Introduction

Organisms and environments are entwined, as the relationship between organisms and the environments they are embedded within, is in constant flux through inextricable links and flows of energy. The relationship between organisms and environments varies through both space and time and is influenced by a mosaic of dynamic biotic and abiotic drivers [?, ?]. Organisms are active participants in constructing their environment, from altering seawater biogeochemistry through physiological processes to organisms constructing biogenic structures; plenty of studies demonstrate that organisms influence their environment [?, ?]. Organisms and ecosystems, while playing an essential role in structuring the physical and biological environment, are simultaneously governed by the ability to perform and function under a myriad of complex interactions, as each act to influence one another non- contemporaneously and contemporaneously through direct and indirect feedback loops [?, ?]. Organisms must physiologically cope with the conditions of the environment they are situated within, which inevitably influences community structure and populations [?]. Further, the biogenic structures created by organisms are highly dependent upon the environmental regime the organism develops in, living beyond the life of the organism itself; organisms are thus simultaneously creators and products of the environment. In a geological epoch of rapid ecological change, it is increasingly imperative to understand how and the extent to which organisms can respond and perform to abiotic drivers and how the legacy of the structures (e.g., shells, reefs) that organisms create may influence other species indirectly. Understanding physiological responses, interactions, and constraints of marine organisms to anthropogenic climate change is perhaps the sine qua non for understanding the changes between marine organisms and the ecosystems they construct. This research intends to inform how the changing oceanic environment may affect organismal physiology by teasing apart the relationship between environmental drivers and physiological performance. This research also intends to elucidate how changes within physiological processes in one organism may have indirect effects on other species long after the organism persists. In this regard, the fate of organisms is intertwined as the abundance and growth of one species codetermines the other, illustrating that organisms are directly or indirectly the subjects and objects of ecological change [?].

Organisms as the Subjects of Ecological Change

Environments are governed by natural spatiotemporal variation of abiotic and biotic drivers that, in turn, influence the structure and processes of communities, drive ecological change, and create a mosaic of microhabitats [?, ?, ?]. For example, within marine ecosystems, the combination of oceanographic processes and local coastal geography may create an array of patterns and variability in abiotic drivers such as temperature, flow, pH, dissolved oxygen, etc., that may impact the structure and processes of ecological communities on distances ranging from microscale to macroscale [?, ?]. Such heterogeneous patterns are naturally occurring and create complex gradients that shape ecological communities and influence physiological processes within individual organisms [?]. However, due to the connotation of stress as a negative response and the ability for organisms to adapt and evolve to changing conditions over time, the term driver has been utilized to describe an environmental parameter that influences organisms and environments across a spectrum ranging from enhancing, optimal, or stressful conditions [?, ?]. Many organisms have evolved to withstand complex and variable environmental gradients through physiological mechanisms such as phenotypic plasticity and acclimatization [?, ?]. According to the metabolic theory of ecology, environmental gradients and changes in abiotic factors may result in physiological trade-offs due to the alterations within the energetic partitioning of an organism's metabolism [?, ?]. The physiological processes of metabolism are the total sum of biological and chemical processes in converting energetic resources and materials into biomass and activity [?]. Comparing physiological responses to gradients of abiotic drivers may allow us to quantify and compare the tolerance limits of organisms [?, ?]. The role of biotic and abiotic drivers in influencing metabolic processes has been of primary interest to the field of ecology as changes in metabolism directly affect the survival, behavior, and energy requirements of organisms, thereby impacting fitness and ecosystem function [?].

Temperature and pH are important for determining physiological processes and metabolic rates for marine organisms and thereby play a large role in affecting the functioning and physiology of ecosystems [?]. Temperature is the key driver in determining physiological rates of organisms as the kinetic energy of biochemical reactions is temperature dependent [?, ?, ?]. Biological processes such as organismal and ecological interactions are also strongly influenced by temperature [?]. The relationship between temperature and body-size exemplifies this as organisms develop faster yet decrease in size under elevated temperatures [?]. Metabolic rates are strongly influenced by an organism's body size and temperature and are subject to change due to changes in abiotic drivers and the natural variability of drivers [?, ?]. Further, organisms adapt to local temperatures to match optimal conditions for physiological processes and acclimatize to a range around these values [?]. Any range too far beyond the ability of an organism to acclimatize influences survival, fitness, and population densities [?]. Studies have shown the influence of sea surface temperature on metabolic processes such as growth, feeding, reproduction, and influencing the range of species distributions [?, ?, ?]. However, it is essential to note that temperature is not the only driver of biological processes and temperature has interactive effects with other abiotic drivers [?]. pH is also an important abiotic driver that impacts the physiological performance of marine organisms and influences the biogenic structures that organisms create [?]. pH plays a vital role in metabolic processes due to its effect on biochemical pathways and internal acid-base balance [?]. For example, low pH is often associated with elevated metabolic rates due to the increase in energetic costs in creating calcified structures such as the formation of shells in mollusks or the skeletons of corals and echinoderms [?, ?]. Due to differences in the energetic costs associated with calcification, there are significant differences in the ability to control acid-base regulation between species [?]. Consequently, changes in physicochemical parameters of the environment affect species differently, impact the interaction between species and, in turn, affect the structures of ecological communities; therefore, studying how differences between abiotic drivers affect organismal physiology will have ecosystem-level implications [?, ?].

