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REVIEW

Avenues of reef-building coral acclimatization in response to rapid environmental change

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ABSTRACT

The swiftly changing climate presents a challenge to organismal fitness by creating a mismatch between the current environment and phenotypes adapted to historic conditions. Acclimatory mechanisms may be especially crucial for sessile benthic marine taxa, such as reef-building corals, where climate change factors including ocean acidification and increasing temperature elicit strong negative physiological responses such as bleaching, disease and mortality. Here, within the context of multiple stressors threatening marine organisms, I describe the wealth of metaorganism response mechanisms to rapid ocean change and the ontogenetic shifts in organism interactions with the environment that can generate plasticity. I then highlight the need to consider the interactions of rapid and evolutionary responses in an adaptive (epi)genetic continuum. Building on the definitions of these mechanisms and continuum, I also present how the interplay of the microbiome, epigenetics and parental effects creates additional avenues for rapid acclimatization. To consider under what conditions epigenetic inheritance has a more substantial role, I propose investigation into the offset of timing of gametogenesis leading to different environmental integration times between eggs and sperm and the consequences of this for gamete epigenetic compatibility. Collectively, non-genetic, yet heritable phenotypic plasticity will have significant ecological and evolutionary implications for sessile marine organism persistence under rapid climate change. As such, reef-building corals present ideal and time-sensitive models for further development of our understanding of adaptive feedback loops in a multi-player (epi)genetic continuum.

KEY WORDS: Epigenetics, Parental effects, Adaptive capacity

Introduction: challenges of a changing marine environment

As more benign ocean conditions rapidly shift to extremes owing to ongoing and amplifying climate change factors, a greater proportion of marine organisms are being pushed beyond their physiological limits. Based on the Intergovernmental Panel on Climate Change representative concentration pathway climate scenarios, substantial changes in a suite of environmental factors impacting marine life are currently intensifying, with dire forecasts for marine ecosystems in the foreseeable future (IPCC, 2019). For example, anthropogenic greenhouse gas emissions are driving an increase in background sea surface temperatures (IPCC, 2019) and the magnitude and duration of marine heatwaves (Oliver et al., 2021). Together, these thermal stresses are driving the collapse of reef-building coral symbiosis (Oakley and Davy, 2018), with detrimental impacts through losses in coral cover and shifts in community assembly and function (Hughes et al., 2017a, 2018). Further, ocean acidification, or the uptake of increasing atmospheric CO_2 by surface ocean waters and the resulting decline in pH, is contributing to shell and skeletal reductions and abnormalities in marine calcifiers (Kroeker et al., 2010) and increased energetic costs for development and daily metabolic demands in a high CO_2 world (Pan et al., 2015). Additionally, warming-induced stratification is causing ocean deoxygenation, contributing to alarming capacity for shifts in oceanic biogeochemical cycling (Keeling et al., 2010). In combination, these environmental changes along with a myriad of local anthropogenic impacts generate a challenging multi-stressor environment within which marine organisms are struggling to cope (Boyd et al., 2015).

As global climate change escalates, a clear canary in the coal mine has emerged in coral reef ecosystems (Hughes et al., 2017b). Reef-building corals are the key habitat engineers for a massive ecosystem valued on the order of hundreds of billions of dollars annually (Bishop et al., 2011; Costanza et al., 2014). Corals are holobionts (see Glossary), or metaorganisms composed of multiple living partners. For example, corals house millions of endosymbiotic single-celled dinoflagellates in the family Symbiodiniaceae (LaJeunesse et al., 2018) that are responsible for the essential function of nutritional recycling in tropical oligotrophic waters. Specifically, the coral provides a stable habitat in the photic zone and access to inorganic nutrients and metabolic byproducts for the Symbiodiniaceae, which in turn photosynthesize and release excess organic products to the coral host in the forms of sugars and lipids (Venn et al., 2008). In addition to Symbiodiniaceae, corals host a microbiome (see Glossary) composed of bacterial symbionts, fungi and viruses (Bourne et al., 2016; van Oppen and Blackall, 2019). To date, the most functional information for these microbial partners is available for bacteria. The bacterial community plays essential roles in providing vitamins (Agostini et al., 2012; Robbins et al., 2019), nitrogen cycling critical in oligotrophic waters (Pogoreutz et al., 2017; Rädecker et al., 2015) and carbon cycling (Brown and Bythell, 2005; Kimes et al., 2010; Rohwer and Kelley, 2004), among other functions. As such, there are a wealth of functional outcomes stemming from the host and dynamic interactions with their microbial symbionts.

The productivity generated through holobiont nutritional recycling can also be a vulnerability, as external environments become more stressful for each of these constituent taxa under climate change. Temperature stress can drive shifts in prokaryotic communities (Bourne et al., 2008) towards opportunistic, or even pathogenic, communities (Littman et al., 2011). For example, analysis of corals under thermal stress identifies enrichment for genes involved in virulence (Littman et al., 2011) and a shift to bacterial communities associated with disease (Thurber et al., 2009). Ocean warming also drives dysbiosis between the coral host and its endosymbiotic dinoflagellates. Coral bleaching is the loss of pigmentation of the Symbiodiniaceae cells from the coral tissues, such that the white skeletons can be seen through the clear host tissues. Mass bleaching is the primary threat to coral energetics and survival worldwide

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Glossary

Acclimation
A rapid physiological or biochemical change within the life of an organism resulting from exposure to new environmental conditions in a laboratory or experiment (Hochachka and Somero, 2002; Willmer et al., 2009).

Acclimatization
A rapid physiological or biochemical change within the life of an organism resulting from exposure to new environmental conditions in a natural environmental setting (Hochachka and Somero, 2002; Willmer et al., 2009).

Carryover effects
Phenotypic consequences of environmental exposure from prior developmental stages (Byrne et al., 2020).

Epigenetics
Mechanisms that cause changes to gene expression that are not dependent on changes to DNA sequence and persist across cells and generations, through mitosis and meiosis, respectively (Cavalli and Heard, 2019; Deans and Maggert, 2015).

Epigenetic inheritance
The passing on of epigenetic marks or gene regulation states that are not due to changes in DNA bases.

Genetic inheritance
A trait passed on due to genetic factors.

Holobiont
Also meta-organism. The functional combination of a host organism and its associated symbiotic community.

Inheritance
Generally defined as the capacity for a trait to be passed on.

Intra-generational plasticity
A general term for carryover effects at any life stage.

Microbiome
An organism's intimately physically or functionally associated community of microbial taxa (eukaryotic and prokaryotic).

Multi-generational plasticity
Phenotypic consequences of the environment of previous generations is evident for several offspring generations (Byrne et al., 2020).

Non-genetic inheritance
A trait passed on due to environmental influences or biological response modulated by environmental influences (including aspects such as parental effects).

Plasticity
Multiple phenotypic outcomes from the same organism across varied environmental conditions.

(Hughes et al., 2017a). For example, in the mass bleaching of 2016 on the Great Barrier Reef (GBR), 91.1% of the 1156 surveyed reefs showed signs of bleaching. In short order, this mass bleaching event negatively impacted community composition, physical structure and ecological function of approximately one-third of 3863 studied reefs on the GBR (Hughes et al., 2018), as well as having cascading impacts on GBR reproduction and recruitment (Hughes et al., 2019).

