Thermal Response of Metabolic Rates, Feeding and Growth in the corallivorous gastropod *Drupella* spp.

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Abstract The corallivorous gastropod genus *Drupella* is known for causing large amounts of damage across Indo-Pacific reefs, yet little is known about the genus's thermal sensitivity, limiting our ability to predict how ocean warming will affect the impact of *Drupella* on reefs. Combining physiological and behavioural experimentation, the current study investigated the thermal response of metabolic rate, feeding, and growth of *Drupella* spp. Snails collected off the coast of Moorea, French Polynesia, were held in the laboratory at one of four temperature treatments: 28 °C (annual mean), 30 °C, 32 °C (annual maximum in 2021), and 34 °C (+2 °C warming scenario, SSP2-4.5). Using intermittent flow respirometry, metabolic rates were estimated under both acute ramping and prolonged thermal exposure. During acute thermal ramping, *Drupella* spp. acclimated at 28 °C and 34 °C were exposed to a rapid temperature increase from 29–38 °C. Temperature was increased in 1 °C increments over 30 minutes, followed by a 30-minute measurement period at each temperature. Metabolic rate increased consistently across the thermal range tested, indicating that *Drupella* spp. can tolerate high short-term temperature changes, at least under well-oxygenated laboratory conditions. In prolonged exposure, both standard metabolic rate (SMR) and routine metabolic rate (RMR) increased between 28 and 32 °C for all acclimation durations. After three days of acclimation, SMR and RMR increased between 28–32 °C by 67.3% and 39.3% respectively, but then both declined by ~30% at 34 °C, indicating metabolic suppression beyond a thermal optimum. In contrast, snails acclimated for 19–23 days showed lower increases, with SMR and RMR rising between 28–32 °C by 26.9% and 19.1% respectively, and no suppression after 32 °C. These results demonstrate that *Drupella* spp. can thermally acclimate, particularly in RMR, which was significantly higher at 34 °C after longer-term acclimation compared to shorter-term. The same trend was observed in SMR, however this was not statistically significant. Unlike metabolic rate, feeding and growth showed no significant effects of temperature and did not increase with metabolic demands. Although this suggests that feeding and growth may not simply rise with warming; both remained unchanged compared to lower temperatures, indicating that *Drupella* spp. can sustain functional performance at elevated temperatures. The combined ability to withstand acute warming up to at least 38 °C, show signs of thermal acclimation, and maintain feeding and growth under elevated temperatures, suggests high thermal resilience in *Drupella* spp. Thermal resilience in the corallivorous snails raises concerns that corallivory may continue during periods of reef thermal stress, when corals themselves are less resilient to damage.

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Author's declaration

I declare that, except where explicit reference is made to the contribution of others, that this dissertation is the result of my own work and has not been submitted for any other degree at the University of Glasgow or any other institution.

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Abbreviations

SMR	Standard Metabolic Rate
RMR	Resting Metabolic Rate
MMR	Maximum Metabolic Rate
AS	Aerobic Scope
COTS	Crown-of Thorns
spp.	species pluralis (multiple species)
ATP	Adenosine Triphosphate

1 Introduction

1.1 Temperature as a Driver of Ectotherm Metabolism and Ecology

Anthropogenic climate change is increasingly impacting ecological systems, with shifts in abiotic conditions driving behavioural and physiological changes in organisms, which can have cascading effects throughout ecosystems. Consequently, there has been a rise in research focused on understanding and predicting organismal response to environmental change (Azra et al., 2022; Dillon et al., 2010; Harvey et al., 2020; Islam, Kunzmann & Slater, 2021). Temperature is considered the most important abiotic factor affecting ectotherms, whose body temperatures, and thus physiological processes, are primarily determined by external environmental conditions (Kern, Camp & Franklin, 2015; Paaijmans et al., 2013; Schulte, 2015) Even slight thermal changes can influence ectothermic metabolism, behaviour, and performance, ultimately causing changes in species distribution, phenology, and food web structures (Amarasekare, 2024; Gibert, 2019; Paaijmans et al., 2013). For example, increased temperatures can alter activity levels, feeding rates, predator avoidance strategies, and reproductive behaviours including spawning timing and mate selection (Jansen & Gislason, 2011; Li, Rodriguez-Muñoz & Tregenza, 2025). Thermal changes in behaviour and performance can, in turn, affect the physiological pathways themselves, highlighting the complexity of these relationships (Farrell, 2007; Verberk et al., 2016). Given the temperature dependence of physiological functions and their cascading impacts, as well as the increasing concern surrounding the consequences of climate change, there has been a particular increase in studies investigating the influence of changing temperature on ectotherm physiology and behaviour (Islam, Kunzmann & Slater, 2021; Kordas et al., 2022; Minuti et al., 2021).

Metabolism is defined as the totality of chemical processes within a living organism, and collectively supports functions such as survival, growth, and reproduction. In ectotherms, metabolic reactions major physiological pathways which are influenced by temperature (Clarke & Fraser, 2004; Huey & Kingsolver, 2019; Schulte, 2015). Metabolic pathways depend on enzymes to catalyse reactions by lowering their activation energy (Feller, 2010). As temperatures rise, increased kinetic energy results in increased molecular motion and diffusion, resulting in

enzymes and substrates colliding more frequently and enzyme-substrate complexes forming more rapidly. Higher temperatures also increase the percentage of collisions that are energetic enough to reach a transition state, where bonds in the substrate(s) are broken or formed to create the product(s) (Schulte, 2015). This increases the catalytic turnover rate and accelerates the overall rate of metabolic reactions consistent with the Arrhenius relationship, which describes the exponential effect of temperature on reaction rates in relation to the probability of molecules surpassing activation energy (Arrhenius ,1889). However, in biological systems, the increasing metabolic reaction does not always rise as predicted by Arrhenius, but also is affected by protein stability, enzyme-substrate binding, and high-level processes, including membrane interactions (Clarke & Fraser, 2004; Feller, 2010; Schulte, 2015). Within the catalytic cycle, temperature can therefore increase multiple steps simultaneously, including the encounter and binding of the enzyme and substrate, the chemical conversion during the transition state, and, in some systems, the release of the product. This increases the likelihood that activation energies will be surpassed, and the reaction will continue.

Temperature-driven acceleration of enzyme-catalysed reactions only occurs up to a species-specific thermal optimum, with most enzymes having a curved temperature activity relationship, where efficiency declines even before protein denaturation (Feller, 2010; Schulte, 2015). This decline is caused by changes in protein motions and active-site organisation that alter the efficiency of enzyme catalysis, rather than being attributed solely to denaturation. As temperatures rise, enzymes show wider ranges of conformation, which can reduce the tightness of the active site and result in less effectively stabilised transition states. This lowers the probability that an enzyme substrate-complex will cross the transition state, decreasing catalytic efficiency even before denaturation (Somero,2004; Daniel & Danson, 2010). Overall, this explains why warming increases enzyme-catalysed metabolism up until a certain thermal optimum, whereafter further increases constrain pathways.

As temperature rises, cellular respiration accelerates, increasing oxygen demands as organisms need to meet elevated aerobic energy needs (Clarke, 2004; Pörtner, 2002; Schulte, 2015). Oxygen requirements come from the increase in enzyme activity as well as the knock-on effect when an organism uses elevated physiological rates to increase routine behaviours, further

elevating oxygen demand. To meet this rise in oxygen demand, organisms may increase ventilation and circulation to deliver more oxygen to tissues, however several constraints can limit this capacity (Porter, 2001). Biophysical constraints include geometric factors including the finite surface area available for gas exchange, which can limit respiratory structures' ability to increase oxygen uptake enough to meet demand (Rubalcaba et al., 2020). Temperature-induced changes in membrane fluidity further limit function by destabilising interactions between proteins and lipids as well as increasing proton leak across mitochondrial membranes, which all can cause issues for metabolic reactions (Clarke & Fraser, 2004; Murata & Los, 1997). At higher levels of organisation, these molecular and biophysical constraints can limit physiological systems. For example, when temperatures get too high, circulatory and respiratory systems may not be capable of delivering sufficient oxygen to meet increased metabolic demands, particularly in aquatic organisms, where oxygen availability decreases with warming (Clarke & Fraser, 2004). Taken together these constraints can define boundaries of temperature dependent physiological performance and set thermal tolerance limits. If those thermal limits are surpassed, cellular processes will start to fail, causing a cascade of dysfunction across multiple levels of organisation. For example, disruption of enzyme activity and mitochondrial function reduces ATP production, thus reducing the energy supply needed for essential processes (Schulte, 2015). At the same time, if oxygen delivery becomes insufficient to meet increasing demands, organisms may be forced to rely on anaerobic metabolism, which leads to acidosis and accumulation of toxic byproducts. These failures, therefore, can impact a range of eco-physiological processes such as growth, reproduction and behaviour. Ultimately, once a critical thermal maximum is reached, homeostasis can no longer be maintained, leading to mortality. For example, zebrafish typically reach a critical thermal maximum of around 41°C, at which they lose equilibrium; if not returned to cooler water, exposure above this temperature significantly increases the mortality risk (Morgan, Finnoen & Jutfelt, 2018). Variation in thermal thresholds has been seen across ectothermic taxa, demonstrating how the interaction of molecular instability, biophysical constraints, and oxygen supply limitation influences the vulnerability of organisms to rising temperatures.

In recent years, there has been a growing interest in how environmental temperatures affect metabolic processes, the resulting implications for other physiological and life-history traits, and

the role of acclimation in mitigating adverse effects (Chen et al., 2021; Hoefnagel & Verberk, 2017; Silva-Garay & Lowe, 2021).Three widely used indicators of metabolic function in ectotherms are standard metabolic rate (SMR), routine metabolic rate (RMR) and maximum metabolic rate (MMR) (Chabot et al., 2016; Killen et al., 2021). SMR represents the baseline energy requirement of a resting, post-absorptive organism, while RMR includes energy spent on spontaneous activity (Chabot et al., 2016). MMR represents the maximum rate of oxygen consumption an organism can achieve to fuel ATP production aerobically (Norin & Clark, 2016). The difference between MMR and SMR is used to estimate an organism's aerobic scope (AS), which represents the metabolic rate available to an organism above maintenance levels (Clark et al., 2013). SMR, RMR, MMR and AS are all are used to investigate physiological responses to environmental conditions and are associated with life-history traits such as growth and energy allocation (Ohlberger et al., 2011; (Chabot et al., 2016). However, rather than metabolic traits simply determining life-history traits, they are thought to have evolved to meet the energetic demands required to complete an organism's life history, consistent with the principle of symmorphosis, which proposes that metabolic and oxygen-supply systems evolved to match, rather than exceed, energetic requirements (Weibel, Taylor & Hoppeler, 1991).

In ectotherms, metabolic rate scales with body mass due to larger organisms having more biomass that must be maintained, increasing their total energetic demand. At the same time, mass-specific metabolic rate declines with size because internal exchange and transport systems do not scale directly proportionally to body volume. Therefore, each gram of tissue in a large ectotherm uses less energy than in a smaller one, producing the well-studied allometric scaling of metabolism (Brown et al., 2004). However, this relationship between body mass and metabolic rate is complicated, and can be influenced by temperature (Killen et al., 2010). Warming raises oxygen demand faster than supply, causing aerobic scope to decline more strongly in larger aquatic organisms (Rubalcaba et al., 2020). Rubalcaba et al. (2020) showed that these size effects arise because oxygen delivery systems, including gills and circulation, cannot scale their supply capacity fast enough to match increasing metabolic demand in warm water. As temperatures rise, metabolic level increases while the body-mass scaling exponent becomes smaller, meaning metabolism may scale less steeply with size under warmer conditions. Studies have shown that larger individuals have smaller proportional increases in metabolic rate with warming than

smaller ones, reflecting these supply limitations rather than reduced thermal sensitivity (Killen et al., 2010; Kordas et al., 2022. Therefore, it is important that when considering the influence of body mass on metabolic rate at different temperatures, as the with the magnitude of this interaction will depend on oxygen-supply constraints and differ across taxa and environments (Killen et al., 2010).

1.2 Thermal Acclimation and Climate Resilience in Ectotherms

When temperature rises above an organism's threshold at which they can no longer meet metabolic demands, physiological processes may start to break down, reducing performance and compromising survival, growth, reproduction and maintenance (Portner, Bock & Mark, 2017; Tattersall et al., 2012). To cope with challenges posed by thermal stress, many ectotherms exhibit physiological acclimation. Acclimation is a reversible form of phenotypic plasticity that allows organisms to adjust physiological systems to changing environmental conditions, including metabolism, cardiovascular function, and neural activity (Lagerspetz, 2006; Rohr et al., 2018; Sandblom et al., 2014; Zhu et al., 2022). When environmental change effects homeostasis, organisms may respond by acclimating which involves adjusting their physiological processes to regulate biological functions, reduce waste and cellular damage, or preserve energy (Hardison et al., 2023). Acclimation involves mechanisms used to maintain ATP production and overall function which include enzyme regulation, restructuring of organs, and mitochondrial adjustments (Duan et al., 2024; Levet et al., 2025; Sollid, Weber & Nilsson, 2005; Voituron et al., 2021). For example, crucain carp and goldfish have been seen to show reversible gill plasticity when exposed to hypoxia or high temperature, gill surface area is increased through induced apoptosis and suppressed mitosis in the intracellular cell mass causing the lamellae to protrude (Sollid & Nilsson, 2006).

The capacity for thermal acclimation varies across species and individuals and has received growing research attention in the past years as a key aspect in determining resilience to climate change (Shah, Funk & Ghalambor, 2017; Stillman, 2003). Acclimation ability has been seen to be influenced by numerous factors including latitude, body mass and methodological factors (Allen et al., 2016; Rohr et al., 2018; Somero, 2010). For instance, organisms that live in areas of high temperature variability such as temperate zones, are thought to have evolved to select for

greater acclimation abilities than those inhabiting areas with little temperature variability (Allen et al., 2016; Rohr et al., 2018). Additionally, smaller organisms have been seen to have faster but overall lower acclimation abilities than larger animals (Rohr et al., 2018). These differences in acclimation capacity can influence an organisms thermal range and can determine which species are most resilient to climate change. Variation can even be seen interspecifically, for example, a study on brook trout populations saw variance in upper thermal tolerance and acclimation abilities between populations (Stitt et al., 2013). In a world of global climate change, low acclimation abilities is a documented cause of mortality driven population declines. Differences in acclimation between species has also been seen to disrupt ecological interactions (Rohr et al., 2018). This exemplifies the importance in researching species acclimation to understand how they may cope with ongoing environmental change, and the knock-on effects this may cause in community structure. Although thermal acclimation has been well studied there are significant knowledge gaps remain regarding how numerous species adapt to temperature fluctuations, with taxonomic and geographic biases remaining (De Bonville et al., 2025). Certain groups, such as fishes, have received disproportionately more attention, while many others remain poorly studied (Bennett et al., 2018; Seebacher, White & Franklin, 2015). Research has been disproportionately concentrated in well studied areas including North America, Europe, and parts of Australia, while a lot of other tropical, polar and freshwater areas remain comparatively underrepresented (White et al., 2021).

1.3 Acute and Longer-term Responses to Thermal Stress

In addition to raising global mean temperatures, climate change is altering temperature variability across multiple temporal scales, including acute, diurnal and annual scales (Kefford et al., 2022). To understand organisms' thermal acclimatory abilities, it is important to investigate both short term and more sustained, longer term, thermal acclimation. Due to changing global temperatures, organisms are undergoing gradual shifts in temperature (Johansen et al., 2021). The timing of thermal acclimation differs in various physiological processes, and also between species, some responses take a few days, while others take weeks to fully stabilise. For example, tropical coral reef fishes exposed to a +3 °C warming showed variations in the timings of different physiological adjustments (Johansen et al., 2021). In the first week, shifts were

primarily associated with stress responses in the blood and gills. For instance, in the first week, *Caesio cuning,* a marine ray-finned fusilier fish*,* increased blood glucose levels, likely enhancing energy delivery, which supports aerobic oxidative phosphorylation and allows for improved performance.

Additionally, in the first week, *C.cuning* showed increases in gill lamellar width, improving capacity for oxygen transport. Between weeks two and three, there were changes in the gills, and the lamellar perimeter increased. Following five weeks at high temperatures, the concentration of haemoglobin in the spleen was still increasing, showing that the oxygen transport within the species was still adjusting (Johansen et al., 2021). Therefore, it is important for studies to consider acclimation time and choose a duration which is sufficient for recording responses when studying thermal acclimation.

In addition to long-term thermal change, due to climate change, organisms are increasingly being exposed to more short-term, acute fluctuations in temperature. Marine heatwaves are emerging as the principal threat to coral reefs though driving coral bleaching, characterised by rapid warming in the upper ocean caused by a range of factors including large scale atmospheric pressure anomalies (Holbrook et al., 2019). Marine heatwaves are defined as periods when sea temperature exceeds a seasonally varying 90th percentile threshold for more than five consecutive days, with most heatwaves typically lasting between 10 and 30 days (Wang & Yao, 2025). Heatwaves are increasing in both frequency and severity, showing the importance in understanding how organisms will respond to these faster intense temperature rises (Holbrook et al., 2019). Numerous studies using short-term acute heat stress studies to investigate how heatwaves may influence marine ectotherms (Marzonie et al., 2022; Lang et al., 2021). Another reason it is important to understand more rapid responses to temperature change is the increasing diel temperature variability due to climate change. For instance, air temperatures have been estimated to have increased by up to 1.4°C in polar regions and 1.0°C in temperate regions between 1975 and 2013 (Wang & Dillon, 2014). It has also been recorded that shallow aquatic habitats sometimes exhibit even larger diel shifts than their surrounding air (Kefford et al., 2022; Marchant et al., 2011; Wang & Dillon, 2014). Even if an organism is functioning within its usual tolerance levels, rapid temperature changes can lead to metabolic disruptions, the breakdown of homeostasis, and damage to tissues due to the lack of compensatory biological acclimation

(Tattersall et al., 2012). Therefore, assessing the acute effects of temperature along with the potential long acclimation times is important for predicting a species' survival and for conservation efforts related to climate change. (Schulte, 2015; Somero, 2015).

Temperature's effect on metabolism has been well studied, increasing our knowledge of environmental change influence on organisms (Kordas et al., 2022; Marshall & Mcquaid, 2020). In aquatic gastropods, thermal sensitivity has been relatively well studied in intertidal species, whereas sublittoral species have received considerably less attention (Diederich & Pechenik, 2013). One key example is the coral-eating snail, *Drupella* spp. Increasing temperatures from climate change and an increase in corallivore numbers are two of the greatest threats faced by coral reef ecosystems, and numerous studies have focused on the consequences of these threats as well as their synergistic effects (Lang et al., 2021; Sully, Hodgson & van Woesik, 2022; Thirukanthan et al., 2023). However, less is known about how rising temperatures specifically affect the physiology and behaviour of key coral predators like *Drupella* spp.

1.4 Thermal Sensitivity and Acclimation in Coral Reef Ecosystems

The extent to which organisms tolerate and acclimate to temperature changes is often impacted by the thermal variability of their environment (Tatersall et al., 2012). Ecosystems differ in the amount of thermal fluctuation they experience which can cause influence to the thermal plasticity of species. Organisms which live in variable temperate environments tend to have higher acclimatory capacities than those that live in stable conditions (Somero, 2010). For example, coral reef ecosystems are relatively thermally stable and thus tend to be dominated by stenothermal organisms that have evolved under historically consistent thermal environments often resulting in narrow thermal optimal ranges and limited acclimation potential (Johnasen et al., 2021; Sunday et al., 2011; Tewksbury, Huey & Deutsch, 2008). Such limited plasticity may heighten the vulnerability of reef-associated species to climate change when their thermal tolerance is low, especially those which are sedentary or sessile that cannot easily escape thermal stress. As sea temperatures continue to rise and marine heatwaves become more frequent, coral reefs are experiencing increasing thermal stress which highlights the importance of understanding the physiological responses of reef organisms to temperature change (Fordyce et al., 2019; Sully, Hodgson & van Woesik). While research on thermal tolerance of tropical reef

fishes has expanded in recent years, revealing species-specific differences, comparatively little is known about the thermal physiology of reef invertebrates (Donelson et al., 2012; Johnasen et al., 2021; Nilsson, Östlund-Nilsson & Munday, 2010).

1.5 Thermal Sensitivity and Knowledge Gaps in a Key Corallivore *Drupella* spp.

One marine invertebrate that plays a key role in coral reef health, but whose thermal physiology remains understudied is the gastropod genus *Drupella*. *Drupella* spp. feed on live coral tissue and are found throughout the Indo-Pacific. These snails have been associated with severe reef degradation; for example, they caused a 35% decline in coral cover in Toga Bay, Japan, and up to an 86% decline on Ningaloo Reef, Australia (Turner, 1994; Ayling & Ayling, 1987). Despite their ability to cause severe damage to coral reefs, their physiology remains poorly understood, with no studies to date investigating their metabolic rate. Whilst field observations in Hong Kong have shown that *Drupella* spp. survive seasonal temperature fluctuations from 14 °C in winter to 33 °C in summer, there has been limited research examining sublethal effects of temperature on metabolism, growth, or behaviour. Laboratory studies examining thermal effects on *Drupella* spp. have been limited to small-scale behavioural trials, without formal assessment of thermal performance (Tsang & Ang, 2019). Studying *Drupella* spp. metabolic rate, as well as how factors such as temperature and body size influence metabolism, could provide valuable insights into feeding rates and ecological impact. Such knowledge would help explain how environmental conditions influence *Drupella* spp. damage capabilities on coral communities, especially under warming scenarios where coral is already more vulnerable (Guan et al., 2020; McLeod et al., 2010).

