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Editorial: Adaptation and Phenotypic Plasticity to Climate Change

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Editorial on the Research Topic

Adaptation and Phenotypic Plasticity to Climate Change

Anthropogenic activities are driving rapid changes in aquatic environments. Numerous studies suggest that climatic shifts and anomalies will convey severe consequences for ecosystems worldwide, leading to disruptions in key processes within populations including larval development, individual growth, and reproductive success. This is further exacerbated by the negative impacts on between-species interactions, and changes to biodiversity and ecosystem services (Munday et al., 2013). Understanding the responses of organisms to environmental shifts is imperative to help predict their fate on a changing planet. Particularly, the capacity of individuals and populations to cope through phenotypic plasticity and adaptation is of critical interest, with advances in genomics and epigenomics techniques helping to unveil the underlying molecular mechanisms (Eirin-Lopez and Putnam, 2019). However, major knowledge gaps remain about the adaptive potential of marine organisms to respond to future ocean conditions. The aim of this Research Topic was to bring together novel research approaches that examine acclimation and adaptation processes in marine organisms, their role in population resilience, and implications for geographical distributions and range shifts under rapid climate change. Contributions to the topic span a broad range of taxa, and investigate a diverse array of response mechanisms such as thermal safety margins (Bennett et al.), thermotolerance *via* endosymbionts and gene expression (Naugle et al.), tolerance *via* changes in allele frequencies (Knöbel et al.), local adaptation and maternal effects (Richards et al.), transgenerational plasticity (TGP; Chang et al.), environment-dependent reproductive success (Wanzenböck et al.), and phenological shifts to long-term seasonal changes (Xia et al.). Furthermore, the importance of environmental variability (not only mean changes) at different time scales, the role of developmental or life history stage in phenotypic responses, as well as future challenges for plasticity research (both within and across generations) are outlined in Bautista and Crespel.

THERMAL TOLERANCE

Organisms can cope with fast changing environments either by staying in place and tolerating local conditions, adjusting *via* plasticity or genetic change, or shifting their distribution to more favourable environments (Gienapp et al., 2007). As discussed in Bennett et al., species distribution models often assume that thermal sensitivity is the same along the species´ geographic distribution, and do not account for local adaptation or thermal plasticity. Bennett et al. conducted a comparative study using populations of four foundation species (two seagrass and two seaweed) that occur across a west-east temperature gradient in the Mediterranean. They found the greatest variability in thermal performance between species, but also site-specific differences in thermal safety margins within species (e.g., *Posidonia oceanica*), and that species retain deep "pre-Mediterranean" evolutionary legacies (genetic differences) for thermal sensitivity. Their study demonstrates differing thermal sensitivities of species despite similarities in realised thermal distributions. Around the island of Tutuila in American Samoa, Naugle et al. investigated thermal tolerance of coral colonies (*Acropora hyacinthus*) from sites with baseline differences in nutrient pollution. This multi-stressor experiment showed that in 2014, polluted sites had more thermotolerant corals due to higher proportions of heat-tolerant endosymbionts, whereas by 2019, there were small difference among sites because most colonies had undergone "symbiont shuffling" towards the heat-tolerant forms. These two studies demonstrate population-specific thermal tolerance, which has important implications for species conservation and management strategies.

GENETIC CHANGE AND NON-GENETIC INHERITANCE

Although it is often assumed that genetic adaptation may be too slow to keep pace with climate change, major shifts in allele frequencies can occur in one generation. Plasticity and non-genetic inheritance are faster and have multiple pathways from which to act. However, how plasticity shapes selection strengths is debated (Merilä and Hendry, 2013). To examine local adaptation to salinity in blue mussels (*Mytilus* spp.), Knöbel et al. conducted a common garden experiment using high salinity "western" and low salinity "eastern" mussels from the Baltic sea and found that laboratory-bred larvae showed local adaptation for several traits. Testing larvae derived from a F1 west-east hybrid population to predicted future desalinisation and warming, they found that when larval populations were exposed to lower salinity, there was a shift toward the "eastern" alleles, indicating that salinity acts as a selection force during the pre-settlement phase driving local adaptation to low salinity, ultimately shaping the genetic composition of populations along the salinity gradient.

Both within- and across-generation plasticity have been shown to contribute to the adaptive potential of populations (Donelson et al., 2018). Exposing six populations of the foundation species, red mangrove (*Rhizophora mangle*), to both increased salinity and nitrogen in a common garden setting, Richards et al. found plasticity in response to salinity for some traits, but that other trait responses co-varied with both stressors. Significant population effects in the common garden suggest local adaptation and/or heritable plasticity, but the strongest predictor for nearly all traits was maternal family, indicating non-genetic inheritance mechanisms. Maternal effects are known to play a large role in offspring phenotypic variation, however, paternal effects are starting to gain attention (Crean and Bonduriansky, 2014). Using laboratory-bred F3 generation sheepshead minnows (*Cypriniodont variegatus*) as parental fish, Chang et al. exposed both parents and offspring to two temperatures in a split-cross TGP experiment. They found that offspring growth was lowest when there was no thermal history match among parents and offspring, but highest when all three matched. That is, TGP effects were additive across the sire-offspring and dam-offspring interactions. Strong paternal effects suggest an epigenetic basis underlying TGP.

REPRODUCTIVE BEHAVIOUR

In addition to shaping key fitness-related traits such as growth, changing environmental conditions can also influence reproductive behaviours like mate choice and the onset of breeding (Fox et al., 2019). Using a mesocosm experiment, Wanzenböck et al. tested for differential reproductive success among stickleback (*Gasterosteus aculeatus*) plate morph phenotypes by genotyping egg clutches laid in either ambient or +4°C conditions. They found that low-plated males sired more eggs at +4°C, likely due to their smaller size (relative to other morphs), and hence, lower metabolic demands at higher temperature. However, more low-plated fish under ocean warming may have implications for range shifts, since their migration distance is limited due to missing keel plates. In silver carp (*Hypophthalmichthys molitrix*), spawning periods are influenced by both temperature and river discharge (which can affect oviposition habitat). By correlating time-series data of temperature and hydrological regimes with larval fish abundance, Xia et al. found that spawning times of populations showed local adaptation, and that the spawning period has shortened over the last decade, with clear implications for reproductive output of this commercially important species.

FUTURE CHALLENGES

The diverse array of mechanisms to cope with rapid climate change compiled in this Research Topic are reviewed in Bautista and Crespel. They highlight that within-generation responses such as thermal tolerance, plasticity and/or relocation are a first line of defence. If organisms manage to reproduce, then climate change effects can be transferred across generations *via* genetic change (adaptation) and/or non-genetic inheritance *via* parental effects, TGP and/or heritable epigenetic modifications. Importantly, they advocate for the inclusion of more environmental variability in future experiments to provide ecologically relevant predictions, and to investigate consequences of early exposure on later stages (carryover effects) and fitness traits. Key research areas for the future include the role of non-genetic inheritance in evolution, neutral and quantitative genetic adaptive potential, interactions between within- and transgenerational plasticity, and coupling genetic sequence data with epigenetic patterns to assess the heritability of epigenetic marks. The collection of papers in this Research Topic demonstrate empirically how adaptation and phenotypic plasticity contribute to population resilience, and propose new research directions to further understanding of their importance under future climate change.

AUTHOR CONTRIBUTIONS

LS, JD, JE-L and TR together wrote this editorial. All authors contributed to the article and approved the submitted version.

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