As reef decline becomes more pronounced, human-assisted evolution of corals (van Oppen et al., 2015) has been proposed as a means of enhancing or restoring damaged and degraded reefs. The overarching goal of human intervention is to mitigate the loss of reefs by generating and outplanting 'climate-resilient' corals. There is a wide spectrum of initiatives proposed under this umbrella, ranging from the less invasive end of environmental hardening (Putnam et al., 2020) to symbiont evolution in the laboratory (Buerger et al., 2020; Chakravarti and van Oppen, 2018; Chakravarti et al., 2017), biobanking coral genetic diversity through cryopreservation (Hagedorn et al., 2019) and/or a Noah's Ark of living coral managed by a global aquarium consortium (Zoccola et al., 2020), host-selective breeding (Quigley et al., 2020), 3D coral bioprinting (Wangpraseurt et al., 2020) and, at the most aggressive end of interventions, coral genome editing (Cleves et al., 2018) and synthetic biology (Anthony et al., 2017). Regardless of outstanding questions of scale and implementation, the future of coral reef management, conservation and restoration rests on our understanding of the avenues of coral holobiont acclimatization (see Glossary) and adaptation.

Corals as metaorganisms with complex life cycles

Several important aspects of coral biology focused on in this Review provide the potential for a variety of rapid response mechanisms in corals. The first is the fact that corals are a metaorganism (Bosch and McFall-Ngai, 2011), where the holobiont function is dependent on both the host and its symbiotic partners. The second is that corals have complex life cycles that interchange between pelagic gametes and/or larvae and a benthic adult stage (Baird et al., 2009; Marshall and Morgan, 2011). In this way, all coral life stages can be influenced by the environment, which provides the opportunity for ontogenetic shifts in holobiont response to have cascading effects (Fig. 1). Together, these aspects of the metaorganism and a complex life cycle provide an array of genetic and non-genetic opportunities for coral acclimatization and adaptation. Here, I describe various aspects of coral as metaorganisms (section 'Metaorganism response mechanisms to rapid ocean change') and discuss the roles of ontogeny (section 'Roles for environmental interactions across ontogeny in generating plasticity') in an adaptive (epi)genetic continuum [section 'Adaptive (epi)genetic continuum'] with multiple avenues of response to rapid environmental change.

Metaorganism response mechanisms to rapid ocean change

Reef-building corals are metaorganisms (Bosch and McFall-Ngai, 2011; Pogoreutz et al., 2020) living within a symbiome (Ainsworth et al., 2020; Gates and Ainsworth, 2011). These intimate and dynamic symbiotic interactions provide acclimatory response within the host's lifetime.

Bacteria, archaea and viruses

Rapid acclimatization capacity is possible through the genetic and functional breadth of bacteria, archaea and viruses associated with coral hosts. As the extent of knowledge of microbial contributions to the holobiont is growing rapidly, I also point to key reviews on this topic (Bourne et al., 2016; Epstein et al., 2019; Hernandez-Agreda et al., 2017; McDevitt-Irwin et al., 2017; Morrow et al., 2018; Rosado et al., 2019; Thurber et al., 2017; Torda et al., 2017; van Oppen and Blackall, 2019). Prokaryotic taxa have very rapid generation times and, importantly, fill key metabolic roles for the host. Mechanistically, holobiont acclimatization could occur through shifts in the genetic material available within a microbial community and horizontal gene transfer (van Oppen and Medina, 2020). For example, rapid transition of the bacterial community to new members and, therefore, functions can be seen when fragments of corals are moved to new environments. Specifically, transplantation from a moderately variable thermal pool to a highly variable thermal pool in an American Samoa back reef resulted in a microbiome shift to match that of corals from the highly variable pool (Ziegler et al., 2017). Furthermore, following acquisition of the bacterial community characteristic of the highly variable pool, corals showed enhanced thermal tolerance. Although it is not yet possible to fully manipulate the microbiome to assign causation, there are clearly links between the prokaryotic microbiome and environmental temperature (Bourne et al., 2008; Littman et al., 2011).

Inheritance of the microbial community is posited as a means of microbiome-mediated transgenerational acclimatisation by Webster and Reusch (2017). Experimentally, inheritance of the prokaryotic

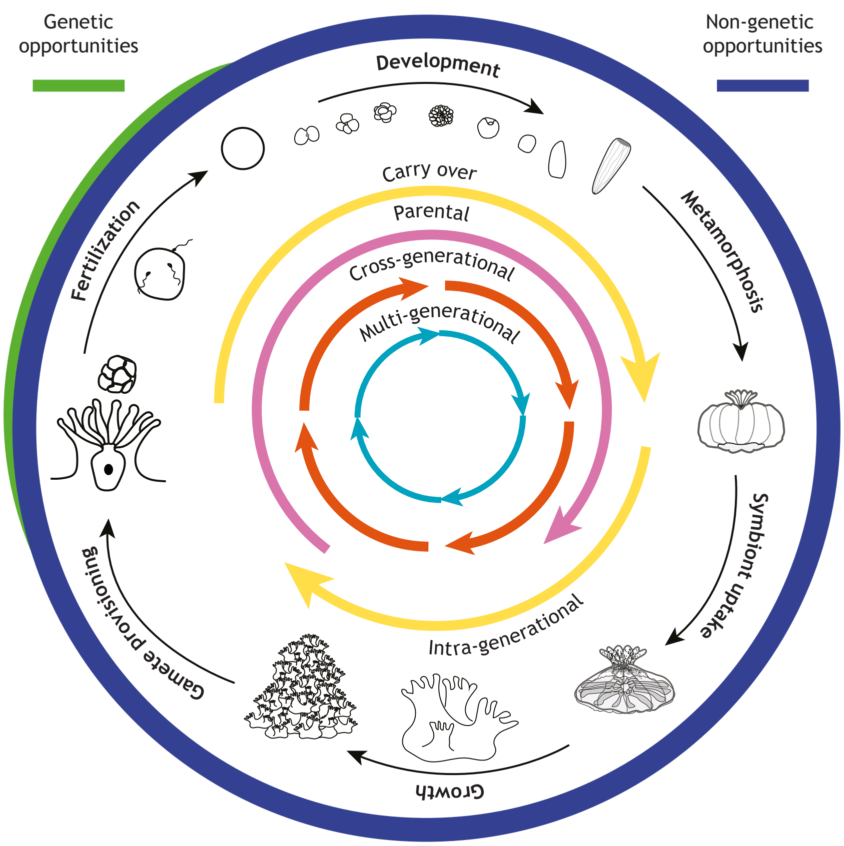

Fig. 1. Acclimatory and adaptive opportunities in organisms with complex life histories. While genetic opportunities (outer green line) to contribute to rapid adaptation are more temporally limited (e.g. germline formation, sexual recombination and fertilization), there are a wealth of opportunities throughout the life cycle for environmental signals to elicit non-genetic opportunities (blue line) for acclimatization. This is the case in organisms with complex life histories (coral broadcast spawning life cycle shown by images and black lines and arrows), such as corals. The types of opportunity are shown in the center of the circle (colored lines indicate the type and general life stages over which these acclimatization mechanisms occur).

microbiome is supported by data of vertical transmission in *Porites astreoides* (Sharp et al., 2012), *Pocillopora meandrina* (Apprill et al., 2012), *Acropora gemmifera* (Zhou et al., 2017) and *Mussismilia hispida* (Leite et al., 2017). The inheritance of the prokaryotic microbiome remains poorly characterized for the majority of coral species (Quigley et al., 2018; van Oppen and Blackall, 2019).