Along with *Drupella* spp., Crown-of-Thorns Starfish (*Acanthaster* spp., or COTS) are among the most damaging corallivores, capable of causing significant coral loss during population outbreaks. Unlike *Drupella* spp., whose thermal physiology has received few studies, COTS physiology has been the focus of many studies. Temperature effects on COTS growth, metabolism, movement, and larval development are well documented, and this knowledge has been used to inform predictive population models (Lamare et al., 2014; Lang et al., 2021; Lang et al., 2022). Establishing a comparable understanding of *Drupella* spp. thermal sensitivity and acclimation capacity is important, not only to understand better how they will respond to changing temperatures, but also to support comparisons between *Drupella* spp. and COTS to aid corallivore management. However, it is important to note that whilst COTS provide a useful

point of comparison due to the amount of research available, comparisons between starfish and *Drupella* spp. must be made cautiously. The two groups differ fundamentally in physiology, including locomotion (water vascular system and tube foot vs. muscular foot) and feeding mechanisms (external digestion via an eversible stomach vs. a rasping radula (Deaker & Byrne, 2006; Dennis et al., 2021; Morton, Blackmore & Kwok, 2001; Pratchett et al., 2017). Therefore, COTS studies cannot be used to predict how *Drupella* spp. will respond to temperature, but comparing the two taxa can still provide useful ecological context by highlighting how the two corallivores may contribute to reef degradation under warming conditions.

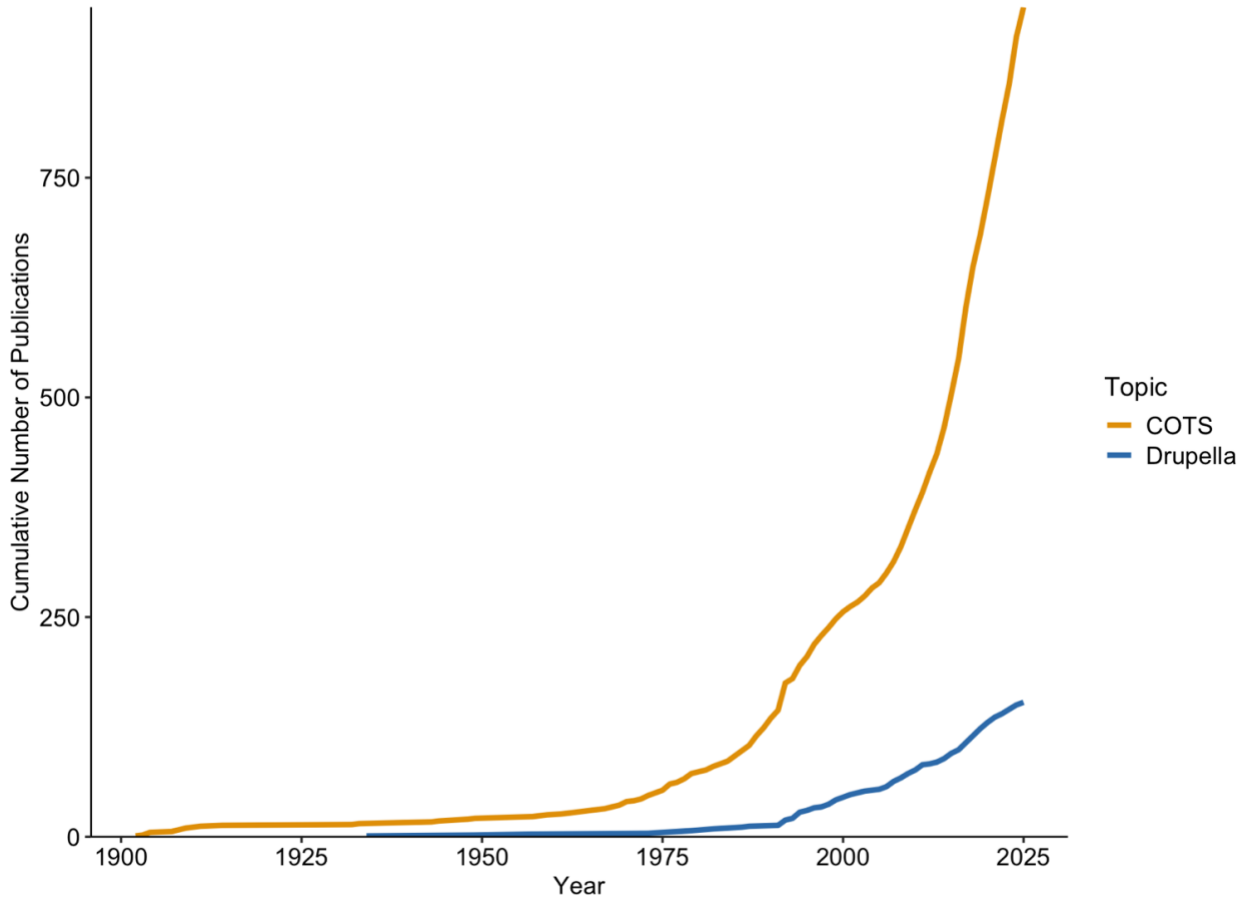

Figure 1.1 Cumulative frequency of Web of Science Core Collection papers on Crown-of-Thorns Starfish (*Acanthaster* spp.) and *Drupella* spp. published per year from 1902 to 2025. Plot shows the results from Web of Science Core Collection search for both genera, giving 944 papers on Crown-of-Thorns and 153 papers on *Drupella* spp.

Figure 1.2 Distributions of *Drupella* spp. studies across countries. The size of green dots indicates the count of published papers which focus on *Drupella* spp. in each respective country. Numbers under dots specify the number of publications per location. Dots do not represent specific locations of the studies, just the country of study.

1.6 Trends in *Drupella* spp. Literature and Research Gaps

Drupella (Thiele in 1925), recognised as a distinct genus within the family Muricidae, was defined by its corallivory and the shape of its radula compared to other Muricidae (Thiele, 1925; Fujioka, 1982, 1984). The radula of *Drupella* spp. is long with reed-like later teeth that are forked or denticulate at the tip. After discovery, a small number of studies were published in the following years (Arakawa, 1957; Cernohorsky, 1969; Taylor, 1978). Nevertheless, it was not until 1982 that the first account of *Drupella* spp. causing severe damage to a reef was recorded in Miyake-Jima, Japan, which led to growing research about the genus (Moyer et al., 1982). Since 1982, a range of studies have been conducted on the genus across the Indo-Pacific, with papers discussing *Drupella* spp. populations in Australia, Hong Kong, Thailand, the Maldives, the Red Sea, and more (Ayling & Ayling, 1987; Bruckner et al., 2017; Morton, Blackmore & Kwok, 2002; Scott et al., 2017) (Fig. 1.1 & Fig. 1.2). The majority of *Drupella* spp. studies are conducted in the field, focusing on either population dynamics, spatial distribution, and/or prey preference (Baird, 1999; Boneka, 2013; Cumming, 1999; Lei et al., 2022; Scott et al., 2017). Fewer laboratory studies have looked at prey attractants, development, and genetics (Al-Horani et al., 2011; Claremount et al., 2011; Morton et al., 2002). When compared to the research on COTS, considerably more studies have been conducted on the starfish than the snail (Fig 1.1). Therefore, reef management may be disproportionally focused on COTS, as we know a lot more about their biology, ecology, and outbreaks. *Drupella* spp., on the other hand, are under-recognised and this may affect our ability to model and predict damage from them on to reefs. The reason that research may be focused more on COTS may be partly because they are more widely recognised as major drivers of rapid reef loss; however, no studies have directly compared the relative damage caused by COTS and *Drupella* spp. While an individual COTS consumes more coral, *Drupella* spp. can reach very high densities during outbreaks, leading to substantial cumulative damage. Therefore, it is important that research on *Drupella* spp. is also prioritised.

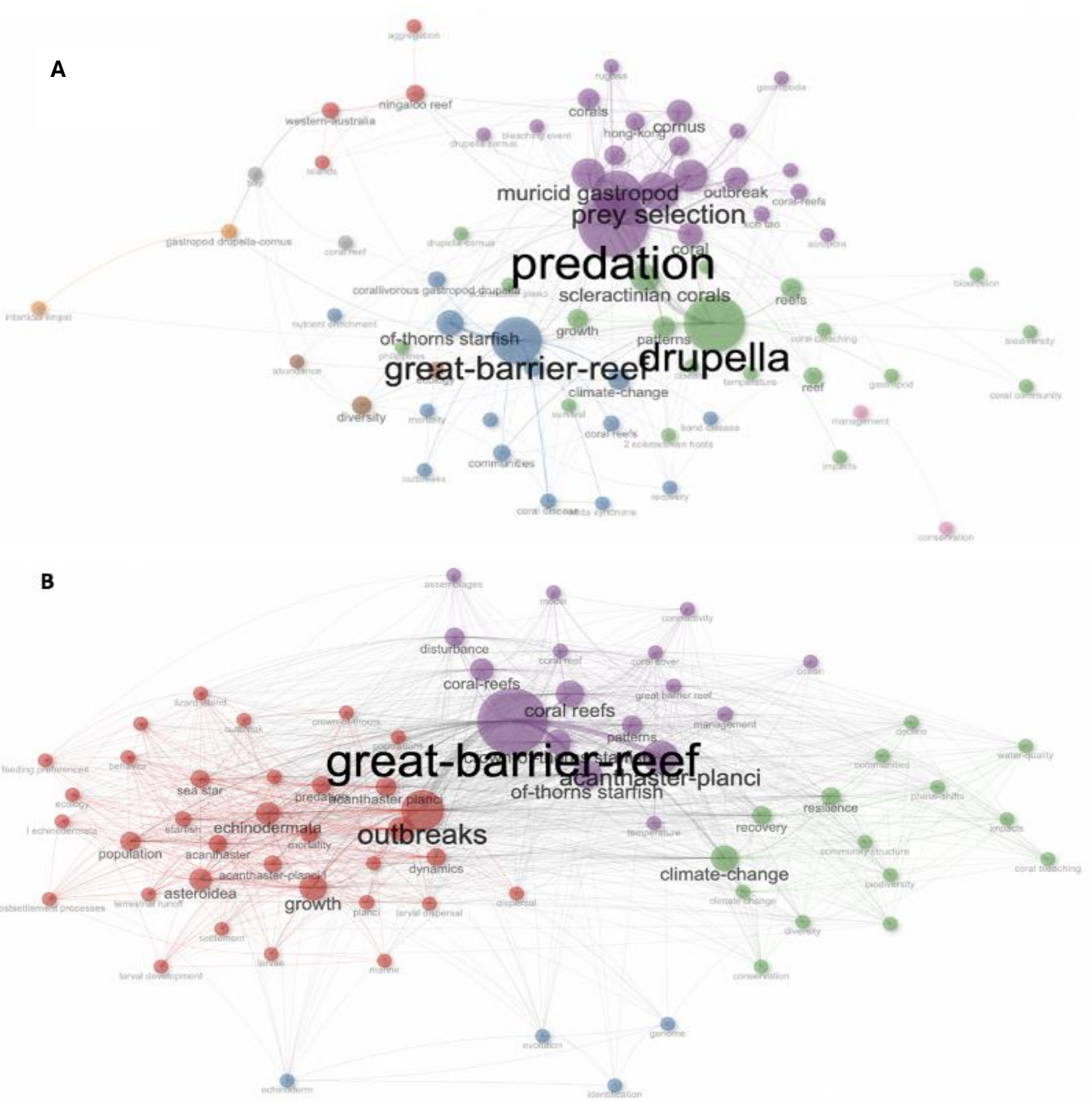

Figure 1.3 Keyword co-occurrence network of related literature on (A) *Drupella* spp. and (B) Crown of Thorns. Created in Biblioshiny (Bibliometrix R package) from the Web of Science Core Collection (74 documents for *Drupella* spp. and 510 for Crown of Thorns). The network is based on Keyword Plus terms, which are generated algorithmically by Web of Science from frequently appearing

words/ phrases in the titles of an article's cited references. Nodes represent top 70 keywords, with node size being proportional to keyword frequency. Lines connect keywords when they appear together in at least two documents, placing frequently co-occurring terms closer together terms which do not co-occur further apart. Line thickness reflects the strength of co-occurrence, how many documents contain both keywords.

A keyword co-occurrence network of *Drupella* spp. literature (Fig. 1.3) illustrates the fragmented state of the current research available on these snails. The network shows no prominent terms relating to physiology, thermal tolerance, acclimation or metabolic processes. Despite their ecological relevance, terms associated with temperature change, climate impact, or environmental shifts are absent. Not having these terms in the papers on *Drupella* spp. suggests that research is yet to address how these organisms respond to environmental stressors, indicating key gaps in understanding their resilience under changing ocean conditions. Additionally, clusters are weakly connected and thematically inconsistent, suggesting sparsity and fragmentation in the research rather than an integrated understanding of the gastropods. Strong geographic bias is evident, with location-based keywords poorly linked across the clusters, for example, "Koh Tao," "Great Barrier Reef," and "Philippines" occur in entirely different clusters with few or no connections between them. Methodological diversity is also limited, with almost all keywords being ecological descriptors (e.g. predation, aggregation), or geographic location, with no keywords referring to experimental techniques or analytical tools such as laboratory experiments or modelling. Overall, the network suggests that *Drupella* spp. research is still in its early stages with key gaps in their understanding. By contrast, the COTS network (Fig. 1.3,b) is much denser and thematically diverse when compared to the *Drupella* spp. network, with a higher number of connections between terms suggesting more integrated and developed research. Clusters are larger, more cohesively interconnected and span more themes including population dynamics, larval ecology and climate resilience. The contrast between the two networks illustrates the relative immaturity of *Drupella* spp. research compared to that on COTS, particularly with respect to climate resilience and physiology while highlighting the breadth and applied focus of crown-of-thorns studies.

One topic that is often discussed in *Drupella* spp. research, but not well understood or defined, is the occurrence of *Drupella* spp. population 'outbreaks'. Many studies have reported occurrences

of population outbreaks, with suggested causes including overfishing of predators, elevated temperatures, and eutrophication (Cumming, 2009; McClanahan, 1989). Despite these hypotheses, the confirmed drivers of such outbreaks remain uncertain, and the mechanisms of interactions between corallivory and anthropogenic stressors are still not well understood (Boucher, 1986; Rice et al., 2019). A key difficulty in research regarding outbreak causes is due to the ambiguity of what an outbreak consists of. Terms such as high density, aggregation, and outbreak are often interchanged and confused, and clear definitions of each in the literature would benefit future research. High density refers only to the number of individuals in a given area, whereas aggregation describes the behaviour of individuals clustering together on a particular coral colony (Bruckner et al., 2017). *Drupella* spp. may form aggregations that could lead to considerable damage to the targeted coral colony, even when overall reef densities are low (Bruckner et al., 2017; Hamman, 2018). An outbreak, on the other hand, implies broader and longer-term ecological consequences of coral decline. The lack of clear definitions and inconsistent use of terminology have created confusion in the literature, making it difficult to identify the true causes of outbreaks and coral damage.

The definition of an outbreak is "any population or elevated density that causes extensive mortality of corals and persists for months or years over large areas of reefs". However, this definition is very vague and does not expand on what constitutes a large area or extensive mortality. Additionally, many subsequent studies have not even applied this definition and instead have used a simple density threshold when determining 'outbreak' or 'non-outbreak'. The commonly referenced density threshold for a *Drupella* spp. outbreak is when populations exceed two individuals per square meter of reef area, as established by a 2009 Australian study that considered coral reef growth rates and *Drupella* spp. feeding rates (Cumming, 2009). Cumming (2009) cautioned that due to *Drupella* spp. densities often being patchy on small scales, high densities recorded from only a few quadrats to transects should not be considered an outbreak, with the minimum sampling effort reported being three transects of 0.5 × 20 m. Although Cumming (2009) explains the importance of considering coral community health when applying the $>2m^2$ threshold, many following studies have focused solely on snail density (Saponari et al., 2021; Zhang et al., 2024). By only focusing on *Drupella* spp. density, spatial context and ecosystem-specific factors such as coral cover and stress may be neglected. For

instance, a recent review on *Drupella* spp. defined an outbreak as being over two individuals per metre squared (Zhang et al., 2023). Relying solely on density to define an outbreak can be problematic because the threshold for ecological damage varies between reefs. Densities of *Drupella* spp. that a reef can sustain without causing considerable damage will depend on several factors including snail feeding rates, coral species composition, local stressors, and the spatial extent of the affected area. While Cumming's (2009) threshold of two individuals per square meter has become the reference for many outbreak definitions, Bessey et al. (2018) reported that densities as low as 0.62 individuals per square meter of reef area could result in *Drupella* spp. consuming coral faster than it can regrow in the study area. Such findings highlight how relying solely on density to define an outbreak could be problematic. For instance, if a study measures a population density of 1.5 individuals m^{-2} they may classify it as non-outbreak based on Cumming (2009) definition, however, this may overlook the potential threat posed by such a population if the prey corals are simultaneously experiencing additional stressors such as thermal stress or bleaching. For example, elevated sea temperatures may reduce coral growth and recovery capacity, making reefs less resilient to predation, meaning that even lower-density populations can become ecologically damaging under the right conditions (Bessey et al., 2018). Rather than a simple density-only based definition for outbreaks, a more effective approach to assessing *Drupella* spp. impact may be to focus on the risk presented by a population. An outbreak could be considered to occur when the combined impact of *Drupella* spp. metabolic rate (and thus feeding rate) and population density exceeds the regenerative capacity of the coral community, i.e., when coral mortality outpaces growth and recruitment.

Compared to *Drupella* spp. much more research has been done on defining and predicting outbreaks in COTS, making them more standardised and relying less on local density and more on a consumption vs growth criterion. COTS outbreaks are also defined as densities high enough whereby COTS consume coral faster than it can grow (Babcock et al., 2020). Crown of thorns models allow outbreaks to be measurable by predicting when COTS consumption exceeds coral growth, through information on different life stages, coral consumption patterns, and coral growth rates (Morello et al., 2014). Future research should aim to develop models similar to those used for other coral predators like *Acanthaster* spp. (Morello et al., 2014), to better

evaluate outbreak densities and predict the ecological damage posed by *Drupella* spp. populations.

1.7 Thermal Sensitivity and Range Dynamics of *Drupella* spp.

Since *Drupella* spp. are ectotherms, their physiology will likely be closely linked to ambient temperature, making thermal information valuable for risk prediction and useful in outbreak modelling. A few studies have discussed the impact of thermal change on *Drupella* spp., with indications of a potential positive correlation between rising temperatures and *Drupella* spp. outbreaks on a reef (Al-Horani et al., 2011; Moyer et al., 1982). The literature is lacking; however, an understanding of the physiological thermal sensitivity of *Drupella* spp. For example, a review by Rice et al. (2019) discussed the effects of ocean warming stressors on corallivory yet only mentioned how temperature will affect coral regeneration without any discussion of how temperature might affect the corallivores themselves.

The most common topics of investigation in *Drupella* spp. studies are population dynamics and spatial distribution (Boucher, 1986; Lei et al., 2022; McClanahan, 1995; Scott et al., 2017). Several long term population studies have noted a correlation between sea surface warming and *Drupella* spp. densities, suggesting a potential role of temperature in instigating aggregations and outbreaks (Morton & Blackmore, 2009; Moyer et al., 1982). The discussion of warming temperatures impacting *Drupella* spp. dates to the first observed aggregation of *Drupella fragum*, where thousands of *D.fragum* was discovered in September and dispersed two months later alongside a decrease in water temperatures (Moyer et al., 1982). Morton and Blackmore (2009) also recorded the lowest densities of *D.* rugosa in Hong Kong during the coldest months (November to February), followed by an increase in spring and a peak in the warmest summer months (May to August). Some studies have suggested that spawning in *Drupella* spp. may be triggered by rising temperatures and could explain the increased number of aggregations observed in summer (Haslam et al., 2023). However, studies by Morton and Blackmore (2009) and by Moyer et al. (1982) stated that temperature-driven changes in *Drupella* spp. densities and aggregations recorded were not related to reproductive activity. However, neither Morton and Blackmore (2009) nor Moyer et al. (1982), offered any alternative physiological explanations for the trends seen. Despite temperature being one of the most influential abiotic factors on

ectotherm physiology, including metabolism and growth, both studies fail to address the thermal impact on *Drupella* spp. physiology and how this may influence their population growth rate.

Temperature shifts are known to have caused shifts in ectotherm geographical range, sometimes leading to range expansions, but in other cases resulting in range contractions (Buckley et al., 2013; Szuwlaski et al., 2021). Recent observations suggest that *Drupella* spp. are undergoing geographical expansion, with rising temperatures suggested to be the cause (Haslam et al., 2023). Haslam et al. (2023) observed extensions in the southernmost spawning of *Drupella cornus* from Houtman Abrolhos (28°S) to Rottnest Island (32°S), where sea surface temperatures had been continuously higher than average since August 2020. *Drupella* spp. are usually associated with tropical regions, and the survival of *D.cornus* through winter temperatures at the temperate sub-tropical Rottnest Island, unlike many of the tropical fish in the area, raises questions about the thermal tolerance and adaptability of the species. As subtropical reefs are anticipated to serve as refuges for coral species in the case of rising ocean temperatures (Berger et al., 2013), understanding the potential risk of *Drupella* spp. to these reefs is important. Information on *Drupella* spp. thermal range would aid in predicting the risk of *Drupella* spp. to temperate reefs and help identify other potential reefs to which *Drupella* spp. may expand.

1.8 Metabolism, Feeding Rate, and Temperature-Driven Behaviour

While metabolism has been well studied in other gastropods (Chen et al., 2021; Minuti et al., 2021; Vladirmiova, 2001), there is an absence of papers that focus on *Drupella* spp. metabolic rates. Additionally, only a limited number of *Drupella* spp. studies make mention of metabolism at all, and when they do, the topic is often underdeveloped. For example, Sam et al. (2017) observed a shorter rearing time for *Drupella rugosa* larvae compared to a previous study and suggested that this was due to warmer temperatures in their study increasing metabolic rate. However, the connection between temperature and metabolic rate was only briefly mentioned and not discussed further. Maoka et al. (2011) investigated the carotenoid composition of *Drupella fragum* and identified metabolic modifications, including the esterification of peridinin, with the aims of determining how these compounds reflect the species' coral-based diet.

However, the study focused on chemical characterisation and did not explore how these modifications relate to metabolic rates or broader physiological processes.

