Symposium on "Climate change and molluscan ecophysiology" at the 79th Annual Meeting of the American Malacological Society

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Climate change has already had many observable effects on Earth. On land, glaciers and snowpacks have shrunk, tropical forests are being replaced by savannahs, and coastal areas have increased risks of flooding (*e.g.*, IPCC 2007, Allan and Soden 2008, Dai 2010, NOAA 2010, Chen *et al.* 2011). In addition to sea-surface warming, climate change has altered the physical and chemical nature of the marine environment, including ocean acidification and expanding hypoxia.

The scope and scale of future environmental change that individuals will undergo on land and in the sea will fundamentally influence the ecological and evolutionary responses of populations and species, dependent on their evolved physiological capacities for environmental tolerance (Parmesan 2006, Hoffmann and Sgrò 2011, Kuntner *et al.* 2014). Although climate change will affect all organisms, molluscs are unique in many respects, and, given their high diversity and evolutionarily flexible body plan, they provide several established and emerging models systems for comparative physiological study in nearly all types of ecosystems, from rivers to rocky shores and deserts to the deep sea. Moreover, many mollusks play pivotal roles as consumers, predators, and competitors in a diversity of ecosystems and habitats. Mollusks also have great economic importance, with many species of mollusks harvested by humans for food, either from natural populations or from aquaculture.

The joint meeting of the American Malacological Society and the World Congress of Malacology in Ponta Delgada, Azores, on July 23rd 2013, brought together malacologists actively pursuing research aimed at addressing the direct and indirect impacts of climate change and the mechanisms mollusks use to compensate for these changes, their natural evolved tolerances, and the energetic, ecological, and biogeographic consequences of compensation. The goal for this symposium was to expose a broad range of malacologists to ecophysiological approaches in the hopes of recruiting and stimulating interest in the emerging questions of this field. Speakers included those whose talks addressed the effects of climate change on mollusks across a wide range of time scales and levels of biological organization, describing the results from recent research as well as considerations of some of the challenges facing ecophysiological research on mollusks in the future.

The symposium began with a wide-ranging keynote presentation by **Peter Ward** that included a broad overview of climate change over geological time as well as preliminary data and video indicating how warming on fore-reef slopes impacts the depth distribution of *Nautilus* Linnaeus, 1758 and its predators in the Indo-West Pacific. Subsequent presentations covered topics including thermal tolerance, changes in species distributions, vertical migration, developmental biology, calcification, metabolism, energy budgets, and circatidal foraging. Several talks focused on the ecophysiology of intertidal rocky shore mollusks; **Folco Giomi** provided an overview of research in this habitat, which is characterized by low tidal aerial exposure, acute solar radiation, and the progressive heating from the substratum, which together contribute to the rapid increase in body temperature of the sessile fauna and associated mobile species on rocky

shores, often above their tolerance thresholds (Helmuth and Hofmann 2001, Helmuth *et al.* 2002, 2006, Marshall *et al.* 2010). Intertidal organisms have, however, evolved morphological, behavioral, and physiological adaptations to cope with environmental variability and endure harsh climatic events (Giomi and Pörtner 2013, Pörtner and Giomi 2013). In particular, mussels and oysters (Fig. 1) constitute remarkable examples of heat tolerance and thermal stress endurance. Owing to their ability to switch to a low energy demanding quiescence and to a maximization of the energy assimilation rate from food intake, rocky shore bivalves are adapted to sustain effective metabolic performances and energy homeostasis during extreme heat events (Marshall *et al.* 2010; Montalto *et al.* 2014, Sarà *et al.* 2014).

