a robust framework for exploring the evolution and trophic ecology of corallivorous gastropods. This research sheds light on their adaptation to cnidarian hosts and contributes valuable insights to broader patterns of marine biodiversity. Understanding how host-parasite interaction mechanisms operate within coral reef ecosystems is a crucial first step in predicting how both gastropods and corals might respond to global environmental changes, such as ocean warming and acidification, which pose threats to their stability and resilience.