ORGANISMAL PHYSIOLOGY IN A CHANGING ENVIRONMENT

As the atmospheric carbon dioxide (CO2) concentration continues to surpass the limits of the earth system, marine organisms will be forced to endure profound transformations of the envrionment, from shifts in temperature to altered geochemistry (richardson2023earth, portner2008physiology}. Ocean warming (OW) and ocean acidification (OA) represent two of the most significant changes occurring in marine ecosystems across the globe, both driven by the unremitted rise of anthropogenic-induced carbon dioxide emissions. OW and OA are not isolated phenomena; they share a common origin, and in a rapidly changing world, their combined impacts on organismal physiology necessitate special attention as multiple drivers of change may act interactively [?]. Since the beginning of the 20th century, the global mean sea surface temperature (SST) has increased by 0.88 [0.68–1.01] °C, and is further projected to warm by 2.89°C [2.01–4.07°C] at the end of the century, which surpasses the thermal tolerance limits of many marine species (following the representative concentration pathway 8.5 emission scenario) [?, ?, ?, ?]. Concurrently, the ocean has absorbed ~30% of anthropogenic CO2 [?], altering the carbonate chemistry of seawater through a decrease in the concentration of carbonate ions CO_3^{2-} and a decline in seawater pH [?]. Mean surface ocean pH values have declined by 0.1 units since the pre-industrial era, with a further projected diminution of 0.1 - 0.4 units by the end of the century [?, ?], posing a unique threat to calcifying marine organisms. Consequently, the impacts of OW and OA will not be consistent across geographic regions, leading to differential effects that will modify already variable spatial and temporal environments. Building a mechanistic understanding of how the combined impacts of ocean warming and acidification affect marine organisms is integral for reliable projections of how climate change may continue to affect marine organisms.

Coastal marine organisms frequently encounter a wide range of temperatures and experience fluctuations in biogeochemistry, resulting from temporal variations, such as tidal and seasonal cycles. The rocky intertidal system is one such system that is known for its variable conditions on both temporal and spatial scales, making them a model ecosystem for understanding how organisms interact and respond to change [?, ?, ?, ?]. Organisms within the rocky intertidal zone must contend with alternating periods of immersion and emersion of tidal fluctuations, which commonly lead to large variations in temperature, oxygen availability, and pH, [?]. Of these naturally occurring changes, thermal variability within the intertidal zone is believed to be a dominant driver in structuring the vertical and latitudinal distribution patterns by limiting upper zonation through abiotic stress and lower zonation through biotic influence [?, ?, ?]. Daily temperature fluctuations are drastic enough to elevate the body temperatures of marine organisms by more than 20°C during a tidal emersion event [?, ?]. Furthermore, changes in pH within tidepools may exceed 1 unit when nighttime respiration rates exceed photosynthetic rates [?, ?]. Such highly variable abiotic changes are naturally occurring and create complex gradients that shape ecological communities and influence physiological processes within individual organisms [?]. Given that organisms within the intertidal zone simultaneously face drastic fluctuations from abiotic drivers, and experience conditions far beyond what is expected in the future, understanding organismal performance in these ecosystems may provide a window for looking toward the future.

The role of biotic and abiotic drivers in influencing metabolic processes has been of primary interest to the field of ecology as changes in metabolism directly affect the survival, behavior, and energy requirements of organisms, thereby impacting organism and ecosystem function [?, ?, ?, ?]. Physiological processes are heavily influenced by environmental factors, and many marine organisms undergo biological responses to natural diel variability present within environments \cite{hofmann2010living. Temperature is the primary environmental driver regulating physiological rates of ectothermic organisms, as kinetic energy of biochemical reactions are temperature dependent [?, ?, ?]. Further, temperature is the key determinant in the regulating rates of biological processes, ranging from metabolic rates [?] to species-interactions [?], such as growth, feeding, reproduction, and determining the range of species distributions \cite{kordas2011community, sanford2002feeding, pinsky2013marine. The physiological processes of metabolism are the total sum of biological and chemical processes in converting energetic resources and materials into biomass and activity [?]. Changes in pH also play a vital role in metabolic processes due to its effect on biochemical pathways and internal acid-base balance [?]. Specifically, declines in seawater carbonate ions and pH attributed to OA are strongly correlated to decreases in calcification and growth rates of many marine organisms [?]. Due to species-specific differences in the energetic costs associated with calcification, there are significant differences in the ability to control internal acid-base regulation between species [?]. Ultimately, changes in the environment that lead to alterations in organismal energetic requirements will scale up to affect the processes of ecological communities; therefore, studying how multiple abiotic factors affect organismal physiology has ecosystem-level implications [?, ?, ?].

