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Review Article

Marine Gastropods in A Warming Ocean: Ecological and Evolutionary Perspectives

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Abstract: Marine gastropods are among the most ecologically important and biologically diverse molluscs which has diverse roles. As ocean temperatures rise, gastropods are exposed to changing thermal regimes that can affect metabolism, growth, reproduction, shell formation and survival, with consequences that extend from individual performance to population persistence and community organization. At the ecological level, warming can alter gastropod feeding activity, mobility and predator–prey interactions. In intertidal systems, species already experience large daily and seasonal fluctuations and many show behavioural thermoregulation, shell thickening and shifts in microhabitat use that reduce heat stress. The evolutionary perspective highlights both plasticity and selection. Gastropods are especially informative because many species occupy narrow thermal niches, yet others persist across broad climatic gradients. The physiological tolerance, shell morphology and life-history traits can evolve in response to thermal stress, particularly where populations are isolated or exposed to persistent selection. Ocean warming does not act alone. In many marine environments, it interacts with acidification, hypoxia and habitat disturbance and these stressors may have additive or synergistic effects on gastropods. Shell formation is particularly vulnerable because temperature and carbonate chemistry jointly influence calcification and shell strength. Thus, the future of marine gastropods will depend on the balance between physiological flexibility, evolutionary potential and the intensity of environmental change. Overall, marine gastropods are likely to show uneven responses to warming: some populations will persist through plasticity and adaptation, while others may decline or shift distribution. Their ecological importance means that such changes will have consequences far beyond the animals themselves, affecting food webs, habitat structure and the resilience of coastal ecosystems. Thus, the paper is an attempt to explore the impact of climate change on ecological and evolutionary perspectives of marine gastropods.
Keywords: Marine Gastropods, Climate Change, Ecological and Evolutionary Perspectives

INTRODUCTION

Marine gastropods are among the most widespread and functionally important invertebrates in coastal ecosystems. They contribute to grazing, nutrient cycling, bioerosion, and the regulation of algal and prey populations, thereby shaping benthic community structure and ecosystem functioning (Lotze *et al.,* 2011). Because many species occupy narrow thermal niches and live close to their upper thermal limits, gastropods are especially sensitive to changes in seawater temperature associated with global climate change (Somero, 2002). Ocean warming affects gastropods through multiple physiological pathways and even modest increases can alter performance and survival. In intertidal habitats, where temperature naturally fluctuates over short temporal scales, many gastropods have evolved behavioural and physiological mechanisms that improve tolerance to thermal stress, such as sheltering in crevices, reducing activity during hot periods, and adjusting energy allocation (Helmuth, 2009; Sanford and Kelly, 2011). However, these mechanisms have limits. Prolonged warming can increase energetic demand, reduce reproductive output and narrow safety margins, especially for larvae and juveniles that often have lower tolerance than adults (Davis, 2000). As a result, warming may cause population decline in some species while favouring others with broader thermal tolerance or higher plasticity. Thus, the paper is an attempt to explore the impact of climate change on ecological and evolutionary perspectives of marine gastropods.

Range shifts and biogeographic reconfiguration

One of the most conspicuous responses of marine gastropods to ocean warming has been the systematic alteration of geographic distribution patterns. As sea surface temperatures rise, many species are tracking their thermal niches poleward, leading to the "thermophilization" of temperate communities and the contraction of cold-water species' ranges (Stuart-Smith *et al.,* 2015). Early evidence for climate-driven range shifts came from the marine gastropod *Acanthinucella spirata*, whose Pleistocene and modern populations revealed a striking pattern of northward range expansion accompanied by the emergence of novel shell morphologies absent in both southern populations and the entire Pleistocene fossil record (Hellberg *et al.,* 2001). The northward expansion was confirmed by mitochondrial DNA sequence data showing significantly reduced variation in northern populations, a signature consistent with recent colonization.

Along the Atlantic Iberian Peninsula, analysis of intertidal gastropod distributions revealed asymmetrical responses to warming: cold-water boreal species most notably *Littorina littorea* which exhibited pronounced range contractions and reduced abundances, whereas the subtropical pulmonate limpet *Siphonaria pectinata* expanded its distribution northward (Chapperon and Seuront, 2010; Rubal *et al.,* 2015). These shifts were significantly correlated with increasing sea surface temperatures along the Iberian coast between 1949 and 2010. Latitudinal range shifts in marine organisms, including gastropods, often exceed terrestrial estimates by several fold (Fenberg *et al.,* 2014). This disparity reflects the relative permeability of ocean barriers to dispersal compared to terrestrial landscapes, combined with the strong thermal sensitivity of physiological processes in ectothermic marine invertebrates.