Three of the four symposium papers in this issue of *American Malacological Bulletin* focus on the ecophysiology of sessile, space-occupying intertidal mussels. First, **Brendon Dunphy and co-authors** (this volume) developed and demonstrated the utility of metabolomics as a tool for characterizing patterns of acute thermal stress in *Perna canaliculus* (Gmelin, 1791), the green-lipped mussel. Metabolomic

profiling (Horning *et al.* 1971) involves the measurement of low-molecular-weight metabolites and their intermediates as a means to identify the chemical signatures left behind by specific cellular processes. The approach is akin to transcriptomics and proteomics, but whereas transcriptomics and proteomics provide information about the potential cause for a phenotypic response, metabolomics provide a snapshot of the physiological or functional state of an organism that is the sum of its genome, gene expression, protein abundance, and environmental influences. Dunphy *et al.* showed that thermally-stressed mussels may be discriminated from unstressed individuals with only a handful of cellular metabolites. Although the development of an assay to accurately measure thermal stress holds great promise as a tool for both field and laboratory experiments, understanding whether specific metabolites associated with stress are merely markers that reveal a perturbed or damaged physiological system, or instead, the signatures of defensive cellular responses to stress, remains an open an exciting question in *Perna* Philipsson, 1788 and other species that can be addressed with this technique in the future.
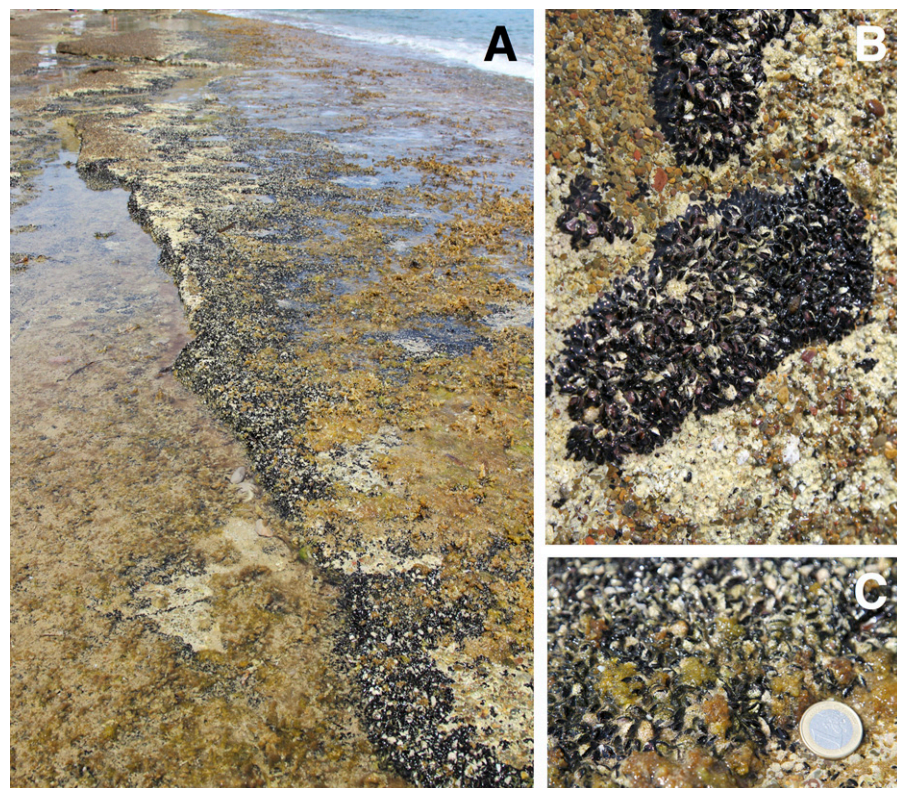

Figure 1. Intertidal mussel beds of *Mytilaster minimus* (Poli, 1795) in Altavilla (Sicily, Italy). **A,** Small mussels' patches (**B, C**) represent an optimal model to investigate the physiological plasticity and the adaptive strategy evolved by these ecosystem engineers to endure acute heat stress and anomalous climatic events. Photo: F. Giomi.

