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ADAPTATION AND EVOLUTIONARY RESPONSES TO HIGH CO_2

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The evolutionary history of fishes spans geological periods where atmospheric CO_2 was much higher than the current-day, yet some extant species are now sensitive to high environmental CO_2. Other species have adapted to live in habitats where they naturally encounter very high CO_2 levels. This chapter explores the evolutionary history of fishes in relation to environmental CO_2 and adaptations to high CO_2 habitats. It then considers the potential for adaptive responses to predicted future CO_2 levels from climate change among extant fishes. Despite a rich theory and well-developed experimental methods in quantitative genetics only a handful of studies have tested for genetic

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variation in CO_2-sensitive traits, which might enable fish to adapt to projected future CO_2 levels. This is a serious knowledge gap that needs a concerted research effort to overcome. Without basic information on genetic variation in fitness-associated traits and the strength of selection, it is not possible to make informed decisions about the impacts of elevated CO_2 on fish populations over the timeframes that CO_2 is changing.

1. INTRODUCTION

Modern fishes began their evolutionary history during a geological period when atmospheric and aquatic CO_2 concentrations were much higher than today (Fig. 1, Clack, 2007; Rummer and Munday, 2017). This evolutionary history has likely helped to shape many of the physiological processes that define modern fishes, especially as they relate to respiration, acid-base regulation, and calcification (Randall et al., 2014). Nevertheless, some extant fishes are sensitive to relatively small increases in environmental CO_2, to levels that are still much lower than their ancestors would have experienced during their evolutionary history. Indeed, experiments over the past decade have revealed that some fish are sensitive to CO_2 levels predicted to occur in the ocean over the next few hundred years due to ongoing anthropogenic CO_2 emissions into the atmosphere (Cattano et al., 2018). These experiments show that CO_2 levels between 1000 and 2000 μatm can affect growth, development, swimming performance, survivorship, reproduction, and a broad range of ecologically

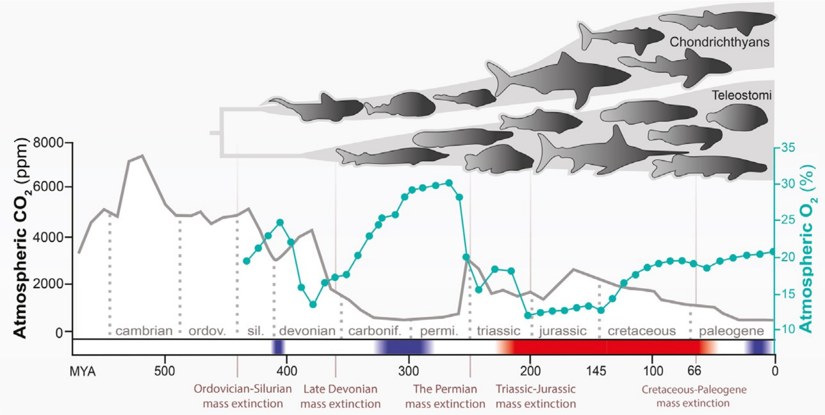

Fig. 1. Geological timeline documenting the evolutionary history of the chondrichthyans and Teleostomi with corresponding atmospheric CO_2 concentrations in parts per million (ppm, left y-axis), atmospheric O_2 percentage (right y-axis) and global warming and cooling periods noted by red and blue shaded bar (Clack, 2007; Erwin et al., 2011; Kardong, 2012; Royer et al., 2004).

relevant behaviors of some marine and freshwater fishes (Cattano et al., 2018; Heuer and Grosell, 2014; Nagelkerken and Munday, 2016; Chapter 9, Vol 37: Munday et al., 2019a). Two important conclusions can be reached from these observations. First, it is clear that many extant fishes are adapted to the low CO_2 levels that have dominated Earth's recent geological history (Masson-Delmotte et al., 2013; Rummer and Munday, 2017). While extant species may have experienced high CO_2 levels in their deep evolutionary history, this does not necessarily mean that they will tolerate high CO_2 levels in the future. Second, to reliably predict how fish populations will respond to higher aquatic CO_2 levels over the next 100–200 years due to accumulating anthropogenic CO_2 emissions, we must consider their potential to adapt to higher CO_2 levels over this timeframe (Munday et al., 2013b; Reusch, 2014; Sunday et al., 2014).