Phenological disruptions and trophic mismatches

Beyond altering where gastropods live, ocean warming is reshaping when they reproduce with potentially cascading consequences for population viability and ecosystem function. Using an exceptional dataset spanning six decades (1946-1949 to 2003-2007) from rocky shores of southwest Britain, Moore *et al.* (2011) demonstrated divergent phenological responses in two congeneric limpets. The warm-affinity *Patella depressa* advanced its peak reproductive development by an average of 10.2 days per decade, while simultaneously extending its reproductive season and increasing the proportion of reproductively active individuals in the population. This advance was strongly correlated with increased sea surface temperatures in late spring and early summer.

Remarkably, the phenological shift observed in *P. depressa* was double the average rate documented for terrestrial and freshwater systems, suggesting that marine species may be responding to climate warming more rapidly than their terrestrial counterparts (Xavier *et al.,* 2010). The cool-temperate winter-spawning limpet *Patella vulgata*, by contrast, exhibited a delayed reproductive development (3.3 days per decade), increased reproductive failure rates, and a reduced proportion of the population reaching advanced gonad stages (Wethey *et al.,* 2011). These divergent responses are among the first to demonstrate that a cool-temperate species can delay its reproductive timing to track cooler, more favourable conditions as the climate warms. The consequences of such phenological shifts extend beyond individual species. Delayed spawning in *P. vulgata* risks creating trophic mismatches between larval availability and phytoplankton blooms, potentially leading to recruitment failures and nonlinear population declines. Similar concerns have emerged from pelagic systems, where emerging mismatches in phenologies may ultimately threaten trophic linkages and ecosystem functioning.

Invasive species have capitalized on these phenological opportunities. Rising seawater temperatures along the northern European Atlantic coast have enhanced the reproductive success of the invasive slipper limpet *Crepidula fornicata*. Comparative histology of a French population between 2000-2001 and 2006-2007 revealed longer brood presence (appearing earlier in the year) and increased gametogenesis intensity during the later period, coincident with significantly higher water temperatures (Valdizan *et al.,* 2011). The proliferation of *C. fornicata* since 1995 when warming became pronounced illustrates how non-native species may exploit climate-induced phenological opportunities to expand their ranges and ecological impacts.

Physiological limits, shell integrity and behavioural impairment

The physiological mechanisms underpinning distributional and phenological responses involve fundamental constraints on metabolism, acid-base regulation and calcification. The western Antarctic Peninsula, one of the most rapidly warming regions on Earth, has provided critical insights into the vulnerability of polar gastropods (Bromwich *et al.,* 2013). Chronic exposure (six weeks) of two common Antarctic gastropods (*Nacella concinna* and *Margarella antarctica*) revealed complex interactive effects of temperature and pH. Righting times in *M. antarctica* showed a significant temperature-pH interaction, meaning that the effect of pH on this behaviour depended critically on temperature (Schram *et al.,* 2014). Maximum escape speeds in this species exhibited an even stronger interaction, indicating that multiple stressors may compromise the ability to avoid predators in ways not predictable from single-factor experiments. The Southern Ocean is particularly vulnerable to ocean acidification due to increased CO_2 solubility and reduced calcium carbonate saturation states at low temperatures, with pH reductions projected for global oceans by 2100 expected to occur in the Southern Ocean by 2050. Antarctic gastropods already possess thin shells prone to dissolution without active maintenance - a pre-existing vulnerability that will likely be exacerbated under combined warming and acidification (Breitburg *et al.,* 2015). However, the intertidal species, accustomed to fluctuating conditions, proved more tolerant, suggesting that habitat history shapes resilience to multiple stressors.

Evolutionary responses and adaptive potential

The evolutionary responses and adaptive potential of marine gastropods to climate change represent a critical arena, as these organisms face unprecedented rates of ocean warming. A central question is whether species can keep pace with environmental change through genetic adaptation or rely on immediate physiological adjustments. Phenotypic plasticity, the ability of a single genotype to alter its phenotype in response to the environment, is often a first line of defence. For example, Arctic gastropods like *Margarites helicinus* have shown an inherent capacity to acclimate to temperatures several degrees above their current summer maximums, a plasticity that may provide a crucial buffer against rapid warming (Richard *et al.,* 2012). However, the extent of such plasticity is not limitless and often involves trade-offs, with warm-adapted species sometimes exhibiting reduced acclimation capacity.