Symbiodiniaceae

The capacity for the Symbiodiniaceae to contribute to holobiont performance is underscored by their massive carbon contribution to the host (Falkowski et al., 1984; Muscatine et al., 1981) and functional differences between Symbiodiniaceae species (Little et al., 2004; Sampayo et al., 2008; Stat et al., 2008). The possibility that Symbiodiniaceae community change leads to a change in holobiont tolerance was proposed as the adaptive bleaching hypothesis (Buddemeier and Fautin, 1993). This posits that corals may increase thermal tolerance through expulsion of thermally sensitive symbionts and uptake of new tolerant types (i.e. switching), or repopulation by the remaining thermally tolerant types (i.e. shuffling).

Symbiont shuffling seems to be the primary mechanism of community change (Berkelmans and van Oppen, 2006; LaJeunesse et al., 2009; Mieog et al., 2007). For example, experimental bleaching of *Orbicella faveolata* resulted in shuffling to a more thermally tolerant symbiont community dominated by *Durusdinium* (clade D), which increased holobiont tolerance (Cunning et al., 2015). Beyond shuffling, there is more rare evidence for the possibility of switching through acquisition of new species from the environment to achieve at least a temporary buffer against stress and starvation (Boulotte et al., 2016; Coffroth et al., 2010). Both shuffling and switching are functionally important as they can result in changes in host–symbiont carbon and nitrogen recycling, and thus impact holobiont energetics, thermal tolerance and growth. For example, *in vitro* experiments comparing Symbiodiniaceae function reported that lower amounts of carbon were released and translocated in synthetic host factor in *Symbiodinium* sp. (clade A) than *Cladicopium* sp. (clade C) (Stat et al., 2008). *In hospite*, faster growth has been demonstrated in *Acropora* spp. juveniles inoculated with *Cladicopium* sp. (clade C) in comparison to those with *Durisdinium* (clade D) (Little et al., 2004). However, there are often trade-offs in holobiont function if the Symbiodiniaceae communities change. Specifically, thermal tolerance can come at the expense of photosynthetic function (Cunning et al., 2015).

Inheritance of the Symbiodiniaceae is possible through vertical transmission, or the packaging of Symbiodiniaceae in the coral eggs during gametogenesis (Padilla-Gamiño et al., 2012; Quigley et al., 2019; Reich et al., 2017; Zhou et al., 2017). Often, however, even if a variety of Symbiodiniaceae are taken up, they can be winnowed out, or outcompeted, with the community returning to the prior state (Coffroth et al., 2010; Dunn and Weis, 2009; Weis et al., 2001). Similarly to the prokaryotic microbiome, further studies are needed on Symbiodiniaceae inheritance and the physiological and ecological consequences.

Endoliths and coral-associated (macro)symbionts

Beyond what are considered the primary players in the holobiont (coral host, Symbiodiniaceae, bacteria, archaea and viruses), there is a growing understanding of functional contributions of other tissue- and skeletal-associated organisms including endolithic algae and fungi (Amend et al., 2012; Wegley et al., 2007). Structural and photophysiological analyses of thick coral tissues and the coral skeleton have documented common occurrences of endolithic organisms such as the *Ostreobium* (del Campo et al., 2017; Fine and Loya, 2002; Massé et al., 2018). Functional investigation of *Ostreobium* identified transfer of

^{14}C-containing products to the bleached *Oculina patagonica* host tissue (Fine and Loya, 2002). A suite of fungi have also been identified in association with corals (Amend et al., 2012). Metagenomic analyses show the potential for fungal contributions to carbon and nitrogen cycling in the coral *P. astreoides* (Wegley et al., 2007). Collectively, this work indicates that holobiont energetic balance is also supported by endolithic organisms.

Aside from organisms living within the skeleton, corals also have the capacity to interact with a variety of coral-associated vertebrates and invertebrates (Stella et al., 2010). For example, corals and their microbiome can take up ammonium and urea deposited in the seawater by coral-associated fishes (Robbins et al., 2019). This can result in enhanced coral growth, likely owing to the addition of limiting nutrients (Allgeier et al., 2014). Further research is needed, however, to more fully characterize the role of these endolithic taxa and less intimately linked coral-associated organisms to coral acclimatization to climate change. Inheritance of these more loosely associated organisms is unlikely, as they are not physically connected to the coral holobiont. It is possible, however, that their nutrient subsidies could have indirect implications for inheritance by affecting the microbiome (Morris et al., 2019), or triggering epigenetic changes (Rodriguez-Casariego et al., 2018), as described below.

Host epigenetics

While gene regulation processes have been implicated in intra- and cross-generational acclimatization (Fig. 1, see Glossary), there has been a recent focus on epigenetics (see Glossary) as the mechanistic underpinnings of these processes through gene regulation (reviewed in Eirin-Lopez and Putnam, 2019). Epigenetics can be defined as molecules and mechanisms generating alternative gene activity states without a change in DNA sequence (Cavalli and Heard, 2019; Deans and Maggert, 2015). Classically, epigenetic mechanisms primarily include: DNA methylation, chromatin structure, histone variants and histone post-translational modifications, as well as non-coding RNAs and RNA methylation (reviewed in Eirin-Lopez and Putnam, 2019; Skvortsova et al., 2018). Inducible DNA methylation and associated phenotypic plasticity (see Glossary) have been demonstrated in cnidarians in response to ocean acidification (Liew et al., 2018; Putnam et al., 2016), symbiosis (Li et al., 2018a), thermal environment (Dixon et al., 2018), nutrients (Rodriguez-Casariego et al., 2018), seasonal environmental changes (Rodríguez-Casariego et al., 2020) and microhabitat (Durante et al., 2019). DNA methylation and its link to magnitude and variability of gene expression (e.g. Liew et al., 2018) have been the primary focus of epigenetic studies to date. However, studies of multiple epigenetic mechanisms in cnidarians including DNA methylation, histone modification and chromatin structure (e.g. Li et al., 2018a; Rodriguez-Casariego et al., 2018; Weizman and Levy, 2019) are beginning to paint a picture of complex epigenetic interplay (i.e. interactions between mechanisms) (Adrian-Kalchhauser et al., 2020).

Inheritance of epigenetic mechanisms, while documented in a variety of taxa, is not an absolute (Ptashne, 2013). In particular, the mechanisms that generate epigenetic ‘memory’ are expected to be maintained by consistent, or predictable, environmental feedback. Thus, often wash-in and wash-out dynamics are to be expected as environments vary (Burggren, 2015). While other marine taxa such as fish (Ryu et al., 2018), urchins (Strader et al., 2019) and oysters (Rondon et al., 2017) show epigenetic inheritance (see Glossary), only a single study has been published to date for corals (Liew et al., 2020). In that study of the coral *Platygyra daedalea*, transmission of DNA methylation was shown between adults, sperm and larvae. Specifically, comparison of corals from extreme conditions (Abu Dhabi) with those from more benign conditions (Fujairah) identified a suite of genes showing origin-specific methylation in the adults and offspring, with methylation strongly correlated to thermal tolerance (Liew et al., 2020). Collectively, the phenotypic response in cross-generational studies of brooding corals (Bellworthy et al., 2019b; Putnam and Gates, 2015; Putnam et al., 2020) and the epigenetic linkages between parent and offspring in spawning corals (Liew et al., 2020) support a capacity for epigenetic inheritance in corals more broadly.