In contrast to the little knowledge on *Drupella* spp. metabolism, there have been numerous metabolic studies on COTS. Research has been conducted on the relationship between metabolic rate and factors such as temperature, size, fecundity, movement and feeding (Deaker & Byrne, 2022; Lang et al., 2021; Lang et al., 2022). Specifically, three studies investigate the impact of temperature on COTS metabolism (Lang et al., 2021; Lang et al., 2022; Yamaguchi, 1974). Results from these metabolic studies have indicated that, despite COTS exhibiting some signs of thermal stress, they have relatively high thermal limits, which have been suggested to give them resilience to short-term marine heatwaves (Lang et al., 2021). Moreover, studies have suggested that high thermal resilience may be responsible for the occurrence of outbreaks by allowing populations to remain active and feed during thermal stress events (Lang et al., 2021). COTS showing signs of thermal resilience has been noted as concerning, as periods of thermal stress suppress coral growth and recovery, increasing the risk that COTS consumption will exceed coral regrowth, a key condition for outbreaks (Lang et al., 2022). Knowledge of the impact of temperature on *Drupella* spp. metabolism similar to that known for COTS would be helpful and would allow for comparisons to be made between the two corallivores.

Feeding rates in ectotherms are influenced by the temperature-metabolism relationship (Bilcke et al., 2006; Wyban, Walsh & Godin, 1995; Rall et al., 2012). Temperature affects the need and ability of ectotherms to predate, as well as their food processing mechanisms involving digestion, nutrient absorption, and storage of surplus energy (Volkof & Ronnestad, 2020). Changes in feeding rates will influence the post-prandial rise in metabolism associated with digestion known as specific dynamic action of feeding (SDA). As SDA represents an additional metabolic cost added onto SMR during digestion, increases in either SMR or SDA will reduce the AS available during digestion for other functions such as locomotion and reproduction. In extreme cases, increases in SMR and SDA reduce AS to near zero, thereby constraining further feeding and creating trade-offs with other oxygen demanding processes. For example, a study on shorthorn sculpin saw that an increase from 10°C to 16°C increased SMR by approximately 82% and SDA by 54%, such that the estimated AS at peak digestion became so large that AS

approached zero. This meant that there was little AS for other essential functions including locomotion or predator avoidance, and digestion itself became metabolically constrained. Although acclimation of eight weeks at 16°C allowed SMR to adjust and AS to partly recover, the study highlighted how acute warming can impose severe short-term trade-offs between maintenance, digestion and other aerobic processes.

Limited research has been done on *Drupella* spp. feeding rates, with one study measuring the impact of temperature on coral predation (Al-Hoarni et al., 2011). Al-Horani et al. (2011) reported a five-fold increase in feeding rates of *D.* rugosa acclimated to 18°C and 30°C, suggesting that this increase may be due to the heightened stress experienced by corals at warmer temperatures. However, the study did not mention any impacts of temperature on *Drupella* spp. physiology, or how that may play a role in the increased feeding rates seen. Another study lacking any physiological explanation is that of Tsang and Ang (2015), which observed *Drupella* spp. acclimated and tested at 14°C to exhibit decreased activity compared to the control group at 22°C, as they took approximately twice as long to reach their preferred prey. As metabolic rates represent the energy production of an organism, it is closely tied to an organism's activity levels (Brothers & McClintock, 2015; Lang et al., 2022). However, the study by Tsang and Ang (2015) offered no physiological explanation for the reduction in activity observed. The absence of a physiological discussion could create difficulties in fully understanding the root causes of the observed changes in *Drupella* spp. behaviour.

The importance of distinguishing between problematic and non-problematic *Drupella* spp. populations are essential for effective management planning, and *Drupella* spp. feeding rates play an important role in calculating densities sustainable by a coral community (Bessey et al., 2018).To establish area-specific densities that the study reef could support, Bessey et al. (2018) calculated the mean *Drupella* spp. consumption rates from 400 individual snails and measured in situ coral growth of the preferred prey in the area *Acropora spicifera*. from this they derived outbreak thresholds ranging from 0.62 to 2.83 individuals per metre depending on coral cover. While comprehensive, requiring such large sample sizes for every new *Drupella* spp. population study may present financial and logistical challenges. Alternatively, developing a model which includes feeding rate and coral growth could prove beneficial for future risk prediction. Given

that laboratory findings indicate temperature influences feeding rates, better investigating the thermal sensitivity of *Drupella* spp. could allow temperature to be integrated into predictive models, potentially leading to more accurate estimates of feeding rates for specific populations. By addressing the gaps in our knowledge of *Drupella* spp. metabolism and incorporating temperature dynamics into predictive models we can improve the effectiveness of future management and conservation efforts.

1.9 Implications for Coral Reef Management and Conservation

Evidence indicating a potential increase in *Drupella* spp. feeding rates under heightened coral stress and elevated temperatures are concerning, as they suggest a possible increase in damage risk posed by *Drupella* spp. under ocean warming, when reefs will already be under stress. Given the already large threat posed by the genus *Drupella* spp., understanding the extent to which they may benefit or be hindered under projected environmental changes is an essential aspect of coral reef conservation. However, the physiological thermal response of *Drupella* spp. to warming remains largely unexplored, particularly in terms of metabolic studies. Accurately predicting the future impact of *Drupella* spp. requires research on their thermal performance, indicating the need for increased study to inform future reef management strategies.

1.10 Objectives, Aims & Hypotheis

By studying the metabolic, feeding and growth responses of *Drupella* spp. to changing temperatures, this research aims to advance our understanding of their thermal performance and sensitivity, assess their potential to cope with future temperature increases, and ultimately evaluate how thermal changes may influence *Drupella* spp.'s impact on reefs.

1.11.1 Chapter 2

Chapter 2 aims to investigate the acute and prolonged response of increasing temperatures on *Drupella* spp. metabolic rates both SMR and RMR. The specific objectives include:

1. Use ramping experiments to quantify the acute thermal sensitivity of *Drupella* spp. metabolic rate.
2. Assess *Drupella* spp. abilities to acclimate by comparing changes in metabolic rate across three and 19–22 days of exposure to elevated temperatures.
3. Examine metabolic scaling exponents with body size, and whether this is influenced by temperature.

We hypothesise that the metabolic rates of *Drupella* spp. will increase with warming temperatures until their thermal optimum is exceeded. If this is the case, *Drupella* spp. metabolic rates will increase until a critical threshold is reached, after which metabolism will decline. We further hypothesise that the longer *Drupella* spp. are acclimated to increased temperatures, the greater their thermal tolerance will be. If this is so, individuals held for longer durations at elevated temperatures will maintain metabolic rates to a higher threshold than those exposed for shorter periods. Finally, we hypothesise that metabolic rates will scale with body size, and that this relationship will be influenced by temperature. If this is the case, metabolic rates will increase with wet weight, but the scaling exponents will become shallower or steeper depending on thermal conditions.

1.11.2 Chapter 3

Chapter 3 aims to determine the effect of elevated temperatures on *Drupella* spp. feeding and growth. The specific objectives are to:

1. Quantify feeding amount of *Drupella* spp. across increasing temperatures.
2. Investigate the relationship between metabolic rates and feeding.
3. Assess *Drupella* spp. growth under different thermal conditions.

Quantifying metabolic and feeding rates of *Drupella* spp. across a range of temperatures will help assess the potential pressure a population may exert under specific environmental conditions. When considered alongside coral growth and regeneration rates, such data can inform thresholds of *Drupella* spp. densities that reefs can tolerate without experiencing net degradation.

Being able to identify these tipping points is important for assessing population risks, improving predictive outbreak models, and ultimately guiding management strategies of the corallivores We hypothesise that the feeding effort of *Drupella* spp. will increase with warming until their thermal optimum is exceeded, reflecting changes in metabolic rates. If this is the case, coral scarring by *Drupella* spp. will increase as temperatures rise, mirroring their metabolic response, until decreasing if metabolic rates begin to decline. We further hypothesise that growth will also increase with rising temperature. If this is the case, thermal effects on growth will parallel feeding effort, with enhanced growth under moderate warming and reduced growth once thermal limits are surpassed.

2 Acute Thermal Tolerance and Prolonged Thermal Acclimation Response in the Corallivorous Gastropod *Drupella* spp.

2.1 Abstract

Outbreaks of the corralivore *Drupella* spp. have caused large scale damage to coral reefs across the Indo-Pacific, yet little research has been conducted on their metabolism or how it is influenced by temperature. Using intermittent flow respirometry, I investigated both the acute and acclimatory metabolic responses of *Drupella* spp. to elevated temperatures. *Drupella* spp. individuals were exposed to one of four final temperatures 28°C, 30°C, 32°C, 34°C. Acute ramping trials used snails that were held at 28° and at 34°C and ran from 29°C to 38°C with thirty-minute measurement and thirty-minute ramping intervals. During acute ramping, metabolic rate increased continuously throughout the temperature range tested suggesting that, during rapid increases in temperature, 38°C falls within *Drupella* spp.'s thermal range. To investigate acclimatory response, *Drupella* spp. were exposed to their respective final temperature for either three or 21-23 days. Oxygen declines were measured over 12 hours to estimate standard metabolic rate (SMR) and routine metabolic rate (RMR). When acclimated to their final temperatures for three days, *Drupella* spp. saw increases in SMR and RMR between 28 °C and 32 °C, followed by declines between 32 °C and 34°C. Snails acclimated for 19-22 days maintained elevated SMR and RMR throughout the temperature range, but the difference between acclimation duration was only significant in RMR. These findings suggest that while *Drupella* spp. exhibit some thermal sensitivity, they also have capabilities for acclimation, which could exacerbate reef vulnerability during times when reefs are already under stress at elevated temperatures. In the acclimation experiment, metabolic scaling exponents were consistent with other studies on Gastropods and decreased further with warming. The decrease in scaling exponents with warming suggests reduced performance in larger individuals under heat stress which may lead to potential shifts in population size structures toward smaller snails. Knowledge on *Drupella* spp. thermal sensitivity should be used in future outbreak monitoring and prediction models, supporting improved management strategies for coral reef conservation.

2.2 Introduction

Coral reef ecosystems are facing increasing threats from climate change and outbreaks of organisms which feed on coral, both of which are recognised as two of the main drivers of reef degradation (De'ath et al., 2012; Baird et al., 2013; van Hooidonk et al., 2016; Mellin et al., 2019; Castro-Sanguino et al., 2021). Since the beginning of the industrial era sea surface temperatures in tropical and subtropical reef regions have risen by nearly 1°C, a trend expected to intensify throughout the century**.** By 2100, ocean warming could reach two to four times the 1971–2018 increase under SSP1-2.6 modelling, and four to eight times under SSP5-8.5 scenarios (IPCC, 2021). Warming ocean temperatures are known to cause severe direct impacts on coral reefs, through processes such as coral bleaching, reduced calcification rates that weaken coral skeletons, and heat stress that disrupts reproduction cycles and lowers the success of larval settlement (Anthony et al., 2008; McNeil, Matear & Barnes, 2004; Richmond et al., 2018). In addition to these direct impacts of warming temperatures to reefs, a growing topic of concern is the indirect effects that warming may have on coral reef ecosystems. For example, how temperature may influence the physiology, feeding behaviour, and population dynamics of corallivores, organisms that feed on coral tissue.

Temperature is a fundamental driver of physiological processes in organisms, with environmental temperature having a large impact on a wide variety of factors including behaviour, growth and reproduction (Jansen & Gislason, 2011; Rosenthal & Elias, 2025). One well documented physiological trait influenced by temperature is metabolism, the rate of energy expenditure that supports an organism's functional capacity (Schulte, 2015). An animal's metabolic rate reflects the energy costs of fundamental processes and activities, thus linking individuals to ecosystem level processes via energy flow (Brandl et al., 2022). Studying the effects of abiotic and biotic factors on metabolic rate helps us learn how organisms adjust to changing environmental conditions and their capacity to cope with stressors (Amarasekare, 2024; Gibert, 2019; Lang et al., 2022). Popular methods for investigating metabolic rate involve measuring standard metabolic rate (SMR) which is the minimum energy required to sustain life in a resting, post-absorptive state, and routine metabolic rate (RMR), which includes the energy expended during spontaneous, low-intensity activity (Killen et al., 2021). Metabolic rate

generally increases with temperature due to the effect of temperature on the kinetic energy of cellular components (Arrhenius, 1889), thereby increasing enzyme-substrate collisions and thus accelerating biochemical reactions. However. the interaction between temperature and metabolic rate is more complex than just an exponential increase and can be influenced by thermal acclimation and constrained by upper thermal limits (Peck & Prothero-Thomas, 2002; Clarke & Fraser, 2004). For example, both SMR and RMR commonly increase with rising temperatures, but this rise is limited by an organism's ability to deliver sufficient oxygen, maintain essential cellular functions, and sustain overall fitness (Pörtner, 2001, 2002; Pörtner et al., 2017).

As climate change is driving temperature variability across different temporal scales, it is important to study *Drupella* spp. response to both short- and long-term thermal changes (Kefford et al., 2022). Acute spikes in temperature, including diel variation in shallow habitats and the increasing frequency and severity of marine heatwaves, can lead to metabolic disturbances at temperatures normally within a typical organism's range (Kefford et al.,2022). Sudden thermal changes can disrupt homeostasis before acclimatory compensatory mechanisms are able to develop, seriously impacting an organism's performance, and in severe cases even leading to mortality (Kefford et al.,2022). While these acute events are increasing in frequency and severity, the more common trend under climate change is a gradual increase in water temperature over time. To cope with thermal stress many ectotherms exhibit physiological acclimation, a reversible form of plasticity involving adjustments at metabolic, cellular, and cardiovascular levels (Franklin et al., 2007; Sandblom et al., 2014). Organisms achieve acclimation through physiological adjustments which include, modifying enzyme kinetics and expression, changes in membrane fluidity, or restructuring of cardiovascular and respiratory organs, all which help to maintain performance during increased temperatures (Duan et al., 2024; Franklin, Davison & Seebacher, 2007; Somero, 2004). For example, in the Spotted rose snapper (*Lutjanus guttatus)*, acclimation to 29-32 °C for 21 days significantly increased expression of lactate dehydrogenase in the gills and muscles, maintaining ATP production via glycolysis at such elevated temperatures (Larios-Soranio, et al., 2020). The abilities and extent of acclimation vary considerably among species and play an important role in determining their resilience to climate change (Stillman, 2003; Somero, 2015). Species with limited plasticity may be particularly vulnerable to warming environments as they may exhibit reduced performance and fitness with

increasing temperatures (Anestis et al., 2007; Stillman, 2003). Whereas organisms with high acclimation capabilities will be less vulnerable to anthropogenic induced climate change (Johansen et al., 2021). In ecosystems where temperature conditions are typically more stable throughout the year organisms often show a reduced capacity for thermal acclimation due to limited evolutionary exposure to thermal variability, this includes coral reefs (Stillman, 2003). For example, prolonged temperature experiments on COTS showed no metabolic adjustments over four weeks of exposure to 32 °C, indicating limited evidence for acclimation (Lang et al., 2022). Lang et al. (2022) discussed the biological implications of COTS's lack of acclimatory ability noting that it creates uncertainty around their long term persistence on warming reefs and suggesting that populations may redistribute to reefs with cooler waters. Unlike the research conducted on COTS, no equivalent studies have investigated the acclimatory ability of *Drupella* spp. to increasing temperatures.

Despite their ecological significance, the thermal physiology of *Drupella* spp. remains largely unstudied (See Fig.1.3, chapter 1). These invertebrates are widely distributed across Indo-Pacific coral reefs and are known to contribute significantly to coral degradation during population outbreaks (Hoeksema et al., 2013; Morton et al., 2002). However, no studies have quantified their metabolic rate, or their metabolic response to temperature change. While field observations indicate that *Drupella* spp. can tolerate a broad seasonal temperature range (14–33 °C), existing laboratory research has focused primarily on behaviour, lacking any metabolic studies (Tsang & Ang, 2019). This knowledge gap is particularly apparent when compared to the well documented thermal biology of COTS, whose metabolic responses to temperature have been extensively studied (Lang et al., 2021; Lamare et al., 2014). Metabolic studies on COTS have contributed to a more comprehensive understanding of the genus and have helped inform reef management efforts (Lang et al., 2021; Lamare et al., 2014). Establishing a comparable understanding of *Drupella* spp.'s thermal limits and acclimation abilities is important, not only to allow for predictions of any potential shifts in their coral predation and geographic distribution under climate change, but also to enable broader comparisons across corallivores. By investigating both the acute and acclimatory metabolic responses of *Drupella* spp. to elevated temperatures the following study aims to enhance our understanding of the thermal sensitivity of *Drupella* spp., to provide insight into their resilience and inform future management.

2.3 Methods

2.3.1 Animal Collection and Husbandry

In April 2024, *Drupella* spp. (n = 140) were collected from *Porites spp.* coral colonies on the north coast fringing reefs of Moorea (17°29′18.86″ S, 149°53′40.69″ W), French Polynesia. Collections were conducted in shallow reef zones (<1.5 m depth), where sea surface temperatures averaged approximately 31 °C at the time of sampling. Individuals were manually removed using 20cm stainless steel forceps and transported by boat in coolers filled with seawater to the CRIOBE research facility. Upon arrival, individuals were randomly assigned (n = 14 per tank) to one of ten experimental aquaria (dimensions: 50 × 30 × 25 cm), each supplied with recirculating, UV-sterilised seawater sourced directly from the adjacent lagoon. Tanks were continuously aerated via submerged airstones and maintained on a 12h light:12 h dark photoperiod using coral specific LED lighting. Water temperature in all tanks was initially held at 28 °C, the annual mean temperature for Moorea's fringing reef, regulated using Inkbird digital thermostats which controlled submersible aquarium heaters. Although snails were collected at ~31 °C, they were acclimated at 28 °C to standardise baseline physiology to the average temperature to ensure all snails started the experiment from a normal baseline, rather than an already elevated thermal state. To be able to identify individual snails, *Drupella* spp. were uniquely marked with two dots of coloured nail varnish on the shell, a non-invasive tagging method which has been shown to cause no adverse effects on gastropod behaviour or survival (Gosselin, 2009).

All snails were acclimated to laboratory conditions at 28 °C for a minimum of six days to standardise baseline physiological states before commencing the experiment. After baseline acclimation, water temperatures in the tanks were gradually increased at a rate of +1 °C per day until the target treatments were reached: 28 °C (annual average), 30 °C, 32 °C (the recorded annual maximum was 32.61 °C in 2021), and 34 °C (a +2 °C warming scenario projected by the mid-century under the SSP2-4.5 intermediate emissions pathway (IPCC, 2021). Each temperature treatment was applied to two replicate tanks, resulting in a total of eight

experimental tanks across the four thermal conditions. The two remaining tanks were left at 28 °C and were kept as spares.

Although the snails were collected in the field from *Porites* spp. colonies, previous studies have demonstrated a strong feeding preference for *Acropora* spp., a faster-growing species with higher regenerative capacity (Al-horani, Hamdi & Al-Rousan, 2011; Cumming, 2009; Morton, Blackmore & Kwok, 2002). Prior to the experiment, a separate group of *Drupella* spp. individuals were offered both *Acropora* spp. and *Porites* spp. coral fragments. In these preliminary trials all *Drupella spp.* consistently selected *Acropora* spp. over *Porites spp.*, leading to *Acropora* spp. being chosen to be used for feeding throughout the study. *Drupella* spp. were fed *ad libitum* with live *Acropora* spp. coral fragments, which were replenished regularly once most of the tissue had been consumed. Tissue consumption was obvious from the exposed white skeleton that results when *Drupella* spp. feed and strip coral tissue from the skeleton (Cumming, 2009).

2.3.2 Measurement of Metabolic Rates

Metabolic rates of *Drupella spp.* were estimated from measurements of oxygen consumption, measured using intermittent flow respirometry (IFR) (Svendsen et al., 2016). The respirometry system consisted of eight parallel glass chambers (volume: 25 ml^3), submerged in a temperature-controlled water bath, which the *Drupella* spp. were held in to measure their oxygen uptake. The water bath had a constant inflow of water pumped form the lagoon through a UV lamp filter, as well as an air stone held in the bath, to bring in oxygenated seawater and ensure mixing. Each IFR cycle included a closed phase (2 minutes) during which oxygen decline was measured, followed by a flush phase (4 minutes in the acute ramping and 5 minutes in the prolonged thermal exposure experiment) during which fully oxygenated seawater was circulated through the chambers. Using IFR allows for repeated metabolic measurements over extended periods of time without animal disturbance. IFR also prevents hypoxia and waste buildup which would otherwise occur without the flush phase, both of which could affect metabolic rates and limit the ability for long term measurements. Extended measurement periods therefore allow for the measurement of sustained periods during which the organism is at rest and functioning at its

baseline metabolic level, which is important for accurately estimating standard metabolic rate (SMR). In addition, real-time oxygen consumption measurements enable the identification of spontaneous, routine activity (RMR).

Water in each chamber was continuously recirculated in a closed loop system using a peristaltic pump connected to gas impermeable Tygon® tubing. Water was drawn from within the chambers, passed through external oxygen sensors, and returned to the same chambers. Continuous recirculation offered several advantages by preventing oxygen stratification within the chambers, maintaining a consistent flow across the sensors to ensure stable and accurate readings, and allowing oxygen concentration measurements to reflect the average oxygen level within the entire chamber volume. Additionally, housing the oxygen probes externally minimised both disturbance to the animals during measurements and the risk of sensor interference caused by contact or movement of the snails within the chamber. Dissolved oxygen concentrations were recorded at two-second intervals by the probes via two four-channel oxygen meters.

All probes were calibrated at their respective experimental temperatures to 100% oxygen saturation in fully oxygenated seawater. Water in the bath, and consequently in the chambers, was maintained to match the specific treatment temperatures required. Thermal control was achieved using a pump driven circulation system that directed water through a submersible stainless steel heat exchanger, which was placed inside a heated freshwater reservoir consisting of a plastic bucket filled with freshwater. The reservoir was heated using two 500W titanium aquarium heaters and maintained at least 6°C above the target bath temperature. An Inkbird thermostat regulated the system by activating the pump whenever the water bath temperature dropped more than 0.3°C below the setpoint. Water levels in the reservoir were checked each morning and evening and topped up when needed to ensure that the heat exchange would work throughout.