Beyond plasticity, evidence for genetic adaptation to thermal stress in gastropods is compelling. Studies on the intertidal snail *Chlorostoma funebralis* have demonstrated clear local adaptation, where southern populations exposed to warmer conditions consistently show higher heat tolerance and faster recovery from heat stress compared to northern populations, all measured under common-garden conditions (Gleason and Burton, 2013). This occurs despite substantial gene flow *via* pelagic larvae, indicating that local selection can be a powerful evolutionary force in the sea. At a more fundamental level, molecular mechanisms such as the heat-shock response are key to thermal adaptation. Research on Tegula snails reveals that while acclimation can shift the temperature thresholds for heat-shock protein synthesis, distinct genetic differences in these thresholds exist between species from different thermal habitats (Tomanek and Somero, 1999). These genetically fixed differences directly influence their biogeographic distribution, as low-intertidal species exhibit protein synthesis that fails at temperatures routinely tolerated by their subtropical congeners. This suggests that the potential for evolutionary rescue may be constrained by pre-existing genetic architecture shaped by a species' evolutionary history.

A broader phylogenetic perspective reveals a complex picture. In a review of marine evolutionary responses to global change, Reusch (2014) noted that the literature is significantly biased towards gastropods and crustaceans, with a focus on their physiological tolerances as a form of "phenotypic buffering". Interestingly, a study on the tropical freshwater snail *Clea nigricans*, which descends from a marine lineage, found an unexpectedly wide thermal safety margin of ~20°C above its current habitat temperatures (Polgar *et al.,* 2014). This mismatch questions the general assumption that tropical ectotherms have narrow thermal windows and high vulnerability suggesting that evolutionary history and ancestral adaptations can significantly influence a species' contemporary resilience to warming.

Consequently, the evolutionary trajectory of marine gastropods will be shaped by an interplay between adaptive plasticity, local adaptation and deep evolutionary constraints. While some populations can adjust their thermal physiology or shift their geographic ranges in response to ocean warming, as seen in nudibranchs during a 2014 warm anomaly (Bond *et al*., 2015), others may be limited by low heritability of key traits. Understanding the balance between selection and gene flow and quantifying the genetic variance for thermal tolerance are therefore essential for predicting which populations can persist through evolutionary change and which will require conservation intervention.

- **Tropical gastropods near upper thermal limits (e.g., Indo-Pacific):** Tropical gastropods are considered highly vulnerable to global warming because they live at or near their upper thermal threshold limits, and the predicted increase in the frequency of warming events in the tropics is expected to be critical for their survival (Chapperon and Laurent, 2011). The vulnerability of these ectotherms is not a simple certainty; there are nuances in how species might cope. For some, the threat appears immediate. The tropical snail *Littoraria scabra* in the Indo-Pacific found that its upper substrate temperature limit is about 33.4°C. When exposed to higher temperatures, it showed behavioural thermoregulation, actively moving to find a cooler site which suggests that an animal's ability to move and choose a favourable micro-habitat is a vital, and often overlooked, short-term survival strategy.
- **Temperate species experiencing heatwaves (e.g., Mediterranean, Western Australia):** Temperate marine gastropods face increasing threats from extreme heatwaves, which have intensified in frequency and severity in regions like the Mediterranean and Western Australia. The 2003 European heatwave caused widespread mass mortality of rocky benthic macro-invertebrates in the Northwestern Mediterranean, with seawater temperatures rising 1–3°C above climatic norms (Garrabou *et al.,* 2009). Similarly, the 2011 "Ningaloo Niña" heatwave off Western Australia led to dramatic changes in kelp forests and fisheries, with gastropod populations showing latitude-specific responses like severe depletion at warmer sites and stability at cooler ones (Short *et al.,* 2015). While some gastropods possess inherent adaptive capacity to thermal stress. A 2013 study on the marine snail *Chlorostoma funebralis* found that southern populations from warmer climates exhibited higher heat tolerance and faster recovery than northern counterparts, indicating local adaptation despite extensive gene flow (Gleason and Burton, 2013). This phenotypic plasticity may provide a buffer against warming, though it is not limitless.
- **Polar and subpolar gastropods facing rapid warming (e.g., Antarctic *Nacella* spp.):** As some of the most stenothermal organisms on Earth, polar and subpolar gastropods face an extreme physiological vulnerability to ocean warming. Their evolutionary history in frigid, stable waters has produced a thermal

tolerance window that is exceptionally narrow and low. For the Antarctic limpet *Nacella concinna*, the temperature threshold for survival is perilously close to current conditions. The up-regulation of its heat shock proteins (HSP70), a key marker for cellular stress, occurs at acutely high temperatures of 15°C or more, levels that bear little relevance to the limpet's natural ecology and do not reflect the complex, low-level thermal stress encountered in its intertidal habitat during events like aerial exposure (Clark *et al.,* 2008). Consequently, for *Nacella concinna* and other polar species, even modest projected warming directly threatens survival. A 2014 study exposed *Nacella concinna* and the snail *Margarella antarctica* to a mere 2°C increase above current ambient temperatures, finding that the combined stress of warming and acidification produced significant temperature–pH interaction effects on righting and escape behaviors, with snails showing increased righting times under multiple stressor conditions (Schram *et al.,* 2014). This indicates that stenothermal polar gastropods exhibit early and clear sub-lethal responses to near-future climate scenarios, where their limited acclimatory capacity provides a very narrow buffer for long-term survival and population persistence.