The use of performance curves can help to quantify the relationship between abiotic drivers and physiological rates to forecast future effects [?] and can allow for comparative assessments across different biological rates and environmental conditions (Figure 1.) [?, ?, ?, ?]. Further, thermal performance curves have been suggested to fill in the gap of uncertainty between multiple stressors as they empirically characterize the relationship between biological performance rates across a wide range of temperatures [?, ?, ?]. Thermal performance curves are a univariate function that describes how some measure of performance (e.g., metabolic rate) varies with temperature. As temperature increases so do the biochemical and physiological rates until they reach a species-specific optimal temperature. Beyond the optimum rate, further increases in temperature denature proteins, stunt growth, and cause reductions in performance and survival [?, ?]. Thermal performance curves are typically left-skewed and hump-shaped and include several metrics, including but not limited to a thermal optimum (TOpt)—the temperature at the highest rate of performance—and a critical thermal minimum (CTMin) and a thermal maximum (CTMax)— the upper and lower thermal limit that an organism can tolerate [?, ?, ?]. These tolerance thresholds and the range they encompass are governed by an organism's ability to respond to sub-lethal and lethal conditions through an organismal-level response and molecular-level responses such as anaerobic metabolism and heat shock response [?, ?]. Further, exposure to concurrent drivers of ecological change, like OA, are expected to constrict an organism's performance curve and thermal limits, such as decreasing the breadth of thermal performance [?, ?]. Comparing physiological responses to gradients of abiotic drivers may allow us to quantify and compare the tolerance limits of organisms [?].

Specifically, we ask the question: how does exposure to decreased pH influence thermal performance curves of respiration of an intertidal gastropod, Tegula funebralis? We anticipate that the thermal optimum (TOpt) for respiration rates will shift towards lower temperatures, indicating a reduced ability to sustain optimal metabolic activity in the face of ocean acidification. Additionally, we expect a decrease in the thermal breadth of the curve (TBr), indicating a narrower range of temperatures at which the gastropod can effectively maintain its respiratory rates. In this study we... (give an overview of your experimental design to set up expectations on how you plan to answer these questions)

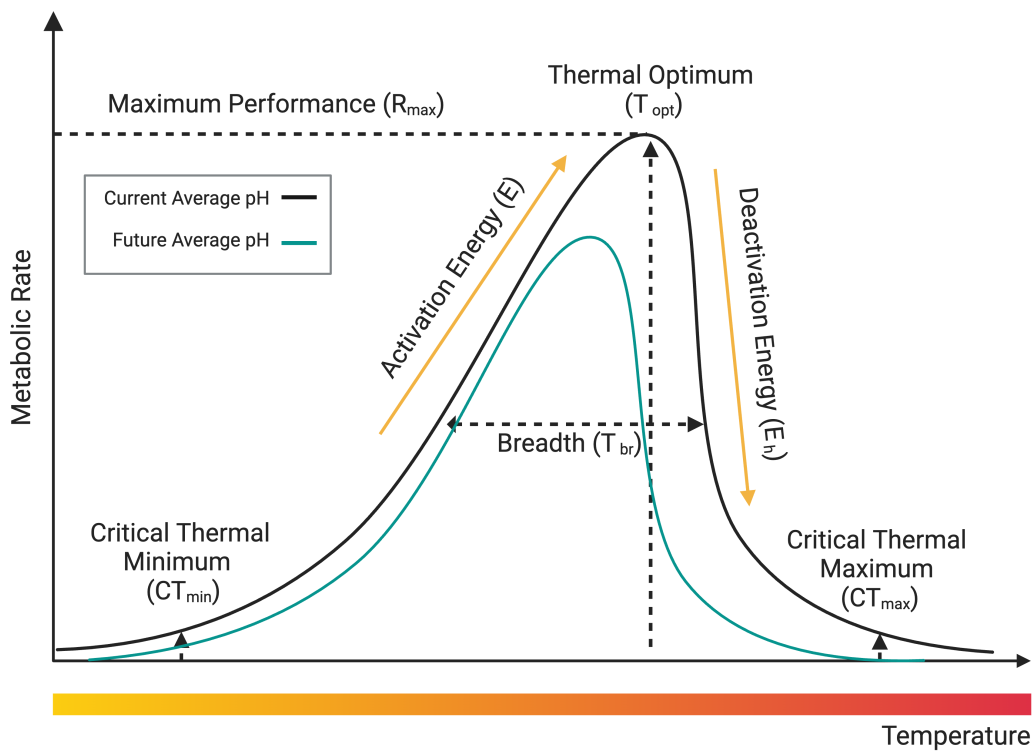

Figure 1: Thermal performance curve schematic illustrating the relationship between biological rates and temperature, including critical thermal maximum (CTMax), critical thermal minimum (CTMin), thermal optimum (Topt), activation energy (E), deactivation energy (Eh), and the thermal breadth of the curve (TBr). Hypothesized characteristics of a thermal performance curve exposed to ocean acidification, including reduced thermal optimum and reduced performance ay maximum physiological rate and breathe of the curve.