Host genetics

A wealth of stress response capacity is due to cnidarian host genetics, along with the greatest potential for inheritance through genetic inheritance (see Glossary) (Falconer and Mackay, 1996). It is clear that genetic variability underlying coral traits exists on reefs (Baums et al., 2013; Drury et al., 2017; Howells et al., 2016; Meyer et al., 2009) and that traits such as growth are heritable and have adaptive potential (Császár et al., 2010; Jury et al., 2019). For example, thermal tolerance, which is a critical trait under ocean warming, was higher in genetically diverged *P. astreoides* populations from warmer inshore areas compared with populations from cooler offshore areas of the Florida Keys (Kenkel et al., 2013). Further study in this same species and location supported a role for genetic differentiation in coral growth, with juvenile corals from the warmer inshore location having higher growth than those from the cooler offshore location when assessed in a common garden experiment (Kenkel et al., 2015).

There is also a clear capacity for more rapid genetic adaptation than previously thought. Specifically, comparison of crosses of *Acropora millepora* colonies from a warmer habitat resulted in offspring with substantially greater thermotolerance than crosses of adults from a cooler habitat (Dixon et al., 2015). A recent genome-wide association study of *A. millepora* that focused on the genetic architecture of thermal tolerance further identified genetic underpinnings of thermal tolerance. In this coral species at least, it appears that thermal tolerance is due to multiple loci of combined effect, not few loci of large effect (Fuller et al., 2020). Scans for functional genes of interest with respect to local adaptation identified the heat-shock co-chaperone sacsin, which has also been identified to be responsive in thermal stress experiments. These studies and others (reviewed in Drury, 2020; Torda et al., 2017) highlight host adaptive capacity, but questions remain on the rates of this genetic capacity for the multitude of coral species on reefs given differences in reproductive mode and fecundity (Baird et al., 2009). Further, the potential for climate change disruption of coral spawning (Shlesinger and Loya, 2019) could dramatically reduce the rate of, and capacity for, genetic adaptation.

The time scale and inheritance of mechanisms of acclimatization and adaptation in the metaorganism partner range from rapid response and weaker inheritance in the microbiome to slower response and stronger inheritance in the coral host (Fig. 2). Non-genetic mechanisms span this range, as they have the capacity to be induced on the order of days to months, yet can drive multigenerational impacts. This indicates that not only are the mechanisms generated by metaorganism partners important, but also their interactions across coral life stages.

Roles for environmental interactions across ontogeny in generating plasticity

The interaction of climate-change-associated stressors with a variety of stages across complex life cycles (Fig. 1, center images and colored arrows) can result in plasticity in terms of parental effects, carryover

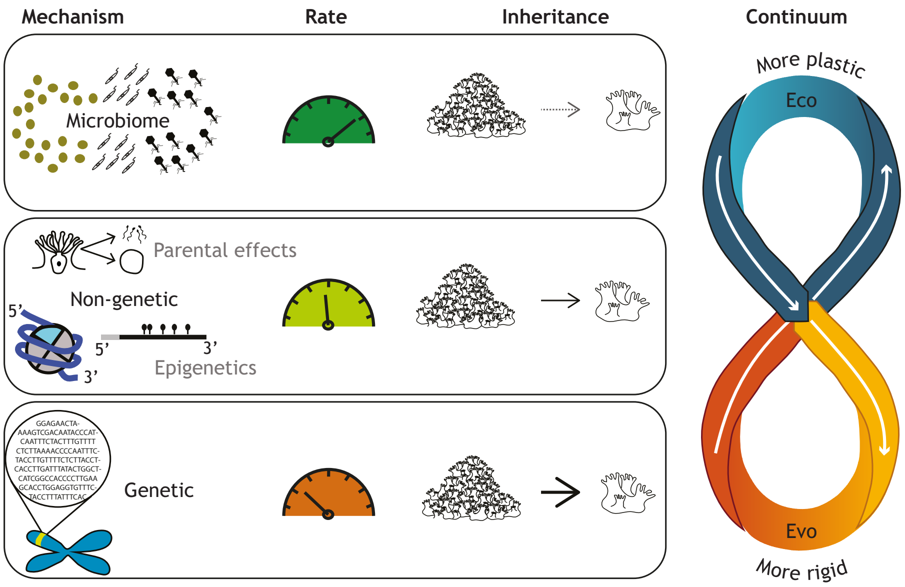

Fig. 2. The adaptive (epi)genetic continuum. Acclimatory and adaptive processes exist on a continuum from the weaker inheritance, plastic end (e.g. microbiome) to higher inheritance, more rigid end (host genetics). Notably, there are feedbacks across these mechanisms where, for example, the microbiome could trigger modifications of the epigenome, and thus gene expression and phenotype. This phenotype could in turn undergo genetic accommodation and evolution.

effects and intra-generational plasticity, cross-generational plasticity and multi-generational plasticity (*sensu* Byrne et al., 2020) (see Glossary). Here, I further define and discuss these ontogenetic sensitivities and opportunities for plasticity and acclimatization.

Parental effects

Plasticity in offspring owing to parental provisioning has been demonstrated in a variety of marine organisms (Marshall and Keough, 2006; Marshall et al., 2008), including corals. This includes the transfer of macromolecules, metabolites, mRNAs, microbiome and mitochondria (Torda et al., 2017). This provisioning is essential for successful embryo development, and protection against environmental challenges such as ultraviolet radiation, pathogens, oxidative stress and energetic demands of homeostasis (Hamdoun and Epel, 2007).

Parental effects in corals can be seen as temporal variation on day of release providing bet-hedging strategies for environmental tolerance (Cumbo et al., 2013; Putnam et al., 2010; Rivest and Hofmann, 2014). Additionally, parental provisioning can be based on integration of site-specific environmental information. For example, *Orbicella faveolata* eggs from adults at 1 m depth had significantly higher concentrations of mycosporine-like amino acid concentrations for UV protection than those eggs released from adults living at 6–8 m (Wellington and Fitt, 2003). In contrast, for corals such as *Montipora capitata* that transmit their symbionts vertically in areas where there are not large contrasts in environmental conditions, parental provisioning shows a coordinated response (Padilla-Gamiño et al., 2013). Specifically, the eggs have significant lipid provisioning (in comparison to adults) for the energetic demands of development, dispersal, metamorphosis and settlement. Simultaneously, the eggs harbor lower symbiont densities and chlorophyll than adult corals (Padilla-Gamiño et al., 2013), likely to reduce the potential for oxidative damage from photosynthesizing at the ocean's surface. Parental effects are also present at the transcriptomic level. This set of parentally provisioned genes (Strader et al., 2018; Van Etten et al., 2020) provides the essential developmental functions (prior to zygotic gene expression initiation) in some of the most sensitive coral developmental stages, namely, fertilization and cleavage.