Seven *Drupella spp.* individuals were measured per IFR trial, with one chamber always left empty to as a blank control measuring background microbial respiration. The control chamber varied between trials to avoid potential chamber-specific effects. Snails were fasted for

approximately 24 hours before each trial to ensure a post-absorptive metabolic state. To minimise external stimuli, including visual disturbance and interactions between individuals, opaque plastic dividers were placed between chambers, and the entire system was covered with a black sheet during trials. Although the chambers were covered, a controlled 11h:13h light:dark cycle was maintained as a precaution to simulate natural diel light cycles. At the end of each trial, snails were removed from their chambers, blotted, and weighed to obtain their wet weights. Shell length and width were then measured using callipers before individuals were returned to their respective aquaria.Between respirometry trials, to minimise microbial oxygen consumption, the system was flushed with 5-9% sodium hypochlorite, then rinsed thoroughly three times with seawater. To prevent damage during bleaching, the oxygen probes were removed. For disinfection, oxygen probes were immersed in 70% ethanol for 5-10 seconds before being rinsed thoroughly with fresh water.

2.3.3 Acute Metabolic Ramping

To evaluate short term metabolic sensitivity to rapid temperature increases, an acute thermal ramping protocol was conducted on a subset of *Drupella* spp. individuals (n=28). Trials were carried out on four dates,18 April, 19 April, 6 May, and 9 May 2024, corresponding to two acclimation treatments: 28°C (18, 19 April and 9 May) and 34°C (6 May). Seven different snails were used on each date, each acclimated for at least 20 days at their respective temperature treatment.

Drupella spp. were placed in their individual respirometry chambers the evening prior to the experiment to allow time to settle at 28°C. Oxygen consumption was then measured using IFR, as described in Section 2.3.3, across a temperature gradient ranging from 28°C to 38°C. Ramping consisted of each step consisting of a thirty-minute heating period, where the temperature of the water bath was increased by 1°C, followed by a thirty-minute measurement phase.

2.3.4 *Drupella* spp. prolonged measurement

To assess the longer-term effects of temperature change and the acclimation abilities of the metabolic rate of individuals held at their respective temperatures were measured using IFR (Section 2.3.2) after three days (shorter-term acclimation) and again after 19-22 (longer-term acclimation) of exposure to their final temperatures.

Each IFR trial began between 11:30 and 13:00, when the snails were placed in their chambers, and continued overnight until 07:00-08:00, lasting approximately 19-20 hours. Water in the bath, and consequently in the chambers, was maintained to match the specific treatment temperatures (28°C, 30°C, 32°C, and 34°C) and maintained at that temperature throughout.

2.3.5 *Drupella* spp. volume

To measure oxygen consumption from IFR, it is necessary to calculate the volume of water from which the oxygen was consumed, therefore it was important to account for the volume displaced by the experimental organism. Due to the presence of calcareous shells and structural variability in *Drupella* spp. an empirical weight-to-volume calibration was created based on water displacement measurements to allow for volume estimation of the snails used in the experiment. A subset of 25 individuals were blotted dry, weighed, and then individually submerged in a graduated cylinder containing a known volume of seawater. The volume of water displaced by each snail was removed using a pipette and weighed on a digital scale. Assuming a seawater density of 1 g/cm³ (which is within measurement error of typical seawater density, 1.024 g cm^{-3}) the weight of the displaced water was used to calculate the volume taken up by each individual snail. To do this a linear relationship between wet weight and displaced volume was established from these measurements. A weight-to-volume conversion factor was then calculated from the relationship, which allowed the volume of the *Drupella* spp. in the experiment to be estimated by multiplying their wet weight by the calculated factor. This method was adapted from previously published approaches used to measure the volume of snail shells (Örstan, 2011) and live gastropods in respirometry studies (Alcaraz et a, 2024).

2.3.6 Data Analysis

All data analyses were conducted in R (R Core Team, 2023) using the dplyr and ggplot2 packages.

In both the ramping trials and the prolonged experiment oxygen consumption rates were calculated by applying linear regressions to the decline in oxygen during closed respirometry phases, making sure to first exclude the initial 30 seconds of the closed period to minimise mixing effects (Killen et al., 2021). In the prolonged experiment, the first two hours of measurements were also not used in analysis to minimse oxygen consumption being effected by stress. To correct for background respiration in the chambers, oxygen consumption measured in a parallel empty chamber was subtracted from each chamber with a snail in it at the corresponding time points, giving the net oxygen concentration decline caused by snail respiration (mg O_2 L^{-1} s^{-1}). To calculate the volume of water available for gas exchange, the total volume of the respirometry system, including chambers and associated tubing, was corrected by subtracting the volume displaced by the snail. This corrected volume was used to convert the net oxygen concentration decline (mg O_2 L^{-1} s^{-1}) into absolute metabolic rate (mg O_2h^{-1}) (Eq.1). Only regression slopes with a coefficient of determination (R^2) ≥ 0.9 were kept for further analysis. RMR was calculated as the mean of all metabolic rate estimates, while SMR was estimated as the lowest 20th percentile of measurements.

Equation 1: used to calculate the oxygen uptake (MO_2; mg O_2 h^{-1}) of individual *Drupella* spp.

$$MO_2 = \Delta O_2 \cdot V \cdot 3600$$

Where:

- $\boldsymbol{MO_2}$ = oxygen uptake rate (mg O_2 h^{-1})
- $\Delta\boldsymbol{O_2}$ = rate of oxygen decline during the closed phase (mg O_2 L^{-1} s^{-1}), corrected by subtracting the rate measured in the empty chamber
- $\boldsymbol{V}$ = respirometer volume (L), corrected for the displacement volume of the snail
- $\mathbf{3600}$ = constant to convert seconds to hours

For use in tables and figures, metabolic rates were size corrected to allow for comparisons across individuals (Eq.2). Metabolic rates (SMR and RMR) were size corrected by standardising to a mean body mass of all the experimental snails (2.98 g), following the allometric scaling approach used by Killen et al. (2016). An allometric log-log regression was first fitted between oxygen uptake rate and wet weight. For each individual, a residual was obtained as the difference between the observed and the value predicted by the fitted regression at that individual's wet weight. To standardise these estimates by size, the residuals were added to the predicted value at the mean *Drupella* spp. body mass (2.98g). The final values were back transformed to return them to metabolic rate units (mg O_2 h^{-1}), giving standardised value of each snail's SMR and RMR as though each were 2.98g in weight. Lastly, to assess thermal sensitivity each temperature interval was used to calculate Q_{10} values (Eq.3).

To evaluate the effect of temperature on snail growth, changes in wet weight, shell length, and shell width were assessed between four days and 20-23 days. Only individuals with complete paired measurements at both time points were included in the analysis.

Equation 2: Allometric Model for Size-Standardisation of Metabolic Rate

$$log10(MO_2) = log10(b) + a \cdot log10(M) + \varepsilon$$

Where:

- $\boldsymbol{MO_2}$ = oxygen uptake rate (mg O_2 h^{-1})
- $\boldsymbol{M}$ = wet weight (g)
- $\boldsymbol{\varepsilon}$ = residual variation
- $\boldsymbol{a}$ = scaling exponent (slope)
- $\boldsymbol{b}$ = normalisation constant (intercept)

Equation 3: Q_{10} Temperature Sensitivity Model of Metabolic Rate

$$Q_{10} = \frac{R_2}{R_1}^{\frac{10}{T_2 - T_1}}$$

Where:

- Q_{10}= temperature coefficient, representing the factor by which the rate changes with a 10 °C increase
- R_1 = mean metabolic rate (mg O_2 h^{-1}) at temperature T_1
- R_2 = mean metabolic rate (mg O_2 h^{-1}) at temperature T_2
- T_1= lower temperature (°C)
- T_2 = higher temperature (°C)

2.3.8 Statistical Analysis

All statistical analyses were conducted in R (R Core Team, 2023) using the dplyr, ggplot2, lme4, and lmerTest packages, with significance accepted at $p < 0.05$.

Linear mixed-effects models were used to evaluate how temperature, wet weight, acclimation duration, and their interactions influenced metabolic rate across both prolonged (SMR and RMR) and ramping trials. Models included individual ID and tank as random intercepts to account for repeated measures. Model selection was guided by comparisons of AIC, BIC, and likelihood ratio tests, and model assumptions (normality, linearity, homoscedasticity) were verified using diagnostic plots. For ramping trials, metabolic rate responses across acute temperature steps were analysed using mixed-effects models with temperature, acclimation treatment, and wet weight as fixed effects, and individual ID as a random intercept.

2.4 Results

2.4.1 Species Identification

It was challenging to determine the species of snails accurately in this study. We are fairly confident that snails in this study were *Drupella cornus* (Röding, 1798) due to the four spiral rows of prominent nodules on most of the snails, which is one of the characteristic features of this species (Röding, 1798). An earlier study in Moorea also reported the snails as *D. cornus* but the research did not explain how they identified them (Hamman, 2018). However, identification on the species level was not always possible since many shells were encrusted and eroded, obscuring key conchological features necessary for confident identification. Therefore, genetic analysis would be needed to identify species with full confidence. Similar identification challenges have been encountered in other *Drupella* spp. studies, which decided to refer to the snails as *Drupella* spp. in order to avoid misidentification (Zhang et al., 2024; Saponari et al., 2021). In alignment with what previous studies established, in this study gastropod snails were identified up to the genus level and referred to as *Drupella* spp.

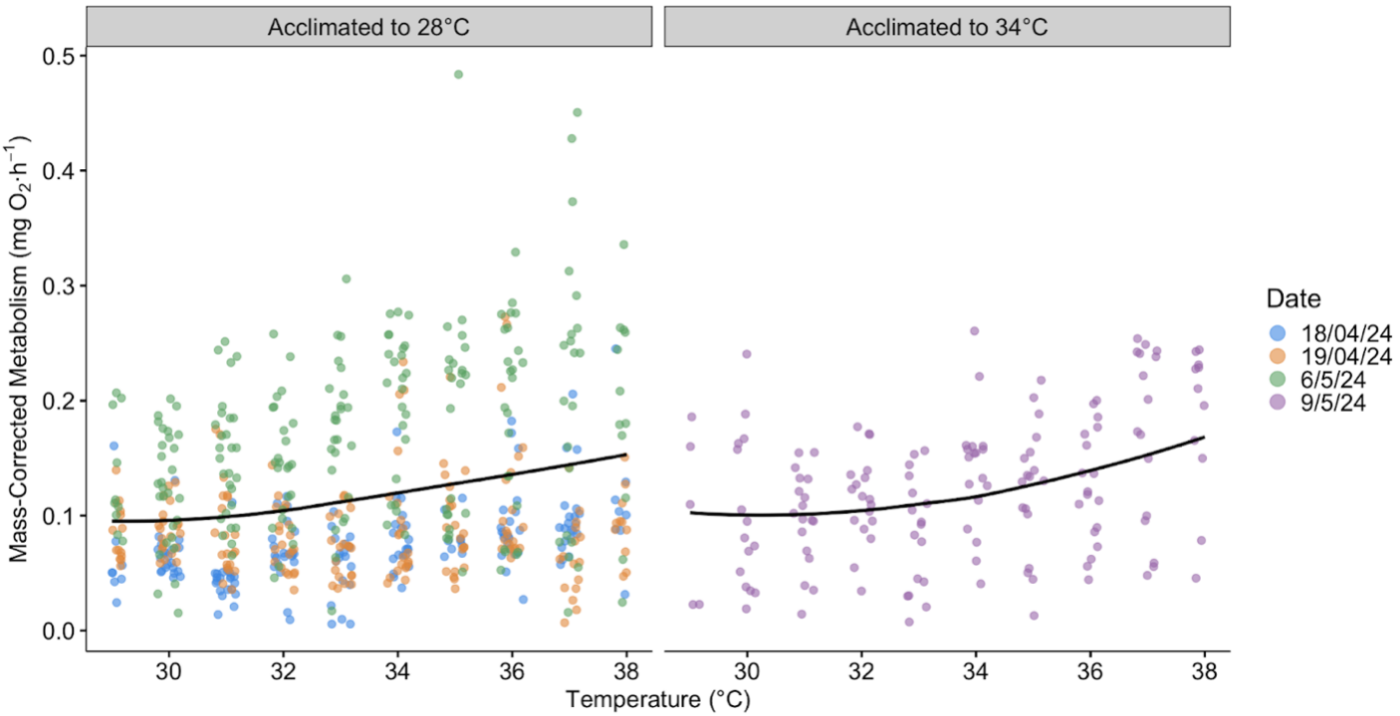

Figure 2.1 Mass-corrected metabolic rates (mg $O_2 \cdot h^{-1}$) of *Drupella* spp. plotted against temperature (°C) during acute thermal ramping trials. Each point represents an individual measurement of metabolic rate for a snail at the given temperature. Colour of dots indicate trial date, shown by the key on the right-hand side. Facets indicate temperature that *Drupella* spp. were acclimated at prior to ramping for at least 20 days: snails acclimated to 28 °C are on the left and those on the right were held at 34°C. Metabolic rates were corrected to the mean mass of snails in the ramping experiment (2.97 g) using residuals from log-log linear regressions of metabolism versus wet weight. Black lines show LOESS curves illustrating overall metabolic trends across temperatures for both acclimation treatments. Graph is made from metabolic-rate measurements collected from seven snails at each date, total n=28, across the temperature ramp. A linear mixed-effect model showed a significant positive effect of temperature on metabolic rate ($t_{913} = 9.89$, $p < 0.001$), while acclimation temperature and its interaction with temperature were not significant ($p > 0.88$).

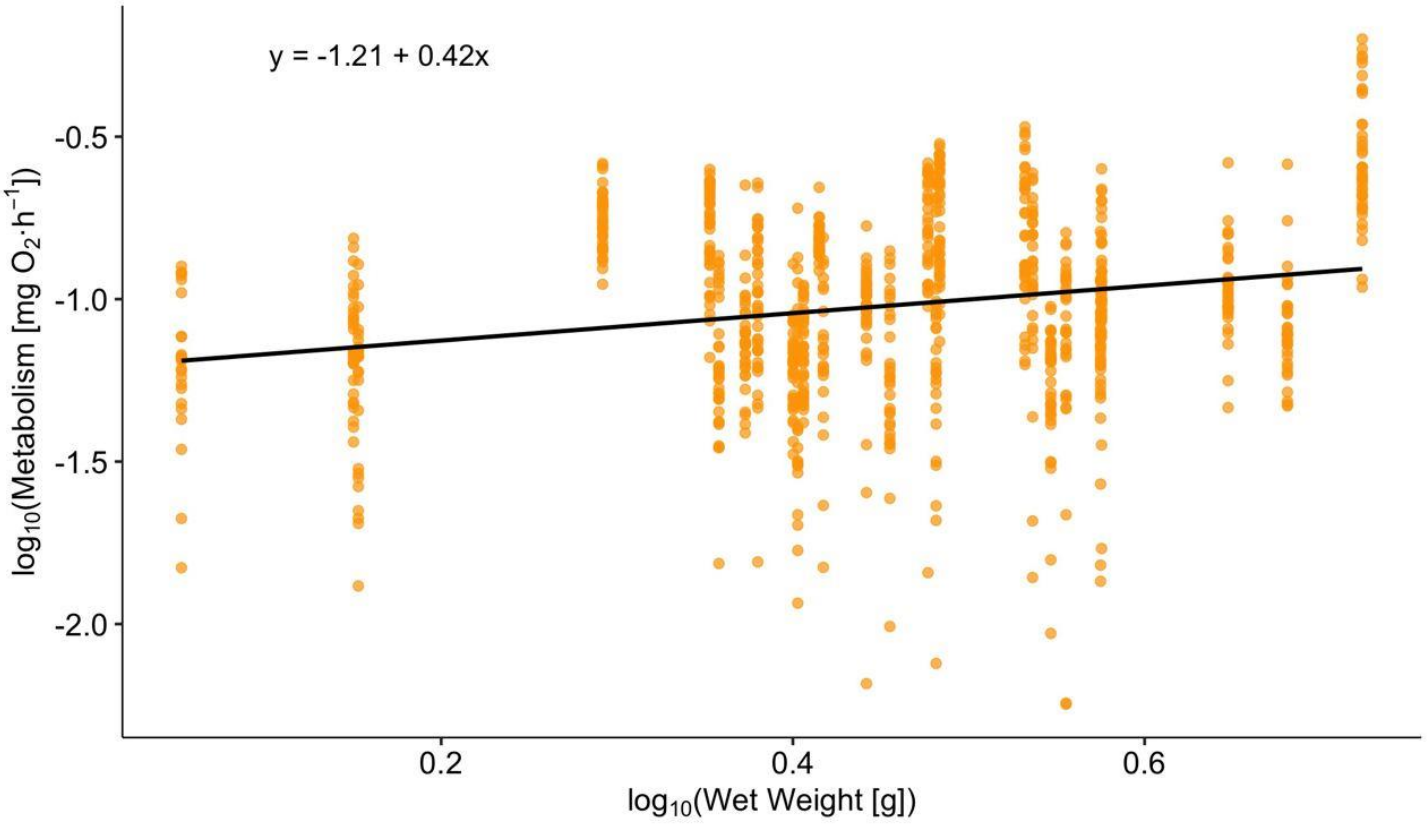

Figure 2.2 Scaling of Metabolic Rate with Body Size during acute thermal ramping from 29°C to 36°C. The plot shows the relationship between $\log_{10}$-transformed wet weight and $\log_{10}$-transformed metabolic rate. Each orange point represents an individual measurement from a snail. Graph is made from 920 metabolic-rate measurements collected from seven snails at each date (n=28) across the temperature ramp. The black line shows the fitted linear regression model ($y = -1.21 + 0.42x$). Metabolic rate increased significantly with body size ($t_{913} = 11.40$, $p < 0.001$), consistent with standard metabolic scaling relationships.

2.4.2 Temperature and Body Mass Effects on Metabolic Rate During Acute Ramping

In the ramping trial, metabolic rate increased with body mass and acute temperature in all *Drupella* spp. across 29-38°C (Fig 2.1 & Fig 2.2). In total 7 snails on four dates (n=28 snails) were measured for their metabolic rates in the temperature ramping protocol. To quantify these effects, two linear mixed-effects models were fitted with temperature, wet weight, and acclimation temperature as fixed effects, and date included as a random effect to account for repeated measurements collected on different days. The first model tested whether body mass modified the acute thermal response, whereas the second examined whether acclimation temperature altered this relationship. Fitting both interaction terms in a single model would introduce multicollinearity and thus were analysed separately to provide clearer estimates for each effect. Full model outputs are provided in Supplementary Figure S2 and S3. The first model showed a significant interaction between wet weight and temperature ($F_{1,913} = 26.9$, $p < 0.001$), indicating that larger animals showed greater increases in metabolism with temperature than smaller animals. In contrast to this, the temperature acclimation interaction did not have a significant effect on metabolism ($F_{1,890} = 0.14$, $p = 0.89$), nor was the acclimation temperature itself as a main effect ($F_{1,2} = 0.01$, $p = 0.93$). This shows that the effect of temperature on metabolism in the acute ramping experiment was homogeneous for those that had been acclimated at 28°C and 34°C.

Table 2.1 Mean (± SD) mass-corrected standard metabolic rate (SMR) and routine metabolic rate (RMR) of *Drupella* spp. across temperature treatments at different acclimation durations. Q_{10} values were calculated between successive temperature treatments and indicate the temperature sensitivity of metabolic rate between the different intervals, expressed as the rate of change between metabolic rates extrapolated to a 10°C increase. Metabolic rates were obtained from 56 individual snails, with 14 snails held at each temperature 28,30,32,34°C. Values are means ± SD based on individual snails and are descriptive indices calculated from mean SMR or RMR between successive temperature steps and were not subjected to formal statistical testing.