Motivated by the fact that rapid anthropogenic changes in climatic conditions necessitate accurate predictions about how species will respond to environmental changes, **Elizabeth Fly and colleagues** (this volume) used species distribution models (SDMs) to understand factors controlling the current and future geographic ranges of the marine mussels *Mytilus edulis* Linnaeus 1758 and *M. galloprovincialis* Lamarck, 1819. What sets this new work apart from their past work on *Mytilus* Linnaeus, 1758 is that Fly *et al.* compared the results from correlative SDMs to results from newly developed mechanistic SDMs. Readers are likely familiar with correlative SDMs, those that use statistical associations between climate variables and species' occurrences to predict a species' range. Probably less familiar are mechanistic SDMs that rely on characterizations of the dominant biological processes that underlie survival and reproduction, deriving model parameters from the phenotypes of organisms that are used to construct distributional models (Helmuth *et al.* 2005, Kearney 2006). Although a mechanistic model that describes all of the important processes constraining a

species' range may be better at predicting range changes (Kearney and Porter 2009), organism-specific mechanistic models are more difficult to construct than correlative SDMs that only require occurrence data. The contribution from Fly *et al.* bears this out: by comparing results between models and species, Fly *et al.* infer that the physiological mechanisms controlling the distribution of *Mytilus* in Europe likely differ both between species and between regions within species. The authors suggest that incorporating local rates of productivity may be the key towards constructing better mechanistic SDMs given that a handful of studies have shown that thermal tolerance and organismal performance under stressful abiotic conditions may depend on the availability of food.

Starting with this same basic idea, that complex interactions between multiple stressors may be important in understanding the realized niche of many intertidal organisms, **Alison Matzelle and co-authors** (this volume) also took a mechanistic approach to model the growth and reproduction of mussels as a function of their environment. Assuming that food availability and body temperature are the primary metabolic drivers for sessile ectotherms, Matzelle *et al.* used a bioenergetics framework that combines aspects of biophysical and dynamic energy budget models to model the cumulative effects of temperature and food availability on growth in *M. californianus*. Rocky shore mussels provide a relatively straightforward but interesting system for understanding the impacts of abiotic and biotic factors given that shore height provides a simple proxy for both thermal stress (emersion time) and food availability (immersion time). The authors also demonstrated how animal behavior can be incorporated into their model; in this case, perceived predation risk or more simply put, the "fear of being eaten" (Trussel *et al.* 2006). Many mollusks are able to detect and avoid predators via chemical cues released by both predators and damaged conspecifics (*e.g.*, Marko and Palmer 1991), a response that appears to comes at the cost of reducing foraging time (Palmer, 1990, Trussel *et al.* 2006). For most rocky shore animals, the most thermally stressful habitats tend to have the greatest predation risk (*i.e.*, habitats with low wave exposure), suggesting some clear expectations about which populations may be more vulnerable to climate change when multiple stressors are considered in the novel framework presented by Matzelle *et al.*