Beyond mRNA and macromolecules, gametes are provisioned with the essential maternal feature of mitochondria. The abundance and capacity of mitochondria in eggs is critical for cellular respiration to generate ATP. For example, in the marine polychaete *Ophryotrocha labronica*, multigenerational plasticity was present through five generations, where those worms exposed to ocean warming had greater mitochondrial capacity and efficiency (Gibbin et al., 2017). Maternal transfer of mitochondrial function is also essential in corals, where 66% of the variance quantified in a heritability study was due to maternal (mitochondrial) influence, which was ∼6 times higher than the variance due to paternal influence or their interaction (Dixon et al., 2015). Together, this breadth of parental and maternal provisioning can contribute to ecological success and fitness, thereby influencing larval settlement and mortality (Quigley et al., 2016), as well as survivorship under thermal challenges (Dixon et al., 2015).

Carryover effects and intra-generational plasticity

Corals have a large capacity for phenotypic plasticity to generate carryover effects, or consequences of environmental exposure from prior developmental stages (*sensu* Byrne et al., 2020). Few studies of coral to date have specifically tested for carryover effects, but those published reveal both beneficial and maladaptive acclimatization. In the spawning coral *Acropora pulchra*, exposure of gametes to increased temperatures [ambient (26°C) +6°C] prior to fertilization resulted in significantly enhanced fertilization success when fertilized at 32°C (Puisay et al., 2018). This enhancement was not present at all temperature treatments, and thermal acclimation (see Glossary) during fertilization and development resulted in some increases in development abnormalities. In the brooding coral *P. astreoides*, swimming larvae exposed to warmer water [ambient (27°C) +3°C] showed no effect of treatment on photochemical efficiency, respiration rate, settlement or survivorship within a few days of exposure, but did have significantly increased catalase (Ross et al., 2013). Post-settlement mortality was significantly higher, however, for these recruits that were previously exposed to 30°C when corals were assayed ∼1 month later.

Beyond carryover effects in these early life stages, corals also display intra-generational plasticity, a general term for carryover effects at any life stage. Some of the earliest studies identifying the potential for beneficial intra-generational plasticity were documented as environmental history driving subsequent response in corals (Brown et al., 2000, 2002). Here, natural solar irradiance-induced bleaching on the exposed portion of the coral colonies resulted in protection against future thermal bleaching in those portions. This environmental hardening phenomenon has since been tested experimentally in *A. millepora*, with short preconditioning periods reducing the stress response and shuffling of the microbiome ruled out, thereby supporting host-beneficial intra-generational plasticity (Bellantuono and Hoegh-Guldberg, 2012). Such a benefit is also seen in natural environmental settings, where protective thermal trajectories (Ainsworth et al., 2016) and high-frequency temperature variation (Safaie et al., 2018; Sully et al., 2019) can reduce coral bleaching.

Cross-generational and multi-generational plasticity

Cross-generational plasticity occurs when the environment of the parent affects the phenotype of the offspring (*sensu* Byrne et al., 2020) (see also 'Parental effects' above). The potential for cross-generational plasticity has been tested in a handful of studies to date in response to temperature, ocean acidification and feeding (Bellworthy et al., 2019a,b; Putnam and Gates, 2015; Putnam et al., 2020). For example, exposure of adult brooding coral *Pocillopora damicornis* (now identified as *P. acuta*) in Hawai'i to ocean acidification and warming results in offspring metabolic benefit (Putnam and Gates, 2015), as well as ecological benefits (settlement, survivorship and growth) lasting up to 1 month post settlement (Putnam et al., 2020). In comparison, in the brooding coral *Stylophora pistillata* from a warmer thermal environment in the Red Sea, exposure to increased temperature during brooding had little impact on either adults or their offspring (Bellworthy et al., 2019a). However, in the case of enhanced feeding of parent *S. pistillata*, offspring of fed parents were greater in number with enhanced protein content, and thus these larvae had lower mortality rates under an ambient (24°C) +3°C thermal challenge (Bellworthy et al., 2019b). For these studies, it is also important to point out that without full knowledge of the timing of gametogenesis relative to the parental exposure periods and brooding of fully developed larvae in the parents, it is possible these results are indicative of either carryover effects or cross-generational plasticity (Byrne et al., 2020).

To date, multi-generational plasticity, where the phenotypic consequences of the environment of previous generations is evident for several offspring generations (Byrne et al., 2020), has not yet been demonstrated experimentally in corals. Experiments are currently focused primarily on fast-growing brooding corals, where expectations are highest for multi-generational plasticity and non-genetic inheritance (Torda et al., 2017) (see Glossary). Importantly for these species, it is possible to obtain reproductive maturity within 18–24 months for some brooding corals. These studies are, however, also essential in spawning corals, owing to the capacity to ensure exposures either exclude or include all of gametogenesis. Parental exposure and quantitative cross designs in spawning corals will help to disentangle the roles of parental effects, epigenetic mechanisms and carryover effects (Byrne et al., 2020; Donelson et al., 2018; Torda et al., 2017).

Adaptive (epi)genetic continuum

From an ecological perspective, these acclimatory mechanisms provide a ray of hope for reef futures. The presence of coral at sites such as CO_2 vents and high CO_2 reefs (Fabricius et al., 2011; Jury et al., 2013; Price et al., 2012), and environmental extremes (reviewed in Camp et al., 2018) provides evidence of natural biological mechanisms of acclimatization and/or adaptation. Evolutionarily, the fate of corals is less clear under the current and expected rate of climate change. There is a paucity of experimental examples of the evolutionary outcomes from the interactions of non-genetic and genetic mechanisms for corals and most marine invertebrates. Theoretical models and work in systems with rapid generation times, however, highlight the importance of examining acclimatization and adaptation together (Ghalambor et al., 2007, 2015; Klironomos et al., 2013; Kronholm and Collins, 2016; Walworth et al., 2020). Here, I advocate for viewing the avenues through which corals can rapidly respond to environmental change, as an adaptive (epi)genetic continuum, with ecological and evolutionary processes intertwined through feedbacks across the continuum (Fig. 2).

The processes of acclimatization and adaptation embody the definition of a continuum, or 'a continuous sequence in which adjacent elements are not perceptibly different from each other, although the extremes are quite distinct' (Lexico, 2021). At the plastic end of the continuum, the rapid generation times and dynamic metabolic capacity of a changing microbiome community can have near real-time phenotypic consequences. The time scale of induction of epigenetic mechanisms has been documented on the order of weeks to months for DNA methylation in corals (Dixon et al., 2018; Putnam et al., 2016). However, the response time, stability and inheritance of the breadth of epigenetic mechanisms have yet to be fully characterized (but see Liew et al., 2020). Genetic adaptation occurs at the slowest rate relative to these other mechanisms and is at the more rigid end of the continuum. Although rapid adaptation is possible in some species (Dixon et al., 2015), rates remain understudied for the majority of coral taxa. Further, study of potential phenotypic–evolutionary feedback through processes such as mutation of CpG sites and codon evolution (Dixon et al., 2016) and genetic accommodation (West-Eberhard, 2003) remain at nascent stages for corals.

Acclimatization and adaptation tend to be artificially divided in most discussions of coral futures in a rapidly changing climate, but it is essential to examine these processes as an interacting continuum with the potential for genetic accommodation of acclimatory mechanisms (Kelly, 2019; Schlichting and Wund, 2014; West-Eberhard, 2003) and subsequent evolutionary consequences. To be clear, the genomic blueprint sets the stage for the existence of epigenetic machinery, as well as for aspects of the specificity or flexibility of interactions with the microbiome. Thus, rapid response mechanisms are ultimately dependent on some genomic aspect(s) of the holobiont partners and the feedback system between high inheritance and low inheritance mechanisms (Fig. 2).