- **Intertidal vs. subtidal gastropods: contrasting exposure and vulnerability**: The stark contrast between intertidal and subtidal habitats imposes vastly different selective pressures on gastropods, shaping distinct patterns of exposure and vulnerability to climate change. Intertidal zones are characterized by extreme thermal variability; for example, individuals of the slippershell snail *Crepidula fornicata* living intertidally in a Rhode Island cove experienced body temperatures as high as 42°C, more than 15°C higher than those recorded for subtidal conspecifics (Diederich and Pechenik, 2013). Remarkably, despite these extreme conditions, both intertidal and subtidal populations exhibited nearly identical thermal tolerances, with a lethal range of 33-37°C following a 3-hour exposure. This finding is particularly concerning because it suggests that intertidal gastropods are already living dangerously close to their upper thermal limits, making them highly vulnerable to even modest future warming. Furthermore, a broader physiological review revealed that warm-adapted intertidal species, especially those from subtropical and tropical habitats, had upper lethal temperatures (LT50s) that were approximately 15°C higher than those of temperate subtidal species (Somero, 2005). However, these same intertidal species also exhibited a limited capacity to further increase their thermal tolerance through acclimation, in contrast to their more cold-adapted subtidal relatives. This combination of living at the edge of their physiological limits and having a reduced ability to acclimate places intertidal gastropods in far greater immediate jeopardy from heat-related mortality than their subtidal counterparts, a vulnerability that will likely be exacerbated as global temperatures continue to rise.

CONCLUSION

The escalating thermal restructuring of the world's oceans presents an unequivocal challenge to marine gastropods, a group whose ecological significance and biological diversity demand urgent scientific attention. The responses of gastropods to ocean warming are neither uniform nor predictable from simple thermal metrics alone. Instead, they emerge from a complex interplay among physiological tolerance, life-history strategy, habitat context and evolutionary heritage. Ecologically, warming has already begun to reconfigure gastropod distributions, with cold-water boreal species contracting poleward while warm-affinity taxa expand, as documented along the Atlantic Iberian Peninsula. Such range shifts are proceeding faster in the marine realm than on land, reflecting the permeability of oceanic dispersal barriers. Parallel to spatial changes, phenological disruptions are altering reproductive timing, as seen in the divergent responses of *Patella depressa* and *Patella vulgata* off southwest Britain. These shifts risk creating trophic mismatches between larval availability and food resources, potentially driving recruitment failures and population declines. Beyond distribution and timing, ocean warming directly impairs physiological performance. Antarctic gastropods such as *Nacella concinna* and *Margarella antarctica* exhibit compromised righting and escape behaviours under even modest temperature increases, especially when warming interacts with acidification. Such multiple stressors may have additive or synergistic effects, undermining shell integrity, metabolic function and predator avoidance in ways not predictable from single-factor studies. The vulnerability of intertidal gastropods is particularly acute: despite experiencing extreme daily temperature fluctuations, many live perilously close to their upper lethal limits and possess limited acclimation capacity, placing them in greater immediate jeopardy than their subtidal counterparts. From an evolutionary perspective, however, there is reason for cautious hope alongside serious concern. Phenotypic plasticity provides a first line of defence, as demonstrated by Arctic gastropods acclimating to temperatures above current summer maxima. Moreover, local adaptation can be a powerful evolutionary force, with southern populations of *Chlorostoma funebralis* showing genetically based higher heat tolerance despite extensive gene flow. Yet such adaptive potential is not universal. Stenothermal polar species, evolutionarily confined to stable cold waters, lack the genetic and physiological flexibility to cope with rapid warming. Similarly, tropical gastropods living near upper thermal thresholds may have narrow safety margins, though unexpected resilience in some lineages reminds us that evolutionary history and ancestral adaptations can produce surprising outcomes. Ultimately, the future of marine gastropods will depend on the balance between their intrinsic adaptive capacity and the pace and intensity of environmental change. As gastropods shape benthic food webs, influence algal dynamics and serve as sentinel species for coastal health, their fate is inextricably linked to the resilience of entire marine ecosystems.

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