Temperature (°C)	Acclimation Days	Mean mass-corrected SMR ± SD (mg O_2 h^{-1})	Q_{10} (SMR)	Mean mass-corrected RMR ± SD (mg O_2 h^{-1})	Q_{10} (RMR)
28	3	0.226 ± 0.155	-	0.318 ± 0.113	-
30	3	0.309 ± 0.141	2.11	0.37 ± 0.123	2.16
32	3	0.378 ± 0.113	2.73	0.443 ± 0.117	2.17
34	3	0.265 ± 0.069	0.17	0.312 ± 0.064	0.2
28	19-22	0.264 ± 0.068	-	0.33 ± 0.062	-
30	19-22	0.318 ± 0.075	2.54	0.369 ± 0.064	1.74
32	19-22	0.335 ± 0.064	1.3	0.393 ± 0.064	1.37
34	19-22	0.349 ± 0.145	1.22	0.427 ± 0.132	1.5

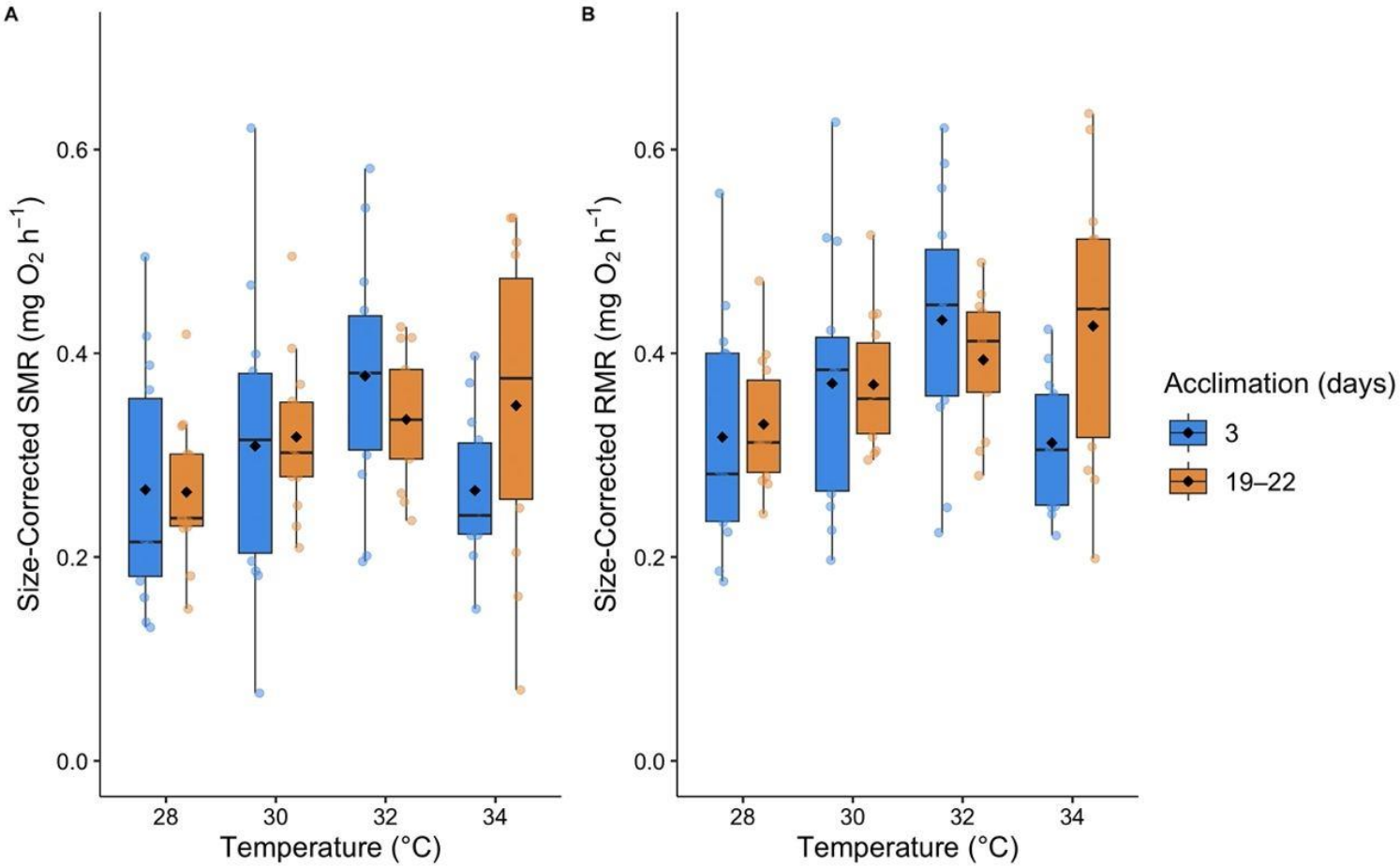

Figure 2.3. Temperature effects on size-corrected metabolic rates in *Drupella* spp. at shorter-term and longer-term acclimation. (A) Standard metabolic rate (SMR) and **(B)** routine metabolic rate (RMR) following either shorter-term (3-day, shown in blue) or longer-term (19-23 day, shown in orange) thermal acclimation to their given temperature (28°C,30°C,32°C or 34°C) from 56 snails (14 at each temperature). Boxplots show interquartile ranges, median shown as a horizontal black line, and 1.5× interquartile range are shown by the whiskers. Points represent individual measurements and means are shown by black diamonds. SMR and RMR were size-corrected using log-log regression against wet weight and standardized to the mean body mass of the study organisms (2.98 g). For both SMR and RMR, temperature ($p < 0.05$) were significant predictors of metabolic rate. Acclimation duration significantly elevated metabolic rate at 34 °C (SMR: $t = 2.15$, $p<0.05$; RMR: $t = 2.47$, $p < 0.05$).

2.4.3 Metabolic Responses to Sustained Temperature Exposure and acclimation

Across all temperature and acclimation treatments, size-corrected SMR of *Drupella* spp. ranged from 0.067 mg O_2 h^{-1} to 0.621 mg O_2 h^{-1}, and size-corrected RMR ranged from 0.176 mg O_2 h^{-1} to 0.635 mg O_2 h^{-1}. Linear models were fitted to test the effects of temperature, body mass, and acclimation group on metabolic rate, including interaction terms to assess whether the influence of temperature varied with body size or acclimation treatment. These analyses were based on measurements from 54 individual snails, 14 held at each acclimation temperature. Full model outputs for both SMR and RMR are provided in the Supplementary Materials (S3 and S4).

Temperature significantly influenced both SMR and RMR, with metabolic rate increasing at 30°C, 32°C, and 34°C relative to 28°C for both metrics (all $p < 0.05$). In *Drupella* spp. acclimated for three days, SMR increased by 67.3% and RMR by 39.3%, between 28°C and 32°C. At 34°C both declined from their peaks at 32 (SMR: -29.9%, RMR: -29.6%), returning close to their values at 28°C (Fig 2.3). *Drupella* spp. acclimated for 19-22 days saw SMR and RMR between 28°C and 32°C increases by 26.9% and 19.1% respectively. Yet unlike those acclimated for only three days, at 34°C both SMR and RMR remained above the 32°C values with SMR increasing by 4.2% and RMR by 8.7% (Fig. 2.3). These findings indicate that for *Drupella* spp. acclimated for three days show stronger thermal sensitivity, with increased metabolic activity with warming and metabolic depression after 32°C, whereas snails acclimated for 19-22 days show more moderate increases and no evidence of metabolic depression.

Q_{10} values for SMR and RMR were calculated between successive temperature steps using treatment means and are shown in Table 2.1. From 28 °C to 32 °C Q_{10} values across both acclimation groups (SMR: 1.30–2.73; RMR: 1.37–2.17, Table 2.1) fell within the range reported in other ectotherms, consistent with metabolic responses to moderate warming (Hue & Kingsolver, 2019). Q_{10} values between 32°C and 34°C differed between acclimation treatments. In *Drupella* spp. acclimated for three days, Q_{10} values dropped below one (SMR: 0.17; RMR: 0.20), indicating metabolic depression, whereas in the 19–22-day group values remained above one (SMR: 1.22; RMR: 1.50). These findings indicate that *Drupella* spp. acclimated for three days show stronger thermal sensitivity, with increased metabolic activity with warming and metabolic depression after 32°C, whereas snails acclimated for 19-22 days show more moderate

increases and no evidence of metabolic depression. This suggests a greater capacity in those acclimated for longer to sustain metabolic performance under increasing temperatures.

Even though metabolic suppression was not seen in either RMR and SMR in *Drupella* spp. acclimated to 34 °C for 19-22 days (Fig 2.3), the statistical significance of the effect of acclimation duration differed between the two measures. For SMR, acclimation duration was not a significant factor at any temperature ($p > 0.05$), and including the interaction between temperature and acclimation duration did not significantly improve model fit ($F_{4,99}=2.10$, $p=0.087$). Contrastingly, a significant effect of acclimation was detected for RMR at 34 °C (Temperature34 × Acclimation 19–22: $t = 2.13$, $p <0.05$), indicating that individuals acclimated for 19–22 days had higher RMR at 34 °C compared to those acclimated for only three days. This pattern is also evident in Figure 2.3, where the longer acclimation group in RMR have a visibly higher median, and overall distribution compared to the shorter acclimation duration, whereas in SMR the medians and spread are more closely together for the two acclimation groups. These findings indicate that *Drupella* spp. show evidence for thermal acclimation, but that longer acclimation to high temperatures has a stronger influence on RMR than SMR.

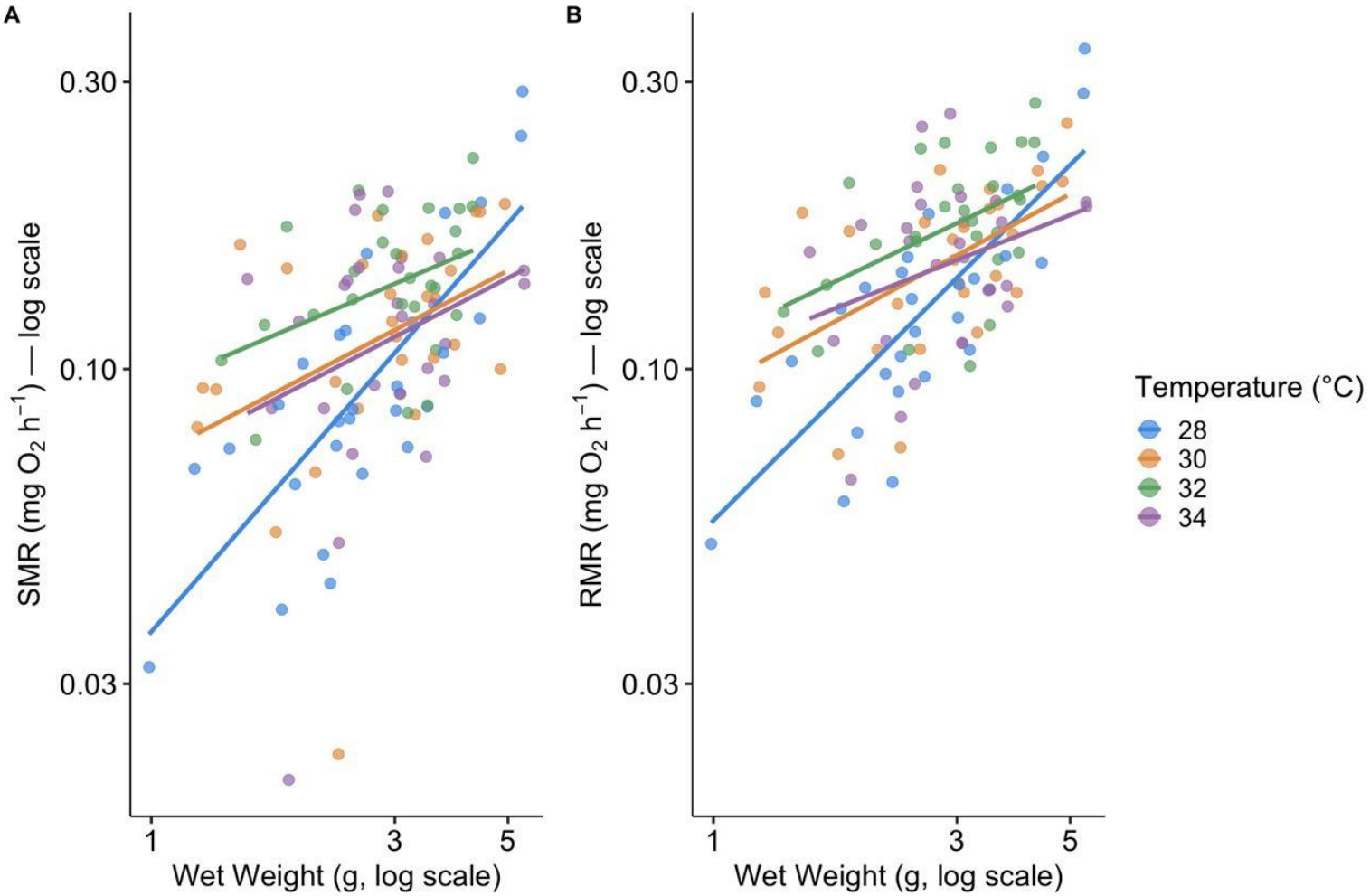

Figure 2.4. Relationship between log-transformed wet weight and log-transformed metabolic rate in *Drupella* spp. across four temperature treatments (28°C,30°C,32°C and 34°C). (A) Standard metabolic rate (SMR) and **(B)** routine metabolic rate (RMR) as functions of wet weight (g), with temperature-specific linear regressions. Points represent individual snails; lines indicate fitted models. The slopes show temperature-dependent shifts in the scaling of metabolic rates with body size. The colours of the different lines correspond with the temperature treatment, shown in the key on the right-hand side.

Table 2.2 Scaling components (b) from log-log regression of metabolic rate on body mass. b values are shown for both standard metabolic rate (SMR) and routine metabolic rate (RMR) at each temperature tested 28°C,30°C,32°C and 34°C. b values shown are the regression slopes, plus/minus standard error (SE), that relates log metabolic rate to log mass indicating how metabolism scales with mass at each temperature.

Temperature (°C)	SMR b ± SE	RMR b ± SE
28	0.971 ± 0.155	0.845 ± 0.123
30	0.445 ± 0.201	0.46 ± 0.126
32	0.362 ± 0.162	0.407 ± 0.151
34	0.441 ± 0.29	0.337 ± 0.199

2.4.4 Body Mass–Temperature Interactions Under Sustained Warming

To investigate how SMR and RMR scaled with body mass across temperatures, linear models were fitted with temperature, wet weight, and their interaction, testing of whether the effect of body mass on metabolic rate changed with warming. Full model outputs are presented in the Supplementary Materials (S3 & S4). Both SMR and RMR increased significantly with body mass across all acclimation temperatures (Fig. 2.4; SMR: $t = 6.94$, $p < 0.001$; RMR: $t = 7.40$, $p < 0.001$), with corresponding mass-scaling exponents of b = 0.64 ± 0.10 for SMR and b = 0.59 ± 0.08 for RMR. Interestingly, the strength of the effect of body mass on both SMR and RMR decreased with increasing temperature (Fig. 2.4; SMR: Temperature × Wet weight t values from –2.35 to –3.49, all $p < 0.05$; RMR: t values from –1.99 to –3.32, all $p < 0.05$). This can be seen by the progressively shallower slopes from 28 °C to 34 °C (Fig. 2.4). SMR scaling exponents (b) decreased by 55 % from 28 °C to 34 °C, while RMR scaling exponents decreased by approximately 60 % (Table 2.2). Therefore, the results indicate a reduction in the influence of body mass on metabolic rate under increasingly warmer conditions.

2.5 Discussion

As coral reefs experience increasing thermal stress the capacity of corallivores to maintain or adjust their metabolic performance will influence both their survival and the extent of their impact on already vulnerable reef systems (Lang et al., 2021; Rice et al., 2019). *Drupella* spp. exposed to acute warming exhibited no limits to metabolic performance up to 38 °C, with metabolic rates increasing across all individuals in line with typical ectotherm thermal responses (Schulte et al., 2011; Lang et al., 2021). This pattern reflects the increased kinetic energy at higher temperatures, which raises enzyme–substrate collision frequency and elevates the proportion of molecules exceeding activation energies. The absence of metabolic downturn suggests that 38 °C falls within their acute thermal tolerance range under well oxygenated laboratory conditions. Such tolerance may enhance the resilience of *Drupella* spp. to heatwaves (which last days to months) or short duration thermal increases lasting a few hours, events that are becoming more frequent with climate change (Hobday et al., 2016; Oliver et al., 2021). While behavioural response to acute thermal increase were not measured here, the ability to maintain metabolic function at elevated temperatures could have implications for their activity during periods when corals are most thermally stressed (Lang et al., 2022).

Drupella spp. which had been acclimated to 28°C and 34°C prior to ramping showed similar increases in metabolic rate with rising temperature, indicating that prior exposure to warmer temperatures did not alter their thermal sensitivity. Similarly, Shirokova et al (2025) found that the depth where freshwater amphipods*, Ommatogammarus,* were found, representing acclimation history, did not alter response to 1 °C h^{-1} ramping experimental. The authors attributed the lack of effect from acclimation history to the species' broad tolerance to heating, for instance noting their robust antioxidant defences under thermal stress. The absence of an acclimation effect on acute warming in *Drupella* spp. may therefore reflect a similarly wide physiological tolerance, allowing similar metabolic increases regardless of recent thermal history. Further research could study underlying physiological markers such as glucose levels, antioxidant enzyme activities, and measures of anaerobic metabolism (LDH activity and lactate), to provide insight into the processes occurring at the cellular level in the snails during acute warming (Shirokoca et al.,2015).

During prolonged exposure, *Drupella* spp. showed temperature-dependent metabolic responses, with SMR and RMR increasing between 28 °C and 32 °C across all acclimation durations. After three days of acclimation at their final temperatures, *Drupella* spp. showed decreases in metabolic rate above 32 °C, with SMR and RMR declining by 29.9% and 29.67%, respectively, unlike individuals acclimated for 19–22 days, in which no metabolic decline was observed. Such reductions may impair movement, feeding, immune response and tissue repair, increasing mortality risk (Lang et al., 2022; Huey & Kingsolver, 2019; Sahoo & Acharya, 2025). Several mechanisms may explain this decline, the most plausible being that individuals were approaching their thermal optimum and physiological processes began to break down. While moderate warming can increase enzyme activity, excessive heat can denature or destabilise enzymes, reduce substrate affinity, or disrupt enzyme complexes involved in aerobic metabolism, leading to impaired ATP production and metabolic depression (Schulte, 2015; Tattersall et al., 2012). Reduced oxygen supply could also contribute, as oxygen solubility declines with temperature; however, this alone would be expected to cause a metabolic plateau rather than the downturn observed (Rubalcaba et al., 2020).An alternative explanation is adaptive metabolic depression, in which organisms actively reduce metabolic rate by downregulating aerobic enzyme production to limit energy use and prevent cellular damage (Guppy & Withers, 1999; Storey & Storey, 1990). For example, the subtidal gastropod *Turritella bacillum* exhibited sustained bradycardia and low oxygen uptake under heat and hypoxic stress, reflecting a regulated hypometabolic state that supports survival without incurring substantial anaerobic debt (Marshall & McQuaid, 2020). However, if the decline in *Drupella* spp. were due to adaptive metabolic depression, it would be expected across all acclimation durations. The absence of metabolic suppression in individuals acclimated for 19–22 days instead suggests that the decrease observed after three days reflected an acute heat-shock response occurring before sufficient time for acclimation.

Drupella spp. acclimated for 19–22 days showed no metabolic decline with warming, and at 34 °C had significantly higher RMR than snails acclimated for only three days. SMR showed the same pattern, though not statistically significant due to greater overlap. This indicates that prolonged acclimation enhances thermal tolerance, with greater plasticity in RMR than SMR. Higher metabolic variation in the 19–22-day group compared to the three days at 34 °C also

suggests individual differences in acclimation capacity. As RMR reflects spontaneous activity rather than baseline maintenance, it may be more responsive to temperature (Norin et al., 2016), as seen in other marine ectotherms where SMR remains stable while MMR and aerobic scope show greater thermal plasticity. Increasing RMR at high temperatures may enable *Drupella* spp. to continue feeding and reproducing during warming events, potentially intensifying their ecological impacts with temperature. This supports the idea that *Drupella* spp. may experience a transient heat-shock response at 34 °C which is resolved once physiological adjustments (e.g., enzyme stabilisation, membrane restructuring) occur during prolonged acclimation, however more research into these physiological underpinnings would be beneficial to fully understand what is happening during this acclimation.

In both prolonged and acute studies, the temperatures at which *Drupella* spp. maintain high metabolic performance coincide with the onset of mass coral bleaching on Indo-Pacific reefs (Fitt et al., 2001; Hughes et al., 2017). This overlap suggests that peak feeding may occur when corals are already physiologically compromised, accelerating reef degradation (Sharp, Brown & Miller, 1997). For example, *Acropora* spp. in northwest Australia experienced severe bleaching and up to 75% mortality at daily averages above 32 °C (Schoepf et al., 2015). Moreover, increases in SMR and RMR do not necessarily indicate that aerobic scope is maintained; if MMR plateaus or declines while baseline metabolic costs rise, aerobic scope will contract, potentially constraining performance despite the absence of metabolic depression. Future work should therefore quantify MMR to determine how warming affects aerobic capacity in *Drupella* spp.

Temperature shaped these patterns differently across experiments. In the prolonged trial, the scaling component at 28 °C was almost double that observed at warmer temperatures, indicating that at lower temperatures larger individuals can fully express size-related metabolic capacity. At 30–34 °C, thermal constraints likely dampened size effects and drove convergence in metabolic rates regardless of body size, consistent with evidence that environmental stress can reduce metabolic scaling slopes (Glazier, 2020; Rubalcaba et al, 2020; Killen et al., 2010). In the acute ramping trial, where temperature increased by 7 °C over nine hours, larger individuals showed steeper rises in metabolism than smaller ones, likely because physiological systems such as gill

ventilation and heart rate can temporarily match rising oxygen demand under well-oxygenated laboratory conditions (Gilbert & Farrell, 2021). In the absence of oxygen limitation, larger snails are able to sustain the increased oxygen requirements associated with warming, supporting their greater energetic demands arising from larger cell numbers and more complex internal transport systems (Brown et al., 2004). This temperature-dependent shift in size effects may alter population size structure and therefore predation pressure on corals, with warming favouring smaller individuals and potentially changing the ecological impact of *Drupella* spp, outbreaks, but more research is needed to assess this.

3 The influence of thermal warming on Feeding and Growth in the Corallivorous gastropod *Drupella* spp.

1.1 Abstract

The obligate corallivore muricid gastropod *Drupella* spp., has been documented to cause extensive damage to reefs across the Indo-Pacific. Increasing ocean temperatures and corallivore outbreaks are two of the biggest risks facing coral reefs. However, little is known about the synergistic impacts of these two stressors, including how thermal shifts may affect *Drupella* spp. feeding and growth rates. In laboratory conditions, we investigated how increasing seawater temperatures (28°C, 30°C, 32°C) influence *Drupella* spp. feeding on Acropora spp. and short-term growth. To measure feeding, *Drupella* spp. were placed individually in floating tubs within their given temperature treatments, each containing a single piece of *Acropora* spp., and left for 18 hours. Feeding was calculated from measuring the area of coral scarring left by the snails. Despite mean feeding area increasing by 26.4% from 28°C to 32°C, temperature had no significant effect on feeding activity. Standard metabolic rate and routine metabolic rate also did not predict feeding performance in *Drupella* spp. Wet weight, on the other hand, showed a significant positive effect on feeding area. Over 20-23 days, *Drupella* spp. showed no significant increase in wet mass and shell length but not shell width, and size metrics were not significantly effected by temperatures. Our results suggest that within the given temperature range *Drupella* spp. can maintain feeding capacity and growth, but temperature alone does not explain the variation. Ecologically, even stable or weak temperature increases in predation coupled with stressed corals could be damaging. Incorporating temperature and feeding rates into outbreak models will improve predictions and management thresholds under progressing climate change.