Interactions of acclimatory mechanisms create additional avenues for plasticity

Although many of the mechanisms and plasticity outcomes discussed here have been described previously (Donelson et al., 2018; Drury, 2020; Eirin-Lopez and Putnam, 2019; Torda et al., 2017; van Oppen and Blackall, 2019), what still remains unclear is the interplay of mechanisms across multiple life stages (Fig. 1) and within the adaptive (epi)genetic continuum (Fig. 2). Here, I present developing areas of research examining interactions of multiple mechanisms and ontogenetic stages discussed above within this continuum.

Epigenetic crosstalk

Although often discussed and measured separately, a complex interaction of epigenetic marks results in gene expression regulation. From higher order chromatin structural arrangement to histone modification, nucleosome interactions, and DNA and RNA methylation, gene expression regulation is a multi-player, coordinated act (Cavalli and Heard, 2019). We are only at the early stages of such analysis of epigenetic interplay in cnidarians. For example, in the sea anemone *Exaiptasia pallida*, histone 3 lysine 36 trimethylation (H3K36me3) marks methylated genes. This evidence supports the hypothesis that gene expression regulation is driven by expression patterns that are activated by the environment. Gene expression in turn recruits proteins for histone modifications that have a binding domain for maintenance DNA methyltransferase (Dnmt3b), thereby inducing DNA methylation of the region. The outcome is reduced spurious transcription from within the gene body (Li et al., 2018a). Not only do epigenetic mechanisms interact to generate emergent properties of gene expression regulation, but there is also significant influence of metabolism and its resulting metabolites and epigenetic modifiers, which act as readers, writers and erasers (Li et al., 2018b), providing opportunities for metabolic regulation and deregulation of epigenetic capacity.

Parental–energetic–epigenetic crosstalk

Parental provisioning and vertical transmission of symbionts and mitochondria energetically prepare offspring for environmental assaults, with potential metabolic–epigenetic implications (Li et al., 2018b) at the earliest developmental stages and through recruitment (Fig. 3). For example, the presence of a greater amount of sugars for cellular metabolism, as well as higher functioning mitochondria, generates the capacity for a greater metabolite pool. In an epigenetic context, this is critical as multiple metabolites generated through cellular respiration act as cofactors for epigenetic modifying enzymes (described and reviewed in Etchegaray and Mostoslavsky, 2016; Li et al., 2018b; Wong et al., 2017). For example, metabolites such as S-adenosyl methionine, alpha-ketoglutarate and nicotinamide adenine dinucleotide act as regulatory metabolites or key cofactors for the activity of epigenetic modifier enzymes including DNA methyltransferases (DNMTs) and ten-eleven translocation proteins (TETs). Together, these enzymes write (DNMT3a), maintain (DNMT1) and remove (TET) DNA methylation in the genome, thus identifying a direct link between metabolism and epigenetics (Fig. 3). Furthermore, the enhanced ATP production owing to symbiotically or mitochondrially enhanced metabolism generates a greater capacity for transcription and translation of these essential epigenetic readers, writer and modifiers, and other stress response capacity. Therefore, this metabolic linkage from parentally provisioned microbiome to offspring energetics and epigenetics (Fig. 3) creates the potential for differing acclimatory mechanisms for vertical versus horizontal symbiont transmission in corals. For example, the vertical transmission mode is hypothesized to amplify acclimatory capacity through this cascade and feedbacks of enhanced energy availability and epigenetic modifying enzymes (Fig. 3).

Microbiome–metabolite–epigenetic interactions

The nutritional role of the microbiome in holobiont performance provides a plethora of metabolites that can act as environmental signals to trigger epigenetic regulation of host expression. A well-studied example of this is the influence of metabolites produced by the human gut microbiome on the epigenetic state of the intestinal cells (Bhat and Kapila, 2017) to facilitate digestion and immune function. In the case of corals, a suite of metabolites are produced during photosynthesis and cellular respiration (Chiacchiera et al., 2013) that provide both energy and cofactors for epigenetic processes (see also 'Parental–energetic–epigenetic crosstalk') (Etchegaray and Mostoslavsky, 2016), as well as change the levels of pH and oxygen. Such metabolite changes have been linked to differential DNA methylation and holobiont growth (Putnam et al., 2016). Shifting and shuffling of microbiome communities in response to environmental change therefore have the capacity for interactive effects on the acclimatory process both directly through the microbiome function (e.g. carbon and nitrogen cycling), as well as through driving changes in metabolite production that influence the internal physiochemical environment and can trigger changes in host epigenetic regulation of gene expression. The interaction of the metaorganism partners with epigenetic variation is thus an area ripe for further exploration (Nyholm et al., 2020). While not studied yet in coral-associated bacteria, there is also the potential for physicochemical microenvironments such as those that exist in coral tissues (Putnam et al., 2017) to induce epigenetic changes in bacteria (Veening et al., 2008).

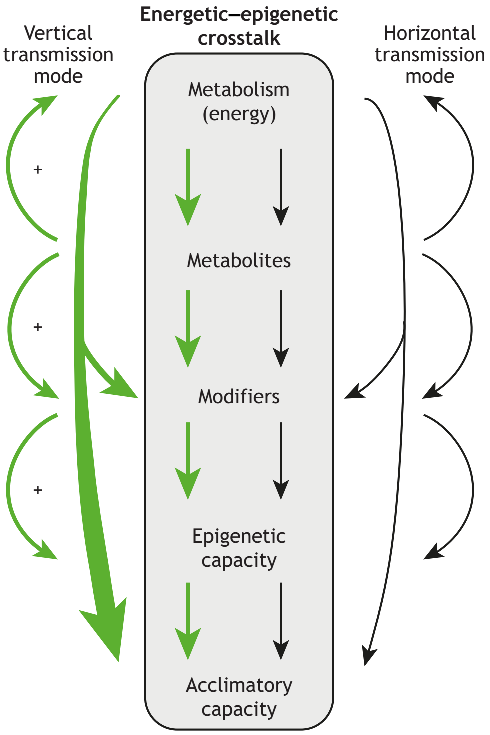

Fig. 3. Energetic–epigenetic crosstalk in horizontal and vertical transmission modes creates cascading effects on acclimatory capacity. Coral metabolism generates energy and metabolites essential for function. These metabolites play key roles in modifying enzymes [e.g. DNA methyltransferases (DNMTs) and ten-eleven translocation proteins (TETs)] and thus facilitate epigenetic capacity, as well as providing a positive feedback to metabolism. The ATP generated also enhances modifier enzyme and other protein production, and therefore enhances acclimatory capacity. In corals that vertically transmit their symbionts and/or high functioning mitochondria (left side, green lines), energetic–epigenetic crosstalk has the potential to be immediately present and generate a positive amplification (growing green arrow and+signs indicating enhancement). In contrast, in horizontal transmitters (right side), this energetic–epigenetic crosstalk would be less and the benefits delayed (smaller black lines) until symbiotic uptake and integration is completed.