Other contributions to the symposium concentrated on the challenges of understanding the thermal landscape of smaller sessile and mobile intertidal mollusks at several different spatial scales. **Govindraj Chavan** provided an overview of planned work on connectivity and local adaptation among isolated Macaronesian (Island archipelagoes of Madeira, Canary, Cape Verde, and Azores) populations of limpets (species of *Patella* Linnaeus, 1758) and better-connected European populations to compare different levels of local adaptation between these two regions. **Nicholas Carey** presented work on the importance of considering allometric scaling of metabolic rates with body size (metabolic rate decreases relative to an organisms' body mass as it gets larger), a phenomenon that precludes straightforward comparisons of metabolic rates between species (Carey, Galkin *et al.* 2013, Carey, Sigwart *et al.* 2013). Emily Carrington discussed ongoing research on the foraging behaviors of the predatory whelk, *Nucella ostrina* (Gould, 1852), in the context of thermal stress (Vaughn *et al.* 2013; Hayford *et al.* 2015). Feeding on its barnacle prey (Fig. 2a) generally requires movement higher on the shore, potentially increasing the risk of thermal stress in *N. ostrina*, but remaining in cooler refuges with little food, potentially leads to energetic stress. When slow moving snails make excursions high on the shore, how do they balance the reward of food with the risk of overheating? In outdoor tidal mesocosms, snails shifted their foraging strategy according to the changing risk of thermal stress on small (weekly) and large (seasonally) timescales. Peak foraging preceded the onset of
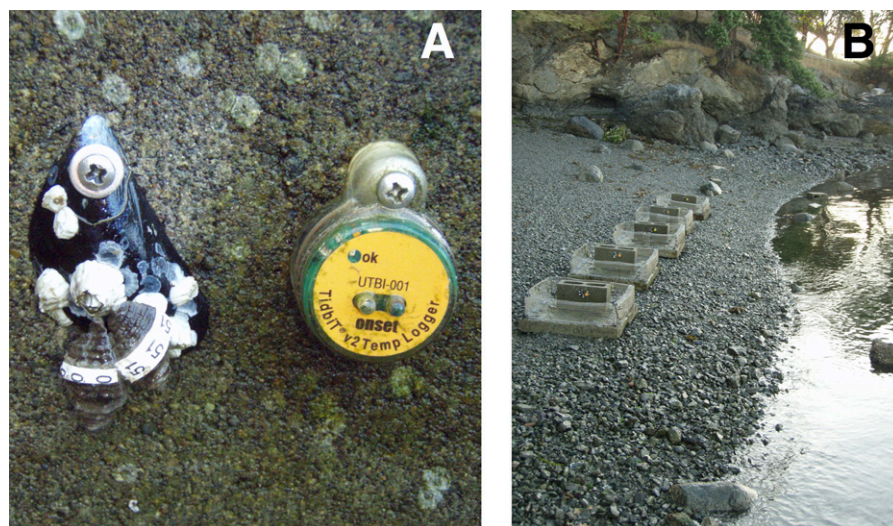
Figure 2. Close-up of two individual *Nucella ostrina* (**A,** left) foraging on barnacles. The temperature logger (**A,** right) records the approximate conditions snails experience when they are foraging. Five experimental islands (**B**) on the shore in Friday Harbor, WA. Each island is a semi-enclosed arena for *Nucella ostrina* predation on barnacle prey, where snails must choose to forage on eastern or western faces (visible here) or shelter in a cool, moist habitat below. See Hayford *et al.* (2015) for additional details. Images provided by Hilary Hayford.

spring tides, when aerial exposure occurred only during early morning hours and was reliably cool. Snails experiencing only nighttime low tides foraged aperiodically and manipulative experiments revealed sex-specific responses to aerial warming. In the field, *N. ostrina* on artificial concrete islands (Fig. 2b) shifted predictably from western to eastern facing surfaces on days with afternoon low tides. These results suggest that *N. ostrina* alters its behavior to capitalize on relatively small-scale spatiotemporal differences in microclimate, a foraging pattern that consistently minimizes exposure to extreme aerial temperatures. In a climate scenario of increased aerial temperature, selective mobility may give this predator an advantage over its sessile prey. These results underscore the importance of characterizing the temporal patterns of microhabitat use when assessing the thermal exposure of mobile organisms.

Several speakers focused on the impacts of ocean warming and acidification on bivalves and cephalopods. **Frank Melzner** presented work on bivalves living in the Baltic Sea, which is characterized by low salinity, which goes along with low carbonate concentrations (Ω). Upwelling of CO_2-rich water also leads to very low calcium carbonate saturation states, which frequently reach values of $<< 1$ (Melzner *et al.* 2013), conditions under which 'abiotic' calcium carbonate typically dissolves. Despite these conditions, the Baltic Sea ecosystem is dominated by calcifying invertebrates. Melzner explained that mytilid mussels, which dominate benthic habitats in the Baltic, can calcify at very high rates even when the seawater is undersaturated with calcium carbonate ($\Omega<1$). In fact, Melzner and colleagues showed that total mytilid calcium carbonate production strongly depends on habitat food density (particulate organic carbon, POC), much more so than on carbonate availability, in coupled laboratory and field experiments (Thomsen *et al.* 2013). However, Melzner and co-authors also showed that larval mytilids are highly sensitive to low seawater carbonate concentrations, with high larval mortality at CO_2 partial pressures (PCO_2) that occasionally occur today. As future ocean acidification will lead to non-linear increases in PCO_2 partial pressure (and equally strong decreases in Ω) in estuarine habitats, strong selective forces will be acting on local mussel populations (Melzner *et al.* 2013). It is unknown, however, if rapid adaptation will allow maintenance of mussel-dominated communities in the future.