3.2 Introduction

Corallivorous gastropods of the genus *Drupella* spp. are among the most ecologically damaging invertebrate predators on Indo-Pacific coral reefs (Bruckner et al., 2017; Morton & Blackmore,

2009; Cumming, 2009; Hoeksema et al., 2013). In contrast to many coral predators whose feeding mechanisms are less damaging, more spatially restricted, or short lived, *Drupella* spp. can cause prolonged and severe coral mortality (Cole et al., 2008; Turner, 1994). Unlike corallivores that feed on coral mucus, these obligate corallivores feed on the actual living tissue of scleractinian corals, with their aggregative feeding behaviour often resulting in significant reef degradation (Turner & Buckley, 2001; Morton & Blackmore, 2009; Hoeksema & Scott, 2020). Outbreaks have been reported across a wide geographical range, from the Red Sea to Japan and Australia, prompting increasing research into their distribution, behaviour, and prey preferences (Cumming, 1999; Antonius & Riegl, 1998; Hoeksema & Scott, 2020; Fujioka et al., 2015). Although research on *Drupella* spp. feeding has increased, there has been a disproportionate focus on prey selection, with comparatively fewer studies examining the rate of coral tissue consumption or the influence of environmental variables on feeding behaviour (Morton & Blackmore, 2009; Al-Horani et al., 2011).

Drupella spp. feed using a specialised radula adapted to rasp coral tissue from the calcium carbonate skeleton, leaving behind distinctive white scars on coral surfaces (Cernohorsky, 1969; Fujioka, 1982). Feeding typically occurs nocturnally, whilst during the day individuals remain cryptic, aggregating in crevices and camouflaged by pink calcareous algae (Boucher, 1986; Cumming, 1999). *Drupella* spp. are rarely observed feeding in isolation, instead, they are commonly found in small groups or dense aggregations, a behaviour that not only intensifies localised coral damage but also complicates management effort (Bruckner et al., 2017; Cumming, 2009). At natural densities on healthy reefs, *Drupella* spp. may play a functional role in shaping coral assemblages by preferentially feeding on fast-growing genera such as *Acropora* and *Montipora*, *Drupella* spp. reduce coverage of competitive dominant coral genera and create space for slower-growing, more stress-tolerant species (Rotjan & Lewis, 2008). By allowing space for slow-growing corals, *Drupella* spp. can help enhance both structural and taxonomic diversity on a reef (Turner, 1994; Morton et al., 2002). However, under the present day impacts of climate change, characterised by widespread coral bleaching, elevated thermal stress and decreased recovery capacity, reefs are less resilient to such predation (Hughes et al., 2017; Edmunds & Lenihan, 2010; Sivaguru et al., 2023).

There are multiple reports of *Drupella* outbreaks following major coral stress events, such as bleaching (Hoeksema et al., 2013; Bruckner et al., 2017) or cyclone damage (Zhang et al., 2024). When preferred fast-growing corals are depleted, such as during bleaching events, *Drupella* spp. may shift to feeding on slower growing, structurally important species that are less capable of recovery (Hoeksema et al., 2013; Kayal et al., 2012; Sivaguru et al., 2023). Such shifts highlight how rising ocean temperatures can indirectly increase reef vulnerability, not only changing *Drupella* spp. feeding patterns but also potentially disrupting the equilibrium between coral recovery and snail predation. Without effective refuges for the coral, or top-down controls prey on the snails, *Drupella* spp. populations may persist beyond the point of prey depletion due to abilities to switch between prey. These dynamics seen in classic predator–prey models where delayed population responses or limited spatial refuges result in ecosystem instability (Huffaker, 1958).

Temperature not only reduces reef resilience to corallivory but may also amplify the ecological impact of *Drupella* spp. by increasing their feeding and activity levels. In marine ectotherms, both behaviour and metabolism are strongly influenced by temperature, with warmer conditions generally driving increased consumption and activity (Wyban et al., 1995; Rall et al., 2012). Results from the previous chapter showed that elevated temperatures (up to 32 °C with three days acclimation, and at least 34°C with longer acclimation), can increase metabolic demands, which in turn will require greater energy intake to sustain basic physiological processes. The resulting increase in energy requirement can drive greater feeding intensity (Wyban et al., 1995; Rall et al., 2012). For example, in channel catfish (*Ictalurus punctatus*), increased water temperatures have been shown to increase food consumption and growth (Buentello et al., 2000). Although the relationship between metabolic rate and feeding is well established, no research has yet explored how metabolic rate relates to feeding behaviour in *Drupella* spp.

Seasonal and thermal patterns in *Drupella* spp. activity have been observed in the field, for example, *Drupella rugosa* populations in Hong Kong showed elevated feeding and increased densities during the summer months when sea temperatures exceeded 27 °C, whereas in winter, when temperatures fell below 20 °C, feeding activity ceased as individuals became inactive (Morton & Blackmore, 2009). The study suggests that temperature impacts *Drupella spp.*

behaviour, influencing levels of feeding intensity and therefore the heightening ecological impact. Despite these field-based observations, experimental data on temperature-driven feeding responses in *Drupella* spp. remain limited. Most existing research on temperature effects in aquatic gastropod feeding has focused on herbivorous or detritivores species (e.g., McLean, 1962; Paine, 1971; Foster & Hodgson, 1998), leaving a gap in our understanding of thermal sensitivity in corallivorous taxa. To date, only one laboratory study has explicitly examined temperature effects on *Drupella* spp., using only two individuals of *D. cornus (*Al-Horani et al., 2011*).* Al-Horani *et al.* (2011*)* reported a fivefold increase in feeding rates between 18 °C and 30 °C. Although limited in sample size, these results raised important concerns that ocean warming could enhance the top-down pressure exerted by *Drupella* spp., particularly when coral tolerance is already compromised at high temperatures. Therefore, there is a need for additional research to better understand how temperature affects feeding behaviour in *Drupella* spp. and the broader implications for reef ecosystems under climate change.

Thermal increases in metabolic rate and consequentially feeding rate has been seen to lead to increasing organismal growth (Volkoff & Rønnestad, 2020). However, just like metabolism, this relationship is often only seen within species specific thermal limits, with excessive or prolonged heat exposure potentially suppressing growth by reducing energy available for tissue synthesis or impairing feeding efficiency (Cloyed et al., 2019; Rall et al., 2010, 2012; Shokri, Cozzoli & Basset, 2024). For instance, Arctic char exhibited increased growth between 5 °C and 13 °C, but growth halted entirely at 21 °C (Beuvard, Imsland & Thorarensen, 2022). Similar patterns have been seen in molluscs, where short-term warming extends foraging and enhances tissue growth whereas prolonged heat induces stress responses that divert energy from growth to cellular maintenance (Vaughn et al., 2013) In a broad comparative study of molluscs, Broell et al. (2017) reported that growth increased with the time spent at optimal temperatures, but declined when temperatures fell outside this range. Understanding how temperature influences growth in *Drupella* spp. is ecologically important as growth rates determine the timing of reproductive maturity and can affect the onset of population outbreaks. Consequently, changes in *Drupella* spp. growth, whether accelerated or suppressed, are likely to impact both feeding pressure and broader reef ecosystem damage.

In contrast to the little research on *Drupella spp.* feeding and growth, the nutritional and developmental responses of COTS to environmental change are far better studied. Numerous studies have shown that COTS show increases in both feeding and growth under ocean warming and acidification. The increases are thought to be driven by elevated metabolic rates as well as changes in prey condition, such as weakened skeletal defences (Lang et al., 2022; Kamya et al., 2017, 2018; Uthicke et al., 2013). Similar mechanisms may apply to *Drupella* spp., where warming may both increase metabolic demand and weaken coral hosts, potentially enhancing predation rates. *Drupella* spp. are known to be attracted to stressed corals, showing preferecne to injured coral tissue over healthy tissue (Hoeksema et al., 2013; Rice et al., 2019). Preference to damaged tissue is thought to result from chemical cues released by stress. For example, Morton, Blackmore & Kwok (2002) found that increased mucus release from stressed corals attracts *Drupella* spp. to the injured area. Warming temperatures could therefore create conditions that both raise *Drupella* spp.'s metabolic, and consequent feeding, while also making coral prey more vulnerable to predation. Such synergistic interactions could potentially lead to intensified and prolonged predation events, yet little research has examined how temperature affects the feeding of *Drupella* spp.

Despite the importance of understanding the relationship between seawater temperature and *Drupella* spp. feeding for predicting ecological damage and defining outbreak densities, this relationship remains poorly quantified under controlled experimental conditions. As climate change accelerates and coral stress events become increasingly frequent, it is even more important now to understand how rising temperatures may influence the behaviour of coral predators. This study investigates the effects of seawater temperature on feeding rates and growth in *Drupella* spp. when presented with their preferred prey, *Acropora* spp. By examining temperature-dependent feeding and growth responses, we aim to evaluate whether ocean warming may influence *Drupella* spp. coral predation and population increases. These findings provide important insights into predator–prey dynamics on coral reefs under climate stress, which can inform strategies for mitigating future coral loss.

3.3 Methods

3.3.1 Feeding Assay and Coral Exposure Protocol

Figure 3.1 Example of coral scarring measurement to estimate *Drupella* spp. feeding. Acropora spp. fragment that *Drupella* spp. was confined with in a floating tub for 18 hours at their given temperature treatment. Scarring is the white area of the coral where the coral tissue has been scraped away by *Drupella* spp. radula. Scarring area measured using Image J as shown by the yellow line. The *Drupella* spp. individual in the image, marked with pink nail varnish for identification, is the snail that consumed the coral tissue.

To investigate the effects of elevated temperature on *Drupella* spp. feeding behaviour, an overnight feeding assay was conducted using live *Acropora* spp. coral fragments. Fragments of *Acropora* spp. (6 cm in length) were placed individually into eight floating mesh containers, each fitted with a secure plastic lid, and held in the same temperature-controlled tanks used to house the snails during acclimation. The mesh design allowed for water exchange between the containers and their surrounding aquaria, ensuring that the water inside the containers accurately reflected the assigned treatment temperatures (28 °C, 30 °C, or 32 °C). Feeding was also trialled

at 34 °C however, the coral consistently bleached under this temperature, making it impossible to reliably distinguish feeding scars from bleaching, and therefore was excluded from any further analysis. Coral fragments were acclimated in their tubs to their respective temperatures for approximately 18 hours prior to the introduction of *Drupella* spp. individuals. During the coral acclimation period, *Drupella* spp. were held in the intermittent flow respirometry (IFR) for measuring of their metabolic rates. To control for postprandial metabolic effects, all snails were fasted for approximately 51 hours prior to the feeding trial, having last been in a tank with food at midday two days earlier. Before being introduced to the experimental containers, each snail was blotted dry and weighed. At 15:00, one *Drupella* spp. individual was placed into each floating container containing an acclimated *Acropora* spp. fragment. One container per trial was maintained without a snail to serve as a control for background coral tissue changes unrelated to feeding. All containers were maintained under a 12:12 h light–dark cycle, with lights switching off at 18:00 and on at 06:00, to simulate natural diel rhythms and provide environmental cues consistent with the species' nocturnal activity pattern.

At 09:00 the following morning, 18 hours after snail introduction, each coral fragment and its corresponding *Drupella* spp. individual were removed from their container and placed on a white plastic tray alongside a metric ruler. Coral fragments were photographed from both lateral sides under consistent lighting provided by a standard adjustable desk lamp positioned overhead. *Drupella* spp. individuals were included in each photograph to allow for accurate identification of snail and coral fragments during image analysis. After being photographed, the snails were returned to their assigned respective aquaria. Feeding amount was identified as areas of white, bleached, or necrotic coral tissue indicative of *Drupella* spp. grazing scars, following methods adapted from Al-Horani et al. (2011). Image analysis was conducted in ImageJ (v1.53), using the freehand polygon selection tool to manually outline grazed areas on both lateral surfaces of each coral fragment. The traced regions were added together to yield a total feeding area (cm^2) per individual, providing a quantitative measure of grazing intensity across the temperature treatments.

3.3.2 Growth Rate Measurements

To assess the growth of *Drupella* spp., measurements of wet weight, shell width and shell length were taken immediately after each time the snail went through IFR (See Chapter 2). Snails were removed from their IFR chambers, gently blotted dry using a clean cloth to minimise surface water from their shells and then weighed to the nearest 0.001 g. Shell length and width were measured using standard callipers to the nearest 0.01 mm. The first measurements were taken after IFR following three days of acclimation, and subsequent measurements were conducted 20 to 23 days later, also directly after metabolic respirometry. For each individual, growth rate was calculated by subtracting the initial measurement from the final measurement for each trait (wet weight, shell length, or shell width) and dividing the result by the number of days between measurements, giving a daily growth rate for each parameter.

3.3.3 Data and Statistical Analysis

The feeding trial was conducted over a fixed duration of 18 hours, but individual feeding activity was not continuously monitored and thus the data represents cumulative feeding area rather than specific feeding rates. Many individuals did not graze during the trial, resulting in a substantial number of zero values in the dataset. To account for these zero inflations, a zero-inflated Gamma generalised linear model (GLM) was fitted using the glmmTMB package in R. Feeding area was modelled separately as functions of SMR and RMR, with both models including interactions with temperature and wet weight. In the model, the conditional component described variation in *Drupella* spp. feeding area that fed on coral (non-zero), whilst the zero-inflation component modelled the probability of a snail not eating at all (zero values). Temperature and wet weight were included as predictors of both the non-zero and the zero values, to see whether these factors influenced the occasion of *Drupella* spp. feeding or not. Likelihood ratio tests were used to compare full models with reduced models for both SMR and RMR, allowing assessment of the overall effect of temperature beyond the main effects of metabolic rate and body size.

To analyse temperatures effect on growth, measured as changes in individuals wet weight, width and shell width over the 20–23-day experimental period, linear models were fitted for each trait.

These models used initial size and temperature as predictors of each growth trait. Additionally, paired t-tests were used to compare growth of the three traits from the start to end to evaluate net change across the individuals. Model fits were assessed using diagnostic plots of residuals to check assumptions of normality and homoscedasticity. All statistical analyses were conducted in R. Graphs and model diagnostics were performed using ggplot2.

3.4 Results

3.4.1 Field Observations of *Drupella* spp. Distribution

In the field, *Drupella* spp. individuals were observed feeding exclusively on branching Porites spp. colonies with no individuals recorded on other coral genera. Despite its presence at other sites around the island, no *Drupella* spp. were seen on Acropora spp. High densities of *Drupella* spp. >100 snails per coral colony were found but were not quantified or further investigated in this study. Individuals were typically found within the coral branches rather than on the surface of the coral.

Table 3.1 Mean feeding area (± SD) of *Drupella* spp. at each temperature treatment (28°C, 30°C, 32°C). Feeding area was assessed after holding individual snails with a piece of *Acropora* spp for 18 hours and was measured as the area of scarring in cm². N = number of individuals of which results were obtained from at each temperature.

Temperature (°C)	Mean feeding area ± SD (cm²)	N
28	2.77 ± 2.42	25
30	2.83 ± 2.87	26
32	3.50 ± 2.44	19

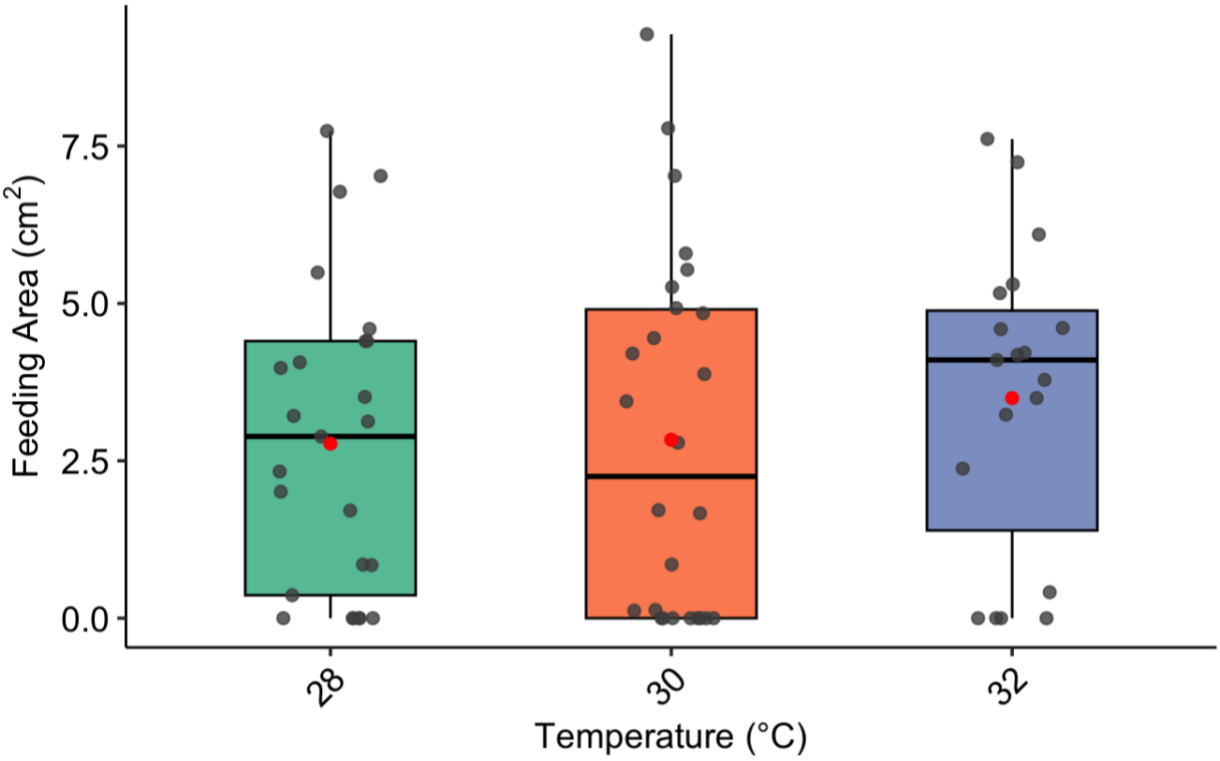

Figure 3.2 Feeding area cm^2 of individuals across three temperature treatments 28,30,32. Boxes represent the interquartile range (IQR), with the median shown as a horizontal black line and the mean shown by the red dot. Whiskers extend to 1.5× IQR, and individual black circles represent raw data points.

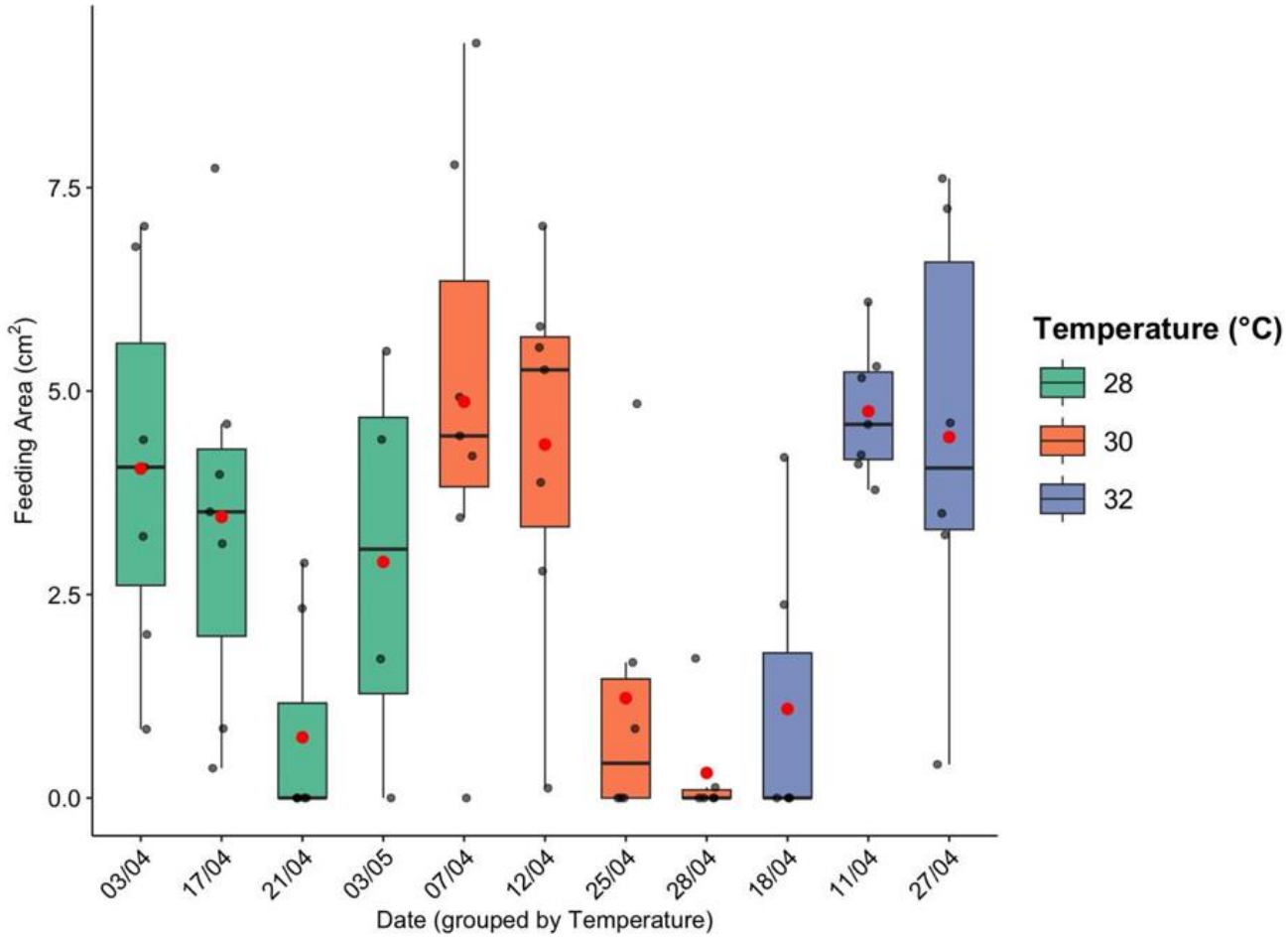

Figure 3.3 Feeding area (cm²) of *Drupella* spp. across experimental dates, grouped by temperature treatment. Boxes represent the interquartile range (IQR), with the median shown as a horizontal black line. Whiskers extend to 1.5× IQR, and individual points represent individual observations. Temperature treatments are indicated by colour, 28°C (green), 30°C (orange) and 32°C (purple). Feeding measurements were taken after 18 hours of holding individual snails with a single *Acropora* spp. fragment at their given seawater temperatures.