Challenges in assessing non-genetic inheritance

The surge of epigenetic studies in corals has pushed the field toward the 'holy grail' of acclimatory epigenetic mechanisms under climate change – epigenetic inheritance (Eirin-Lopez and Putnam, 2019). In the case of epigenetic inheritance, epigenetic mechanisms transition from being context dependent to germline dependent, and are retained through meiosis and development to generate the acclimatized offspring phenotype due to adult conditioning. Epigenetic inheritance has support across a variety of taxa in different forms (Skvortsova et al., 2018). For example, in marine taxa, Rondon et al. (2017) found a set of genes with DNA methylation patterns in the offspring owing to parental exposure to the pollutant diuron (Rondon et al., 2017). In corals, while there is phenotypic evidence for cross-generational effects in multiple taxa (Bellworthy et al., 2019a,b; Putnam and Gates, 2015; Putnam et al., 2020), only a single study supporting epigenetic inheritance has been published (Liew et al., 2020).

Cross-generational effects (Byrne et al., 2020) may vary across taxa due to exposure history, timing of exposure (see below) or the genetic machinery necessary for epigenetic inheritance. Thus the question remains: are we looking for epigenetic inheritance at the right times and in the right places? By this, I mean that if our assumption is that epigenetic inheritance acts through a single mechanism when multiple mechanisms are actually involved, we will not necessarily be focused on the right response variables, or sampling them at their time of action. This topic is addressed in a recent piece by Adrian-Kalchhauser et al. (2020), where they propose that epigenetic inheritance may not be fixed with respect to mechanisms or gene location. Instead, a phenotype may persist, but specific marks would wax and wane, as additional mechanisms are triggered and take over the role of regulating expression. These authors propose considering epigenetic inheritance not in such discrete terms, but in an ‘inherited gene regulation’ capacity, first described as ‘inheritance of the gene interpretation machinery’ by Day and Bonduriansky (2011). Such thinking provides a wealth of hypotheses that require detailed molecular time series and data on the environmental signals over which experience is integrated.

In sexual reproduction, it is clear that the integration of maternal and paternal genetics provides the genetic blueprint for diploid organism development. What is less clear is the complicated nature of inheritance of epigenetic mechanisms and how they may be transmitted through either male or female gametes, or their combination, analogous to their genetic joining. Differences in the timing of oogenesis and spermatogenesis (Soto and Weil, 2016; Szmant, 1991) could therefore create potential for (i) differential maternal and paternal contributions to non-genetic inheritance (Fig. 4) and/or (ii) incompatible epigenetic differences (Fig. 5). In an example of the former case, oogenesis in *Montipora capitata* is ∼10–11 months, whereas spermatogenesis is occurring

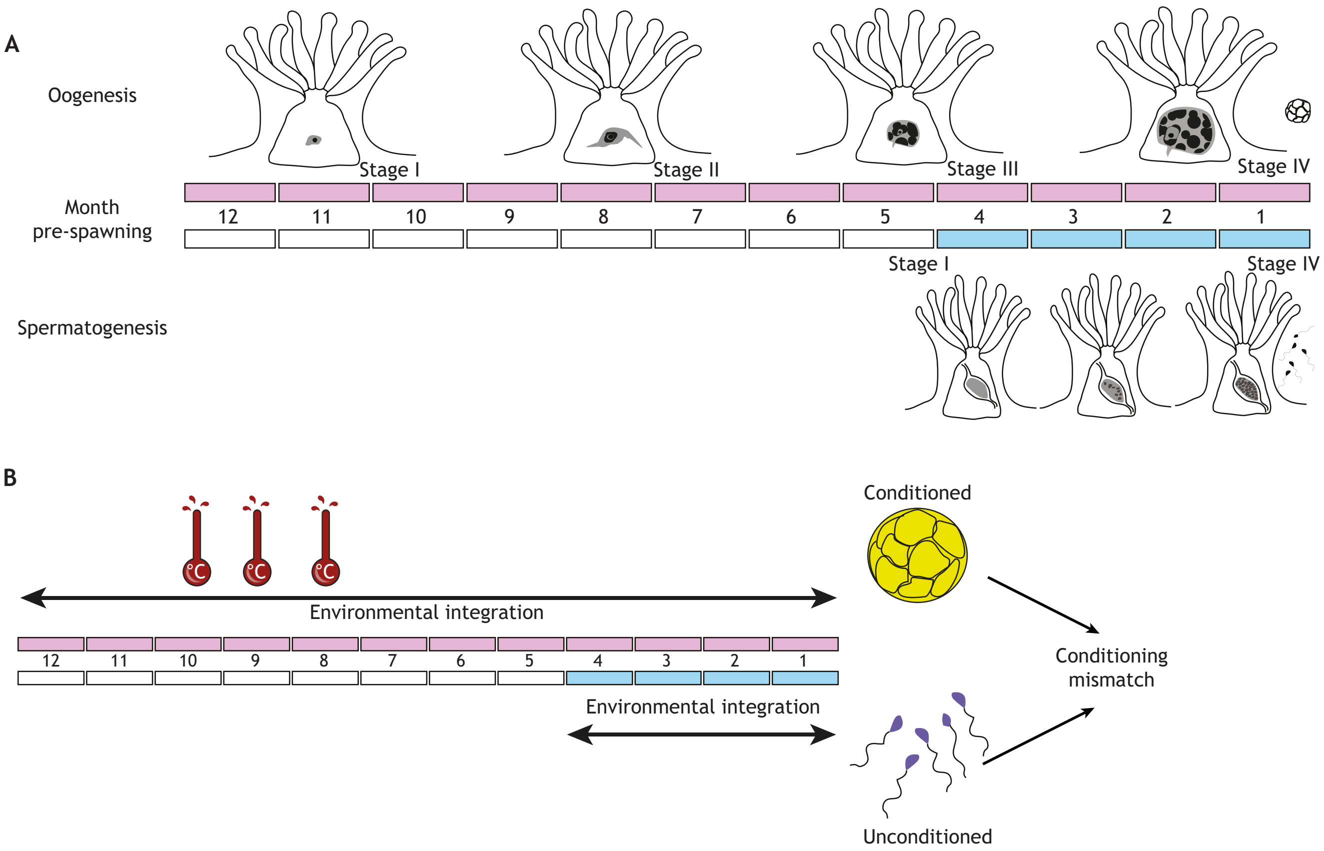

Fig. 4. Potential consequences of differential environmental integration by gametes. The processes of parental effects and epigenetic inheritance will be influenced by (A) differential environmental integration times of oogenesis (9–12 months) and spermatogenesis (1–4 months). Oogenesis occurs through formation by growth of interstitial cells in the mesenteries of the polyps’ gastrovascular cavities (Stage I), followed by the increase of cytoplasm (Stage II) and vitellogenesis (Stage III), and subsequent formation of the cortical layer and vitelline membrane (Stage IV) (reviewed in Randall et al., 2020). In a much shorter time period, spermatogenesis initiates from spermatogonia clustering in the mesenteries (Stage I) and then undergoing meiosis to form spermatocytes (Stage II). The density of spermatocytes and spermatids increases through further meiotic division (Stage III) and develop flagella and become arrayed in bouquet patterns (Stage IV). Eggs and sperm are then packaged into bundles in the hours prior to bundle release (Padilla-Gamiño et al., 2011). These stages are shown as depictions of histological sections placed within the polyps. (B) Integration over a heatwave in eggs but not in sperm may cause a conditioning mismatch between eggs and sperm depending on the running window of environmental 'memory' or integration.