Compared to other mollusks, cephalopods are unusual given their short life spans and large life history plasticity, which may allow them to respond rapidly to new climate regimes. Yet, ocean warming and acidification in the future may impair the more vulnerable early ontogenetic stages, causing shorter embryonic periods and premature hatching (Rosa *et al.* 2012, Rosa *et al.* 2014). In this context, **Rui Rosa** presented recent work demonstrating that, during the embryonic development of the common cuttlefish, *Sepia officinalis* Linnaeus, 1758, there

is a significant rise in the perivitelline fluid (PVF), PCO_2 and bicarbonate levels, as well as a drop in pH and oxygen partial pressure (PO_2) (Rosa *et al.* 2013). The estimated critical PVF PO_2 was lower than the PVF PO_2 measured under conditions that mimicked future warming and acidification scenarios. This suggests that conditions inside the egg capsules of *S. officinalis* may become detrimental to development in the future, promoting untimely hatching and smaller hatchling body sizes. In the fourth paper contributed to this volume, **Brad Seibel** reviewed recent work on the jumbo squid, *Dosidicus gigas* (d'Orbigny, 1835), demonstrating that this species has a remarkable tolerance to hypoxia and a wide temperature ranges. Yet, *D. gigas* lives in regions characterized by strong oxygen minimum zones that influence the depth to which they migrate daily. The hemocyanin (oxygen transport protein) properties from *D. gigas* indicate that their blood remains saturated with oxygen across the full range of temperatures (25 to 10 °C) and oxygen partial pressures (1.6 to 6.0 kPa) that they experience during their nighttime habitat in the upper water column (Seibel 2013). During the daytime, however, squids migrate to depths (300 m) with oxygen partial pressures below the critical PO_2 (Trueblood and Seibel 2013), which triggers a pronounced metabolic suppression (Seibel *et al.* 2014). Interestingly, *D. gigas* recently expanded its range into the California Current, which is less hypoxic and colder than its historical range. In the California Current, *D. gigas* migrates to deeper depths (500 m) to reach its critical PO_2 and suppress metabolism. This suggests that metabolic suppression is an important component of the squid's physiological repertoire (Seibel, this issue).

Finally, the symposium also had contributions from researchers working on terrestrial mollusks. In contrast to marine taxa, the ability of land snails to colonize terrestrial habitats is the result of the evolution of a different set of behavioral and physiological adaptations for maintaining water, ionic, and thermal balance. **Zeev Arad** spoke about the Israeli land snail fauna that inhabits arid and semi-arid habitats, discussing annual cycles of snail activity and aestivation that are related to seasonal changes in temperature, humidity and water availability. **Sandra Troschinski** discussed how terrestrial snails like the Mediterranean *Xeropicta derbentina* (Krynicki, 1836) deal with warm and arid conditions with physiological adaptations at the cellular and biochemical level. Aside from behavioral adaptations, including climbing vertical objects or shifting activity phases to favorable time periods (Pomeroy 1968; Yom-Tov 1971), physiological adaptations at the cellular and biochemical level are of high importance. Troschinski and colleagues, working on populations of *X. derbentina* in Southern France, revealed that different populations from the same habitat have developed different heat response strategies with respect to the histopathological status of the digestive gland (the central metabolic organ of mollusks), and their induction of the stress protein Hsp70. This

has implications for cellular functionality, as low HSP70 levels lead to rapid cellular decay at extreme temperatures. Furthermore, tissue- and cell-specific heat resistance was associated with elevated whole body HSP70 levels (Troschinski *et al.* 2014). They further showed that antioxidant defense mechanisms play an important role in heat tolerance as reactive oxygen species are known to have deleterious effects on DNA, proteins, and lipids (Gutteridge and Halliwell 1990). Based on these facts, a combination of stress proteins (Hsp70) and antioxidant defense mechanisms seem to be essential for the ability of *X. derbentina* to survive extreme temperatures. However, the mobilization of these defense mechanisms seems to be interconnected by an energetic trade-off.

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