3.4.2 Feeding rates across temperature treatments, wet weight, and time

Zero-inflated Gamma models were used to analyse feeding area, with full models including SMR or RMR, temperature, and wet weight as fixed effects, along with interactions between metabolic rate and temperature or wet weight (S5 & S6) . Model selection based on likelihood ratio tests showed that these interaction terms did not improve model fit (SMR model: $\chi^2 = 5.43$, df = 3, p = 0.143; RMR model: $\chi^2 = 3.77$, df = 3, p = 0.288), and the reduced models containing only the main effects provided a better fit, as shown by their lower AIC values. The conditional (non-zero) component revealed no significant main effect of either SMR or RMR on feeding area (SMR: β= 4.84, z = 0.897, p = 0.370; RMR: β= 4.30, z = 0.903, p = 0.366) suggesting that changes in metabolic rate did not influence feeding area. Mean feeding area increased by 2.2% from 28 °C to 30 °C, followed by a further 23.7% increase from 30 °C to 32 °C, resulting in a total increase of 26.4% between the lowest and highest temperature treatments (Table 2). However, temperature did not significantly affect feeding area in the conditional model (SMR model: 30 °C p = 0.431, 32 °C p = 0.192; RMR model: 30 °C p = 0.350, 32 °C p = 0.143). These findings are consistent with the strong overlap in feeding distributions across treatments (Fig. 3.2 which indicates that variation in temperature did not explain differences in feeding activity. Consistently, overlap in interquartile ranges across temperature treatments further illustrates the lack of significant influence of temperature on feeding area (Fig. 3.2. Additionally, the likelihood of zero feeding events was not significantly influenced by temperature (SMR : all *p*s > 0.05; RMR : all *p*s > 0.05). Overall, there was no evidence that variation in SMR, RMR, or temperature explained differences in feeding activity or the chance of grazing in *Drupella* spp.

Feeding activity varied across experimental dates, with moderate grazing observed on some days (e.g., 03/04, 07/04, 11/04) and little to no feeding on others (e.g., 21/04, 28/04) (Figure 3.3). However, adding sampling date as a fixed effect in the zero-inflated Gamma model did not significantly improve model fit ($\chi^2 = 14.36$, df = 8, $p = 0.073$) indicating no consistent temporal trend in feeding behaviour. *Drupella* spp. wet weight had a significant positive effect on feeding area (SMR model: β = 0.182, p < 0.05; RMR model: β = 0.225, p < 0.05), indicating that larger individuals consumed greater amounts of coral when they fed. In the zero-inflation component, the likelihood of individuals that did not feed was not significantly impacted by wet weight (β =

0.086, p = 0.671). Together, these results show that although feeding area increased with temperature, temperature, SMR and RMR did not significantly explain variation in feeding activity or the chance of feeding. Body weight was the only predictor of feeding amount in *Drupella* spp, yet also did not influence whether a snail fed or did not feed.

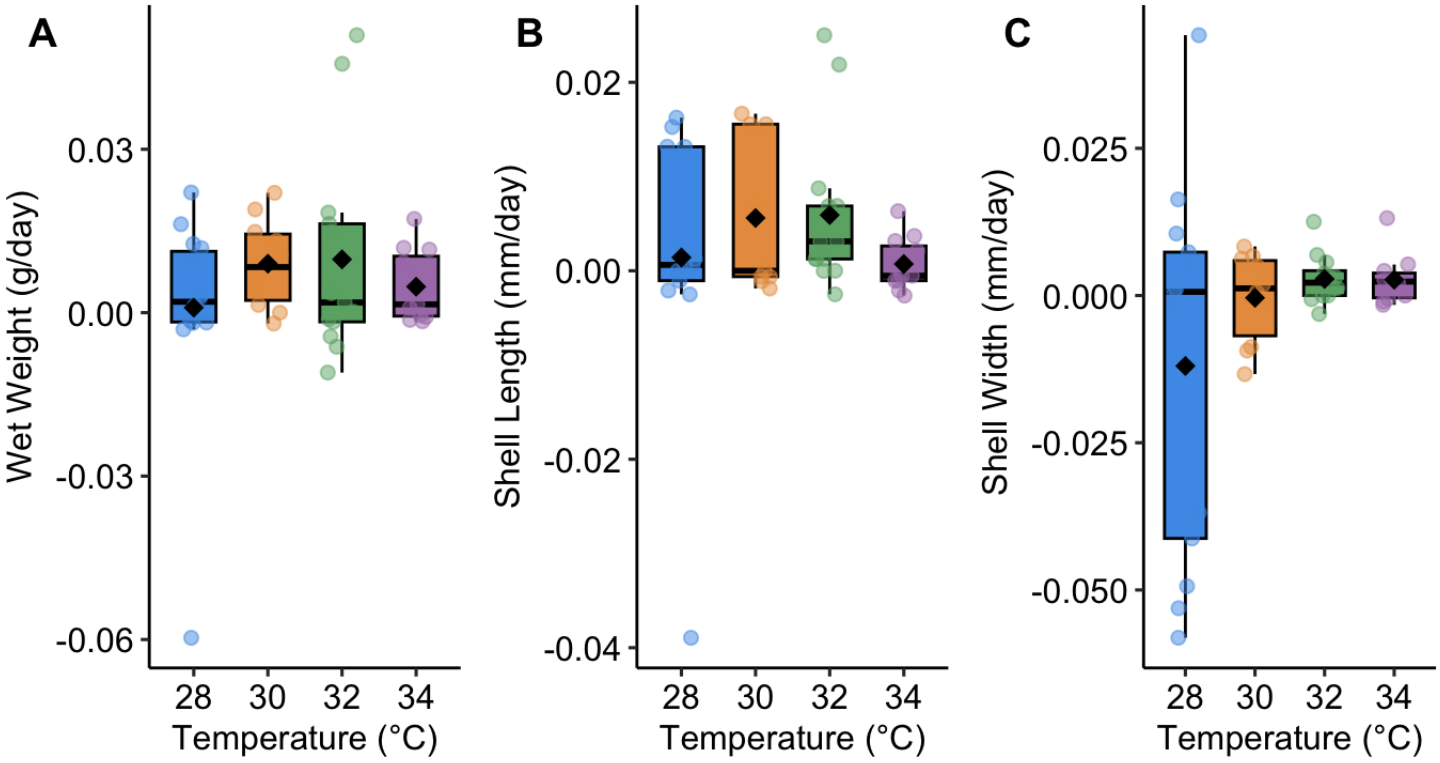

Figure 3.4 Growth rates in shell morphology and wet weight of *Drupella* spp. over 20–23 days of exposure to one of four temperature treatments (28°C, 30°C, 32°C, 34°C). (A) Wet weight (g/day), **(B)** shell length (mm/day), and **(C)** shell width (mm/day) are shown as daily rates of change per individual. Boxes represent the interquartile range (IQR), black horizontal lines show medians, black diamonds are the means, and individual points represent raw observations.

3.4.4 Growth performance and shell morphometrics

Analysis of *Drupella* spp. growth over 20-23 days held at one of 28°C, 30°C, 32°C, 34°C showed that on average snails increased wet weight by 5.88%, shell length by 2.95% and shell width by 0.67%. Paired t-tests between the first and second measurements of growth metrics showed significant increases in wet weight ($t_{47} = 2.58$, $p<0.01$, mean change = 0.099g) and shell length ($t_{45} = 2.23$, $p<0.01= 0.031$, mean change = 0.056mm), while shell width did not change significantly ($t_{44} = –0.61$, $p = 0.55$, mean change = –0.028 mm). Smaller snails grew more than larger ones with initial size significantly affecting growth in length ($\beta = −0.36$, $p < 0.001$; model $R^2 = 0.26$), width ($\beta = −0.84$, $p < 0.001$; $R^2 = 0.68$), and wet weight ($\beta = −0.115$, $p <0.001$; $R^2 = 0.22$). Temperature had no significant effect on any of the growth metrics, shell length ($\beta = 0.006$, $p = 0.56$, $R^2 = 0.26$), shell width ($\beta = 0.006$, $p = 0.63$, $R^2 = 0.68$), or wet weight ($\beta = 0.019$, $p = 0.23$, $R^2 = 0.22$).

3.5 Discussion

In the field, *Drupella* spp. were observed exclusively on branching *Porites spp.* colonies, an interesting observation given their well-documented preference for *Acropora spp.* across much of the Indo-Pacific (Turner, 1994; Schoepf et al., 2010; Moerland et al., 2016). Despite *Acropora spp.* being present elsewhere on the reef, their spatial separation from the sites where *Drupella* spp. were seen suggests that prey availability alone does not fully account for the observed *Drupella spp.* distribution on the reefs of Moorea. This may suggest that local environmental conditions and biotic interactions may also being playing a role in *Drupella spp.* distribution. Branching *Porites spp.* offer structural complexity comparable to that of *Acropora spp.*, potentially providing refuge for cryptic or juvenile individuals (Schoepf et al., 2010). This is supported by field observations, where *Drupella spp.* individuals were frequently found deep within the inner branches of *Porites spp.* colonies rather than on exposed surfaces.

The occurrence of *Porites spp.* predation in Moorea may have important ecological implications as branching *Porites spp.* exhibit significantly slower growth rates (2–4 cm per year; Lewis et al., 1968) compared to branching *Acropora spp.* (6–10 cm per year; Gladfelter, Monahan & Gladfelter, 1978), making them less capable of recovering from sustained tissue loss or structural

damage due to predation. In contrast, the faster growth of *Acropora spp.* will allow these corals to regenerate more rapidly following disturbances. Continued targeting of slower growing *Porites spp.* by *Drupella spp.* could therefore hinder colony recovery, reduce local *Porites spp.* abundance, and ultimately reduce reef resilience and structural complexity in reefs of Moorea. Furthermore, despite it not being the focus of the study and thus was not properly studied, it is important to note that large numbers of at least a hundred of *Drupella* spp. were found on multiple coral colonies. The fact that large numbers of *Drupella* spp. were found on coral species which are not normally reported as their preferred prey highlights the need for further monitoring and studies of the *Drupella* spp. populations on the reefs of Moorea. Although *Drupella spp.* individuals were observed feeding on *Porites spp.* in the field, in the laboratory, when both *Acropora spp.* and *Porites spp.* were presented to the snails, they fed exclusively on *Acropora spp.* and therefore *Acropora* spp. was chosen as the coral to feed the snails throughout the experiment. This preference is consistent with previous research which has seen *Drupella* spp. to have strong feeding preference for *Acropora spp.*, thought to be mediated by species specific chemical cues (Turner, 1994; Schoepf et al., 2010).

Contrary to expectations and previous findings in other taxa (Norin et al., 2016), our results showed no significant relationship between metabolic rate (SMR or RMR) and feeding activity in *Drupella* spp. Increased SMR and RMR with temperature (as seen in chapter 2) will result in *Drupella* spp. needing to increase energy intake to meet these rising metabolic demands. As no significant relationship was seen between metabolic rate and feeding, this suggests that other factors were playing more important roles in affecting feeding behaviour. Large numbers of individuals did not feed across all temperature treatments, and several zero-feeding days occurred randomly across all groups, indicating reasons rather than a thermal effect, as the lack of feeding was not associated with any specific temperature. The isolated conditions used during feeding trials likely influenced the social dynamics that play a key role in feeding in these snails, potentially obscuring effects of temperature or body size (Morton et al., 2002; Bruckner et al., 2017). Isolating individuals in feeding trials likely influenced the social dynamics that play a key role in feeding in these snails, and this potentially obscured effects of temperature or body size (Morton et al., 2002; Bruckner et al., 2017). *Drupella spp.* are known to exhibit social foraging

behaviour, typically feeding in aggregations and rarely found alone in the wild (Morton et al., 2002; Bruckner et al., 2017).

Previous research has shown that *Drupella spp.* respond strongly to conspecific presence, preferentially selecting corals already occupied or damaged by conspecifics over artificially damaged corals (Hamman, 2018). Schoepf et al. (2010) further demonstrated that both juvenile and adult *Drupella spp.* chose to associate with conspecifics when given the choice between conspecifics and food, highlighting the strength of social cues in influencing behaviour. Consequently, the isolated conditions in which this study tested feeding, and absence of social cues, likely suppressed feeding activity and may have masked treatment effects that potentially would emerge under more ecologically realistic, conditions where snails are held in groups. Moreover, the possibility that individuals could detect chemicals from nearby conspecifics, while being physically separated in individual containers, may have introduced behavioural confusion or stress, further influencing feeding responses and causing *Drupella* spp. not to feed at points.

Overall, these findings give insight into the complexity of *Drupella spp.* feeding behaviour. While temperature has clear influence on *Drupella* spp. metabolic processes, it does not appear to be a driver of feeding activity under isolated laboratory conditions. Instead, social interactions may be important for initiating and sustaining feeding. Future research should incorporate group foraging trials at different temperatures to more accurately replicate natural conditions. Given the potential for *Drupella spp.* outbreaks to accelerate reef degradation, a deeper understanding of the ecological and physiological factors regulating their feeding behaviour is important, particularly in the context of climate change, which is increasing coral vulnerability and alter predator prey dynamics on reefs (Rice et al., 2019; Wolff et al., 2018). The absence of a clear link between metabolic rate and feeding activity in *Drupella* spp. may suggest that rising temperatures alone may not directly intensify predation pressure from these corallivores. However, even if feeding rates remain stable, the declining resilience of coral hosts under thermal stress means that similar levels of predation could have more severe consequences. Corals weakened by bleaching or other stressors may be less able to recover from tissue loss, making them more vulnerable to sustained or repeated *Drupella* spp. grazing. Thus, unchanged predation intensity in a warming ocean does not necessarily mean unchanged ecological impact

In contrast to temperature, wet weight had a significant positive effect on feeding area, indicating that larger *Drupella* individuals consumed more coral tissue during feeding trials. This increase in feeding performance with size is consistent with allometric expectations, where larger gastropods possess greater grazing capacity due to increased radular surface area and higher energetic requirements (Keesing & Lucas, 1992; Meirelles & Matthews-Cascon, 2003). Biologically, this means that larger *Drupella spp.* will exert stronger predation pressure on coral colonies, suggesting that it is important to consider size of the snails when assessing the risk of a given population Although most studies on *Drupella* outbreaks only look snail abundance, this study suggests that incorporating size structure is also necessary, as populations dominated by larger individuals may impose greater impacts on coral than those with smaller individuals.

Growth was observed in both wet weight and shell length over the 20–23-day experimental period, while little change was seen in shell width. These changes in growth metrics were the same across temperature treatments, with no evidence of thermal conditions within the 28-34°C range influencing growth. This suggests that *Drupella spp.* are capable of somatic and shell growth under laboratory conditions across a 28–34 °C. No differences in growth across temperatures tested may reflect that the temperatures were still below *Drupella* spp.'s thermal maximum for growth. Therefore, testing a wider range of temperatures over a longer period of time could give more insight into a thermal maximum. Additionally, inter-individual variation in growth rates may have obscured temperature effects including differences in starting age or prior nutritional status. As expected, growth was strongly related to initial body size, with smaller individuals growing more than large ones. This aligns with field studies on *Drupella* spp. which saw individuals around 15mm increasing by 3.8-5.2mm in length over six months, whereas those bigger than 35 mm showed little to no growth (Black & Johnson, 1993). The size dependent effect on growth is consistent with allometric growth, where younger organisms invest more energy into somatic growth whereas larger ones are reproductive mature, so they allocate proportionally more energy into maintenance and reproduction rather than shell growth (Black & Johnson, 1993).

The lack of temperature effects on feeding in our study may explain the lack of changes in growth, as growth will be constrained by energy intake. If temperature did not affect feeding, this could explain the lack of temperature dependent growth. It is also possible that thermal effects on

growth require longer-term exposure to be seen. For example, Hoefnagel & Verberk (2017) reared *Lymnaea stagnalis* for 300 days and found that snails reared under warm conditions (22°C) grew faster and bigger than those reared cold (17°C), illustrating how long-term rearing at different temperatures can show thermal effects on growth that may not have been detectable in the short duration of the current study. A small decline in shell width was observed in some individuals, occurring mainly at 28 °C. This may reflect a temperature-driven response but was not investigated further, and alternative explanations, such as measurement uncertainty or minor shell damage, cannot be ruled out and would require additional study. The lack of a temperature effect on growth implies that *Drupella spp.* may have a relatively broad thermal tolerance for growth, or that increasing temperatures are not enough to increase growth.

Even despite a change in growth with temperature, the fact that *Drupella spp*. maintained growth even at 34°C, a temperature by which most corals will be under considerable thermal stress, has important ecological implications. Higher growth rates in corallivores are often associated with earlier reproductive maturity and increased outbreak potential (Black & Johnson, 1994). The ability of *Drupella spp.* to grow under such conditions suggests that populations may continue developing toward reproductive size during marine heatwaves, when coral hosts are already physiologically stressed. This decoupling between coral vulnerability and predator growth could intensify top-down pressures on reef ecosystems under climate change if *Drupella* spp. populations continue to grow and reproduce even under these stressful conditions.

Overall, these findings suggest that future reef resilience may be compromised not by dramatic increases in *Drupella* spp. predation *per se*, but by the increasingly fragile state of coral hosts and the persistent viability of *Drupella* spp. populations under warming scenarios. Increases in metabolic rate without corresponding increases in feeding or growth raises the possibility of an energetic imbalance at higher temperatures. However, whether this reflects a true energy deficit cannot be determined without a full energy budget. Understanding and managing this dynamic will be essential as climate change continues to reshape the structure and stability of coral reef ecosystems.

4 Conclusion and Future Directions

4.1 Conclusion

This thesis investigated the thermal sensitivity of the corallivorous gastropod *Drupella spp.* using laboratory experiments to measure the effects of elevated seawater temperatures on metabolic rate, feeding behaviour, and growth. Through investigating both physiological and behavioural data, the study gives insight into how ocean warming may influence the ecological impact of this coral predator on Indo-Pacific reef ecosystems. As the first study to measure metabolic rates in *Drupella spp.*, our findings indicate a resilient physiological response to temperature change, which may have concerning effects on reefs. Under well oxygenated laboratory settings, *Drupella* spp. showed increasing metabolic rates across acute temperatures from 28 °C to 36 °C. These results suggest that 36 °C lies within the acute thermal range of *Drupella* spp., which may be concerning as it suggests the capability of the snails to put pressure on coral reefs at temperatures well above coral bleaching. During exposure to prolonged temperature change, metabolic rates increased between 28°C and 32°C across all acclimation durations further indicating elevated energetic demands under moderate warming conditions which may intensify coral predation and accelerate reef degradation. At 32°C, most corals are already undergoing extreme thermal stress and widespread bleaching; therefore, the potential for elevated *Drupella* spp. metabolism, and the increase in activity and feeding which would be needed to meet this demand, is particularly concerning. Although *Drupella* spp. populations may collapse if their energetic demands cannot be met after bleaching, their rising metabolic rate in conjunction with their ability to switch between a large amount of coral prey suggests that they will be able to cause substantial reef damage prior to that point.

For *Drupella* spp. acclimated to their final temperatures for only three days, a decline was recorded in metabolic rates after 32 °C, indicating a potential thermal limit at such temperatures for snails acclimated for a shorter period of time. Sustained exposure to such temperatures could therefore impair physiological functions, including feeding, locomotion, and immune response, eventually compromising survival. However, when acclimated for 19-23 days to their final temperatures, no metabolic suppression was seen in *Drupella* spp. While acclimation duration was not significant in SMR, significant acclimatory plasticity was observed in RMR, suggesting

ability for physiological adjustment. Abilities to acclimate may allow individuals to maintain activity levels during thermal stress, enhancing their ability to survive temperature increases and continue to put feeding pressure on reefs when they are most vulnerable. Therefore, the ability to maintain metabolic rate up until at least 36 °C during acute thermal ramping, in combination with showing signs of thermal acclimation after prolonged exposure, raises questions about the role of *Drupella* spp. in coral damage and delaying reef recovery during ocean warming.

With increased metabolic rates *Drupella* spp. will need to increase feeding to meet energetic demands, yet when tested in the current study no significant changes in feeding rates were seen with increasing temperatures or metabolic rates. The reasons no significant relationship between temperature or metabolic rate and feeding was detected may be due to experimental conditions, such as the isolation of individuals during feeding, which likely disrupted social foraging cues known to feeding in *Drupella spp.* In natural reef environments, these gastropods typically feed in aggregations and are strongly influenced by the presence of conspecifics and coral tissue damage. The absence of increased feeding despite heightened metabolic demand may highlight the importance of social feeding behaviour in *Drupella spp.* In addition to no thermal change in feeding, no clear temperature dependent differences in shell growth or wet weight were detected. The ability for *Drupella* spp. to continue feeding and growth at 34°C may raise concern due to the vulnerability of reefs at such temperatures. The combined lack of temperature driven changes in feeding and growth, despite rising metabolic demand, highlights the role of other factors in influencing energy use under warming conditions. Specifically, the potential importance of social cues in regulating feeding behaviour may be involved.

An important future direction will be the development of temperature-dependent energy budgets for *Drupella* spp., which would allow the relationship between metabolic demand, feeding, growth and overall energetic balance to be quantified. Constructing such budgets would require simultaneous measurements of ingestion rate, assimilation efficiency, respiration and, where feasible, excretion across multiple temperatures to estimate scope for growth. This approach would determine whether the non-significant increases in feeding observed in the present study were sufficient to offset elevated metabolic costs, or whether individuals incur energetic deficits under warming. Establishing complete energy budgets would provide a mechanistic foundation

for predicting how temperature influences net energy allocation to maintenance, growth and reproduction, thereby improving our understanding of the drivers of *Drupella* spp. population dynamics and outbreak potential under climate change.

The findings of this study suggest that rising ocean temperatures considered alongside partial acclimation observed in RMR, this suggests a degree of thermal resilience. *Drupella spp.* may therefore be capable of withstanding warming conditions and resuming feeding once temperatures moderate, potentially allowing them to persist in degraded reef environments. Despite some physiological constraints, the capacity for acclimation and maintenance of physiological functions raise concerns that *Drupella spp.* could continue to exert substantial predation pressure on coral communities, potentially intensifying reef degradation and delaying post-disturbance recovery under future climate scenarios.