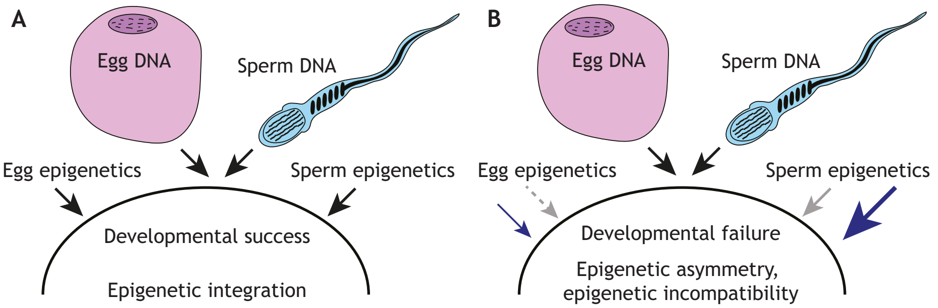

Fig. 5. Epigenetic asymmetry or incompatibility. Intragenerational gene regulation patterns are generated by (A) the interplay of genetic and epigenetic features (black arrows) provided to the embryo in order to successfully complete development. (B) Differences in the extent or location of epigenetic marks (blue arrows), or gamete-specific presence (gray solid arrow) or absence (gray dashed arrow) of epigenetic marks may lead to epigenetic asymmetry and/or epigenetic incompatibility between eggs and sperm, acting as post-fertilization barriers to developmental success.

∼1–5 months prior to summer spawning in June–August (Padilla-Gamiño et al., 2014). Here, it is possible that bleaching (typically peaks in October) falls within the window of gametogenesis, while spermatogenesis would occur following recovery of pigmentation and cell densities in January–February of the following year (Cunning et al., 2016), resulting in differences in exposure history between gametes. In the dominant Caribbean coral *Orbicella faveolata*, where spawning occurs in August to September, oogenesis can begin as early as December of the prior year, while spermatogenesis ramps up in May–June of the spawning year (Szmant, 1991). In this case, later oocyte stages would be affected by thermal stress that tends to appear nearer to coral spawning (∼August–September) and spermatogenesis is more likely to be impacted as well. It is therefore essential to consider the potentially differing intersections of ontogeny (Fig. 1) and thermal stress owing to species-specific reproductive patterns and timing of oogenesis versus spermatogenesis (Fig. 4). Furthermore, research into the potential for and extent of epigenetic inheritance should take into account the timing of experimental exposures relative to germline differentiation (Byrne et al., 2020) and the gametogenic cycle (e.g. Karelitz et al., 2019), which could result in gamete conditioning mismatch (Fig. 4B). Together, these factors may contribute to the contrasting patterns in cross-generational and multi-generational plasticity documented across taxa and locations (Byrne et al., 2020).

It is possible for mechanisms of rapid acclimatization to promote each other, or be at odds with each other. This may be the case with epigenetic differences generated by differences in the integration time of the environment between eggs and sperm (e.g. Fig. 4B). These contrasting epigenetic states could have implications for the critical areas of gamete recognition and fertilization, and the zygotic gene activation and maternal to zygotic transition, and therefore developmental success (Figs 4 and 5). In particular, the packaging of DNA in chromatin in eggs and in protamines or protamine-like structures in sperm (Eirín-López and Ausió, 2009) may generate differing contexts for environmentally induced epigenetic status in sperm and in eggs. Furthermore, differences in epigenetic mechanisms owing to environmental history or parental imprinting can have compatibility consequences (Blevins et al., 2017; Ishikawa and Kinoshita, 2009).

In terms of human interventions in biology, assisted reproduction in humans can result in epigenetic or regulatory incompatibility, with pathological consequences for the embryo (Huntriss and Picton, 2008). For example, intracytoplasmic sperm injection in mammals can result in epigenetic asymmetry, or the potential for epigenetic incompatibility of gametes (Oikawa et al., 2020; Teperek et al., 2016). Epigenetic imprinting serves as a clear illustration of functional non-equivalence between eggs and sperm (Ferguson-Smith, 2011). Epigenetic incompatibility has been implicated in blocking species hybridization (Ishikawa and Kinoshita, 2009). Although this potential for gamete epigenetic or regulatory incompatibility (Fig. 5) has not been examined in laboratory breeding of corals, there are clear cases of paired crosses outperforming others in breeding studies (Willis et al., 1997). Epigenetic compatibility systems could be further assessed in corals with the examination of a suite of epigenetic mechanisms in the context of a quantitative genetics breeding experiment.

While the field is hot on the trail of parental effects and epigenetic inheritance, a broader, more inclusive approach to understanding under what conditions are the various processes of the adaptive (epi)genetic continuum more (or less) important is warranted. More broadly, it is essential to understand whether such mechanisms are present across taxa before consideration of non-genetic interventions by reef managers and restoration practitioners.

Concluding remarks

The acclimatory and adaptive landscape for reef-building corals is dynamic, and multifaceted. The complex life cycles of corals and other marine organisms (Marshall and Morgan, 2011) and exposure to rapidly changing environments generate the potential for antagonism and synergy. As such, contrasting acclimatory outcomes may be generated for marine taxa (e.g. Byrne et al., 2020) owing to the type, timing, magnitude of stressors and the life stage(s) across which the exposure is integrated. Phenotypes will not always be adaptive, but can range on the spectrum from beneficial to maladaptive. The push and pull of phenotypic plasticity and selection may at various times and under various disturbances either enhance or restrict evolutionary responses (Fox et al., 2019; Ghalambor et al., 2015; Kronholm and Collins, 2016).

Many studies to date assume that the stability of a single epigenetic mechanism will underlie epigenetic inheritance. However, there is growing evidence for interplay between epigenetic mechanisms in model systems that needs to be assessed in non-model marine organisms (Eirin-Lopez and Putnam, 2019). Notably, we need to check our assumptions about the stability and inheritance of specific epigenetic marks, and how epigenetic imprinting of eggs and sperm may set the stage for compatibility. A broader perspective will be to consider the potential that epigenetic inheritance may look like inherited gene regulation (Adrian-Kalchhauser et al., 2020) and not the temporal persistence of any one, or a set of, specific marks.

Now, more than ever, it is critical to engage in collaborative cross-scale and multi-omics approaches to push our knowledge of coral holobiont biology forward (Cleves et al., 2020; Cziesielski et al., 2019; Gaitán-Espitia and Hobday, 2021; Nyholm et al., 2020; Williams et al., 2021). Furthermore, this collaborative, multi-scale work will be most effective and efficient through the use of an open scientific exchange framework (e.g. Open Science Framework; Foster and Deardorff, 2017). While maintaining creativity, intellectual freedom and critical thinking about how things are done (and why), we can also share resources, tools and protocol repositories (e.g. github, protocols.io, online lab notebooks, coraltraits.org, reefgenomics.org) to reduce loss of time and resources in duplicative work. The future of coral reefs and their essential goods and services are at risk. Now is the time to tackle complex data integration, to examine the interplay between genetic and non-genetic mechanisms, and to do so in a collaborative and open framework to move coral biology forward for the good of all.

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Competing interests

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