4.2 Future Research

The current study provides an important first step toward understanding the thermal physiology of *Drupella* spp., however, further research is needed to build on these findings. Firstly, more in-depth studies could be done to look more specifically at enzyme activity, gene expression and oxidative stress markers to create a greater understanding of how thermal increase influences *Drupella* spp. physiology. Measuring citrate synthase as a proxy for aerobic metabolic capacity, and lactate dehydrogenase as proxy for anaerobic capacity across multiple temperatures, and then at a single common temperature, would help determine whether changes seen in metabolism are due to a kinetic effect of temperature, an increase in enzyme capacity through acclimation, or a shift toward anaerobic metabolism. Research could use comparison of thermal activity curves to test how the same enzyme extract responds when investigated across different temperatures, to show how much of the increases in reaction rate are purely temperature-affected. In addition, studies could measure enzyme extracts from numerous individuals which have been acclimated to different temperatures and then tested at a single common temperature would show whether warm-acclimated snails have higher activity at the same temperature. If so, this would reveal increased enzyme capacity through acclimation rather than just faster reaction kinetics. Similar techniques were used by Lang et al. (2021), where such enzyme-based approaches revealed

shifts between aerobic and anaerobic pathways under thermal stress. Applying similar analyses in *Drupella* spp. would provide greater insight into the physiological basis of the metabolic increases observed with warming and how acclimation shapes thermal tolerance.

Another factor which could be useful for future research is investigating the combined effects of ocean warming and ocean acidification. Previous studies have investigated the combined effects of ocean warming and ocean acidification on marine molluscs, stressors which co-occur because of rising carbon dioxide concentrations under climate change (Pörtner, 2008). Acidification can impair shell formation, ion regulation and cellular function, and thus may influence metabolic rates in conjunction with temperature. A study conducted on the sea hare *Stylocheilus striatus* showed that while metabolic rate was not significantly affected by temperature or acidification alone, when combined, it caused a significant increase in metabolic rate (Horwitz et al., 2020). This reveals the synergistic effect of the two stressors on mollusc physiology, highlighting the importance of studying the two stressors in conjunction to get a full picture of how climate change could affect *Drupella* spp. physiology.

Beyond cellular physiology, to understand the ecological drivers of *Drupella* spp. outbreaks, an integrated approach that considers both abiotic and biotic factors on feeding and growth are needed. Our findings showed that temperature alone is not a predictor of feeding activity in isolated individuals. Future research should incorporate group foraging trials that allow conspecific interactions to better replicate natural conditions to understand how changes in temperatures may influence feeding. Additionally, to create a fuller understanding of the effects of temperature on *Drupella* spp. growth, longer-term field-based studies are needed. Two approaches could be used including the deployment of in situ temperature loggers combined with repeated measurement of individually marked snails (e.g., via PIT tags) over months or years, as well as analysis of shell growth increments calibrated against oxygen isotope ratios. Such work is essential to understand whether thermal conditions influence *Drupella* spp. growth in the field, and to what extent laboratory observations translate to ecological realities.

A further question arising from this study is whether elevated metabolic rates at higher temperatures create an energetic imbalance if feeding and growth do not increase correspondingly. Future work would be useful to investigate energy budget analyses using

measurements of assimilation efficiency, the energetic content of the consumed coral tissue, and excretory losses. Integrating these components would allow feeding rates to be converted into actual assimilated energy, enabling direct comparison with metabolic expenditure. Quantifying assimilated energy relative to metabolic demand would allow for a greater understanding of how *Drupella* spp. meet increased energetic requirements under warming, and how this could ultimately influence growth, survival or outbreak potential.

In addition to feeding and growth, temperature may influence other behaviours that affect ecological impact which were not investigated in this study. For instance, elevated metabolic rates with temperature increase could increase locomotion, allowing snails to travel across reefs more quickly potentially expanding the area of coral they prey on. Increased temperatures and activity may also cause range shifts into previously unaffected reef systems. Another factor which may be affected by warming is host-selection behaviour, which could change, potentially altering how efficiently *Drupella* spp. locate and target live coral. In addition, if temperature modifies *Drupella* spp. finding mates or spawning cues, behavioural shifts could interact with reproduction and contribute to outbreak dynamics. Future research into these non-feeding behaviours is therefore important to build a more complete understanding of how warming may reshape *Drupella* spp. impacts on reef ecosystems.

Although our measurements of metabolic rate, feeding and growth provide insight into *Drupella* spp.'s physiological sensitivity and ecological influence on a reef in warming waters, alone they do not explain whether temperature is a direct driver of outbreaks. Investigating how temperature influences reproduction would be valuable in trying to see whether temperature might influence population boosts, and thus how it may influence outbreaks. Thermal reproductive studies could include looking at fecundity, larval survival and early development, as has been done for COTS (Lamare et al., 2014). For example, laboratory experiments rearing embryos and larvae at different temperature treatments could monitor fertilisation success and developmental rate to investigate the effects of temperature on *Drupella* spp. reproduction and development. Studies such as these could help identify thermal thresholds for population growth, which may improve our capacity to predict and manage outbreak risk.

Ultimately, integrating physiological data into outbreak models will greatly improve our ability to identify when *Drupella* populations pose a threat to reef health. Such models should include coral cover, coral species composition and growth rates, as well as temperature and its effects on both coral growth and *Drupella* spp. feeding. These models will help with outbreak identification and therefore management, allowing for determination of whether certain populations are at outbreak densities. Additionally, models would allow for prediction, helping monitor which populations may be heading towards outbreak densities. This will allow for more effective management, particularly as intervention becomes increasingly difficult once outbreaks have already occurred.

In conclusion, understanding *Drupella* spp. thermal physiology is important for predicting the snail's impact on future reef ecosystems under climate change. The current study offers a good beginning to understanding *Drupella* spp. thermal response, yet further research into metabolic and reproductive response to long-term temperature changes could help create a fuller picture of the relationship between temperature, feeding, growth and population densities. Integrating this physiological and ecological data into models will help predict populations that may pose specific risks and assist in reef management. Such abilities will not only improve our ability to manage *Drupella* spp. outbreaks but will enhance our ability to provide reef conservation in a warming ocean.

5 List of references

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6 Supplementary Information

Supplementary Table S1. Checklist of 53 essential criteria for reporting methods in aquatic intermittent-flow respirometry. Edited from Killen et al. (2021), "Guidelines for reporting methods to estimate metabolic rates by aquatic intermittent-flow respirometry" (J. Exp. Biol. 224)

Number	Criterion and Category	Response	Value (where required)	Units
	EQUIPMENT, MATERIALS, AND SETUP	Measured post-trial after blotting	2.98 (mean)	g
1	Body mass of animals at time of respirometry	Glass chambers	25	ml
2	Volume of empty respirometers	Continuous recirculation with peristaltic pump		
3	How chamber mixing was achieved	Chambers were mixed by continuous closed-loop recirculation using peristaltic pumps		
4	Material of tubing used in any mixing circuit	Tygon® tubing (gas-impermeable)		
5	Volume of tubing in any mixing circuit	7.32 – 12.32 mL depending on chamber	7.32 – 12.32	ml
6	Confirm volume of tubing in any mixing circuit was included in calculations of oxygen uptake	Yes, volume of tubing was included		
7	Material of respirometer (e.g. glass, acrylic, etc.)	Glass		
8	Type of oxygen probe and data recording	External oxygen sensors and four-channel oxygen meters; recorded using Firesting software		
9	Sampling frequency of water dissolved oxygen	Recorded every 2 seconds	2	seconds
10	Describe placement of oxygen probe (in mixing circuit or directly in chamber)	In mixing circuit, not inside chamber		
11	Flow rate during flushing and recirculation, or confirm that chamber returned to normoxia during flushing	5 min flush phase ensured normoxia during flushing		
12	Timing of flush/closed cycles	Prolonged: 5 min flush / 2 min closed; Ramping: 4 min flush / 2 min closed		
13	Wait (delay) time excluded from closed measurement cycles	First 30 seconds excluded	30	seconds
14	Frequency and method of probe calibration (for both 0 and 100% calibrations)	100% oxygen calibration in fully oxygenated seawater before trials began		
15	State whether software temperature compensation was used during recording of water oxygen concentration	Yes, during calibration		

	MEASUREMENT CONDITIONS			
16	Temperature during respirometry	Prolonged acclimation trials: 28 °C, 30 °C, 32 °C, 34 °C Acute ramping trials: 29–38 °C in 1 °C increments	28, 30, 32, 34 29–38	Degrees Celsius
17	How temperature was controlled	Temperature controlled water bath regulated via Inkbird thermostats that controlled a pump-driven circulation system connected to a heated freshwater reservoir		
19	Photoperiod during respirometry	Simulated diel cycle: 11 h light: 13 h dark during trials. Bath covered but light kept on photoperiod anyways		
20	If (and how) ambient water bath was cleaned and aerated during measurement of oxygen uptake (e.g. filtration, periodic or continuous water changes)	Water bath had a air stone in it. Chambers were aerated during closed phases		
21	Minimum water oxygen dissolved oxygen reached during closed phases	Dissolved oxygen never dropped below levels that would induce hypoxia		
22	State whether chambers were visually shielded from external disturbance	Yes, opaque plastic dividers between chambers; whole system covered with a black sheet		
23	How many animals were measured during a given respirometry trial (i.e. how many animals were in the same water bath)	Seven each in individual chambers	7	Snails
24	If multiple animals were measured simultaneously, state whether they were able to see each other during measurements	No, chambers were visually isolated by the opaque dividers		
25	Duration of animal fasting before placement in respirometer	24 hours	24	hours
26	Duration of all trials combined (number of days to measure all animals in the study)	37 days	37	days
27	Acclimation time to the laboratory (or time since capture for field studies) before respirometry measurements	Minimum 6 days baseline acclimation at 28 °C prior to experiments. Additional acclimation, 3 days and then 19–22 days at final temperatures before IFR measurement		
	BACKGROUND RESPIRATION			
28	State whether background microbial respiration was measured and accounted for, and if so, method used (e.g. parallel measures with empty respirometry chamber, measurements before and after for all chambers while empty, both)	One of the 8 chambers was left empty during every trial; blank chamber rotated between trials. Oxygen decline from the blank was **subtracted** from each occupied chamber		
29	State if background respiration was measured at beginning and/or end, state how many slopes and for what duration	~		

30	State how changes in background respiration were modelled over time (e.g. linear, exponential, parallel measures)	**Parallel subtraction** of the blank chamber at each time point/closed phase		
31	Method and frequency of system cleaning (e.g. system bleached between each trial, UV lamp)	**between trials:** system flushed with **5–9% sodium hypochlorite,** then **rinsed 3× with seawater;** oxygen probes removed during bleaching, then **disinfected in 70% ethanol for 5–10 s** and rinsed with fresh water before reinstalling. supply water went through a UV lamp filter		
	STANDARD OR ROUTINE METABOLIC RATE			
32	Acclimation time after transfer to chamber, or alternatively, time to reach beginning of metabolic rate measurements after introduction to chamber	In prolonged trials the first two hours of measurements were removed as acclimation to the chamber time; in ramping trials, they acclimated overnight (~12 h)		
33	Time period, within a trial, over which oxygen uptake was measured (e.g. number of hours)	Oxygen uptake was measured for around 19–20 h in prolonged trials (after exclusion) and for 30 min at each 1 °C step in ramping trials		
34	Value taken as SMR/RMR (e.g. quantile, mean of lowest 10 percent, mean of all values)	SMR was taken as the lowest 20% of slopes, while RMR was calculated as the mean of all valid slopes		
35	Total number of slopes measured and used to derive metabolic rate (e.g. how much data were used to calculate quantiles)			
36	Whether any time periods were removed from calculations of SMR/RMR (e.g. data during acclimation, periods of high activity [e.g. daytime])	The first 2 house of prolonged trials and the first 30 s of each closed phase were excluded from calculations		
37	r^2 threshold for slopes used for SMR/RMR (or mean)	Only slopes with $R^2 \geq 0.9$ were kept for analysis		
38	Proportion of data removed due to being outliers below r-squared threshold	Mean of 13.2% in the trials tested		
	DATA HANDLING AND STATISTICS			
39	Sample size	56 snails used in the prolonged, 28 used in the ramping	56 and 28	Snails
40	How oxygen uptake rates were calculated (software or script, equation, units, etc.)	Oxygen uptake calculated in R from 2-min regressions of O_2 decline (mg O_2 L^{-1} s^{-1}), converted to mg O_2 h^{-1} using $MO_2 = \Delta O_2 \times V \times 3600$		
41	Confirm that volume (mass) of animal was subtracted from respirometer volume when calculating oxygen uptake rates	Yes, snail displacement volume (from wet mass–volume calibration) was subtracted from chamber volume		

43	State whether analyses accounted for variation in body mass and describe any allometric mass-corrections or adjustments	Yes, rates were size-standardised to 2.98 g using allometric log–log regression and back-transformation		

Supplementary Figure S1. Output of the linear mixed-effects model (LMM) testing effects of Temperature, Acclimation Temperature, Wet Weight, and the interaction of temperature and acclimation metabolic rate in the ramping experiment.

```
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: Metabolism ~ Temperature * Acclimation_Temp + Wet_Weight + (1 |      Date)
   Data: df_cleaned

REML criterion at convergence: -2498.6

Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.7954 -0.5660 -0.0533  0.5325  6.5572

Random effects:
 Groups   Name        Variance Std.Dev.
 Date     (Intercept) 0.002341 0.04838
 Residual             0.003633 0.06027
Number of obs: 920, groups:  Date, 4

Fixed effects:
                                          Estimate Std. Error         df t value Pr(>|t|)
(Intercept)                             -1.801e-01  3.631e-02  5.637e+00  -4.960  0.00305 **
Temperature                              6.573e-03  6.643e-04  9.130e+02   9.894  < 2e-16 ***
Acclimation_TempAcclimated to 34°C      -4.299e-03  7.956e-02  8.105e+00  -0.054  0.95821
Wet_Weight                               2.493e-02  2.188e-03  9.131e+02  11.397  < 2e-16 ***
Temperature:Acclimation_TempAcclimated to 34°C  2.349e-04  1.663e-03  9.130e+02   0.141  0.88772
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) Tmprtr A_TAt3 Wt_Wgh
Temperature -0.608
Acc_TAt34°C -0.443  0.277
Wet_Weight  -0.187  0.000  0.015
T:A_TAt34°C  0.241 -0.399 -0.709  0.008
```

Supplementary Figure S2. Output of the linear mixed-effects model (LMM) testing effects of Temperature, Acclimation Temperature, Wet Weight, and the interaction of wet weight and temperature on metabolic rate in the ramping experiment.

```
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: Metabolism ~ Temperature * Wet_Weight + Acclimation_Temp + (1 |      Date)
   Data: df_cleaned

REML criterion at convergence: -2523.2

Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.7560 -0.5770 -0.0514  0.5538  6.4326

Random effects:
 Groups   Name        Variance Std.Dev.
 Date     (Intercept) 0.002332 0.04829
 Residual             0.003529 0.05941
Number of obs: 920, groups:  Date, 4

Fixed effects:
                                 Estimate Std. Error         df t value Pr(>|t|)
(Intercept)                      0.155273   0.073795  89.994009   2.104   0.0382 *
Temperature                     -0.003496   0.002041 913.005519  -1.713   0.0870 .
Wet_Weight                      -0.087241   0.021755 913.003825  -4.010 6.56e-05 ***
Acclimation_TempAcclimated to 34°C  0.005351   0.056005   2.011486   0.096   0.9326
Temperature:Wet_Weight           0.003368   0.000650 913.002031   5.182 2.71e-07 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) Tmprtr Wt_Wgh A_TAt3
Temperature -0.921
Wet_Weight  -0.885  0.951
Acc_TAt34°C -0.184 -0.008 -0.003
Tmprtr:Wt_W  0.880 -0.956 -0.995  0.006
```

Supplementary Figure S3. Output of the linear model (LM) testing effects of Temperature, Wet Weight, Acclimation duration, and their interactions on SMR.

```
Call:
lm(formula = SMR ~ Temperature * Wet_weight + Acclimation_Group *
    Temperature, data = data)

Residuals:
      Min        1Q    Median        3Q       Max
-0.101332 -0.023853 -0.002469  0.027495  0.072131

Coefficients:
                                  Estimate Std. Error t value Pr(>|t|)
(Intercept)                      -0.015164   0.020265  -0.748 0.456060
Temperature30                     0.076495   0.029588   2.585 0.011185 *
Temperature32                     0.107645   0.034565   3.114 0.002412 **
Temperature34                     0.091914   0.032619   2.818 0.005838 **
Wet_weight                        0.044163   0.006368   6.936 4.21e-10 ***
Acclimation_Group19-22           -0.006370   0.013959  -0.456 0.649120
Temperature30:Wet_weight         -0.025703   0.009327  -2.756 0.006971 **
Temperature32:Wet_weight         -0.025361   0.010726  -2.365 0.020005 *
Temperature34:Wet_weight         -0.034236   0.010052  -3.406 0.000954 ***
Temperature30:Acclimation_Group19-22  0.016347   0.019819   0.825 0.411478
Temperature32:Acclimation_Group19-22 -0.009082   0.019930  -0.456 0.649595
Temperature34:Acclimation_Group19-22  0.033275   0.019768   1.683 0.095464 .
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 0.03693 on 99 degrees of freedom
Multiple R-squared:  0.4532,    Adjusted R-squared:  0.3925
F-statistic: 7.461 on 11 and 99 DF,  p-value: 3.422e-09
```

Supplementary Figure S4. **Output of the linear model (LM) testing effects of Temperature, Wet Weight, Acclimation duration, and their interactions on SMR.**

```
Call:
lm(formula = SMR ~ Temperature * Wet_weight + Acclimation_Group *
    Temperature, data = data)

Residuals:
      Min        1Q    Median        3Q       Max
-0.101332 -0.023853 -0.002469  0.027495  0.072131

Coefficients:
                                  Estimate Std. Error t value Pr(>|t|)
(Intercept)                      -0.015164   0.020265  -0.748 0.456060
Temperature30                     0.076495   0.029588   2.585 0.011185 *
Temperature32                     0.107645   0.034565   3.114 0.002412 **
Temperature34                     0.091914   0.032619   2.818 0.005838 **
Wet_weight                        0.044163   0.006368   6.936 4.21e-10 ***
Acclimation_Group19-22           -0.006370   0.013959  -0.456 0.649120
Temperature30:Wet_weight         -0.025703   0.009327  -2.756 0.006971 **
Temperature32:Wet_weight         -0.025361   0.010726  -2.365 0.020005 *
Temperature34:Wet_weight         -0.034236   0.010052  -3.406 0.000954 ***
Temperature30:Acclimation_Group19-22  0.016347   0.019819   0.825 0.411478
Temperature32:Acclimation_Group19-22 -0.009082   0.019930  -0.456 0.649595
Temperature34:Acclimation_Group19-22  0.033275   0.019768   1.683 0.095464 .
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 0.03693 on 99 degrees of freedom
Multiple R-squared:  0.4532,    Adjusted R-squared:  0.3925
F-statistic: 7.461 on 11 and 99 DF,  p-value: 3.422e-09
```

Supplementary Figure S5. Output of the Gamma zero-inflated GLMM analysing Feeding Area as a function of RMR, Temperature, and Wet Weight.

```
Call:
lm(formula = RMR ~ Temperature * Wet_weight + Acclimation_Group *
    Temperature, data = data)

Residuals:
      Min        1Q    Median        3Q       Max
-0.096262 -0.026312  0.001006  0.026522  0.088775

Coefficients:
                                   Estimate Std. Error t value Pr(>|t|)
(Intercept)                       0.0010526  0.0209824   0.050  0.96009
Temperature30                     0.0705951  0.0306360   2.304  0.02329 *
Temperature32                     0.1037581  0.0357899   2.899  0.00461 **
Temperature34                     0.0910108  0.0337741   2.695  0.00828 **
Wet_weight                        0.0488165  0.0065932   7.404 4.43e-11 ***
Acclimation_Group19-22           -0.0005447  0.0144533  -0.038  0.97002
Temperature30:Wet_weight         -0.0212663  0.0096574  -2.202  0.02998 *
Temperature32:Wet_weight         -0.0221670  0.0111056  -1.996  0.04868 *
Temperature34:Wet_weight         -0.0345296  0.0104085  -3.317  0.00127 **
Temperature30:Acclimation_Group19-22  0.0052966  0.0205215   0.258  0.79686
Temperature32:Acclimation_Group19-22 -0.0145280  0.0206358  -0.704  0.48307
Temperature34:Acclimation_Group19-22  0.0437164  0.0204679   2.136  0.03516 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 0.03824 on 99 degrees of freedom
Multiple R-squared:  0.5229,    Adjusted R-squared:  0.4699
F-statistic: 9.865 on 11 and 99 DF,  p-value: 7.424e-12
```

Supplementary Figure S6. Output of the Gamma zero-inflated GLMM analysing Feeding Area as a function of SMR, Temperature, and Wet Weight.

```
 Family: Gamma  ( log )
Formula:          Feeding_Area ~ SMR + Temperature + Wet_Weight
Zero inflation:                ~Temperature + Wet_Weight
Data: model_data

      AIC       BIC    logLik -2*log(L)  df.resid
    610.1     638.9    -295.1     590.1       121


Dispersion estimate for Gamma family (sigma^2): 0.502

Conditional model:
             Estimate Std. Error z value Pr(>|z|)
(Intercept)   0.94940    0.25122   3.779 0.000157 ***
SMR          -1.65103    1.90288  -0.868 0.385586
Temperature30  0.14122    0.17927   0.788 0.430848
Temperature32  0.23650    0.18139   1.304 0.192306
Wet_Weight     0.18216    0.09005   2.023 0.043089 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Zero-inflation model:
             Estimate Std. Error z value Pr(>|z|)
(Intercept)  -1.38837    0.65052  -2.134   0.0328 *
Temperature30  0.34045    0.46399   0.734   0.4631
Temperature32 -0.27384    0.53607  -0.511   0.6095
Wet_Weight     0.08611    0.20280   0.425   0.6711
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```