Atmospheric CO_2 concentrations have risen from approximately 280 ppm before the Industrial Revolution to over 400 ppm in the current day (www.esrl.noaa.gov/gmd/ccgg/trends/global). While most of the ocean surface waters and large freshwater basins are in approximate gas equilibrium with the atmosphere (Doney et al., 2009), some habitats can have much higher PCO_2 (CO_2 partial pressure) due to a variety of physical and biological processes that concentrate CO_2 inputs (Fig. 2; Chapter 1, Vol 37: McNeil and Matsumoto, 2019). For example, coastal upwelling can bring CO_2-rich water from the oxygen minimum zone to the surface in nearshore habitats (Feely et al., 2008). Furthermore, biological activity in shallow water habitats can enhance aquatic CO_2 content, especially when water flow is limited or constrained (Baumann and Smith, 2018). As an extreme example, small creeks and seasonal ponds that are connected to rivers can attain very high CO_2 tensions (>10,000 μatm) when water flows are restricted and/or CO_2 flux with the atmosphere is constrained by surface growing plants (Borges et al., 2015; Ultsch, 1996). Biological activity, and thus CO_2 production, can be further enhanced in freshwater and coastal habitats by the input of terrigenous nutrients. Despite periods of high CO_2, these aquatic habitats can have diverse fish communities (Junk et al., 2007), demonstrating the capacity of fishes to adapt to habitats that naturally encounter periods of high CO_2. In the most extreme cases, this has involved unique physiological and behavioral adaptations to deal with extended periods of hypoxia and hypercapnia. In contemporary times, the global expansion of aquaculture production has created another environment where fishes are often exposed to very high PCO_2, due to the concentration of metabolic CO_2 in high-density culture (Chapter 8, Vol 37: Skov, 2019). Cultured fishes are also subjected to artificial selection and/or selective breeding of genotypes favoring high performance in aquaculture conditions, potentially also promoting high CO_2 tolerance, but at the expense of physiological and behavioral traits that may be needed to survive in the wild.

Fig. 2. A representative land-sea interface showing a variety of habitats that may experience high PCO_2 due to concentration of CO_2 inputs by biological and physical processes. Drawn by Erin Walsh.

There are two principal ways that animals can adjust to environmental change; they can acclimate through phenotypic plasticity or they can genetically adapt (evolution). Phenotypic plasticity is the capacity of a single genotype to produce different phenotypes depending on the environmental conditions experienced. Therefore, an individual may acclimate to a changing environment by expressing a phenotype that has higher performance under those particular conditions. By contrast, genetic adaptation involves selection of genotypes that have higher fitness under the new environmental conditions, leading to a change in the frequency of alleles in the population and a shift in the mean phenotype of the population toward the fitness peak (Hendry et al., 2011). Importantly, phenotypic plasticity can act relatively rapidly, within an individual's life time; whereas genetic adaptation may take many generations, depending on the strength of selection and the amount of genetic variation in the population for the relevant traits (Chevin et al., 2010; Crozier and Hutchings, 2014; Hoffmann and Sgro, 2011). Phenotypic plasticity and genetic adaptation may also influence each other. For example, within-generation phenotypic plasticity could slow the pace of among-generation genetic change by shifting the mean phenotype closer to the fitness peak and thus reducing the strength of selection (Diamond and Martin, 2016). Furthermore, plasticity exhibited within a generation may be influenced by the environmental conditions experienced in previous generations (parental and transgenerational effects), meaning that plasticity can also be a multigenerational process (Bonduriansky et al., 2012) and can interact with genetic adaptation (Klironomos et al., 2013).

Predicting the adaptive potential of fish populations to future higher CO_2 levels is further complicated by the presence of additional environmental changes, such as global warming. There may be fitness trade-offs and/or genetic correlations between traits under elevated CO_2 and high temperature (or any other environmental stressor) that could either enhance or retard the pace of adaptation (Munday et al., 2013b; Sunday et al., 2014). At the same time, over-harvesting may reduce the genetic diversity of some fish populations and thus reduce their potential to respond to selection. Consequently, predicting whether fish will adapt to the combined effects of elevated CO_2 and other stressors is not an easy task.

In this chapter, we first explore the evolutionary history of modern fishes in relation to global trends in atmospheric CO_2 with a focus on the adaptive radiation of teleost fishes over the past 50 million years. We also consider extant fishes living in high CO_2 habitats and how they have adapted to these environments. We then examine what is known about the adaptive potential of fishes to rising CO_2 levels associated with global climate change. Laboratory experiments show that individual performance and fitness-related traits of some fishes are impacted by elevated CO_2, but there is also the possibility that phenotypic plasticity and/or genetic adaptation could buffer these impacts over the timescales at which CO_2 levels are rising. Therefore, we consider (i) the evidence for acclimation to elevated CO_2 through phenotypic plasticity and (ii) the evidence for genetic variation in phenotypic responses that could provide the raw material for fish populations to adapt to elevated CO_2. To date, only a handful of studies have attempted to test the adaptive potential of fish populations to elevated CO_2. We use these as case studies to describe our current understanding of this important topic and to identify major knowledge gaps for future research. Finally, we consider whether there is evidence for artificial selection and adaptation to high CO_2 in aquaculture, which could be informative for predicting the potential for fish populations to adapt to rising CO_2 in the wild.

2. EVOLUTIONARY CO_2 HISTORY OF TELEOSTS

The geological timescale over which the fishes evolved commenced over 400 million years ago (Ma: Megaannum or million years ago) during the Silurian Period and the Devonian "Age of the Fishes" (Fig. 1). The earliest fossils of the cartilaginous fishes date back 430 Ma (Märss and Gagnier, 2006), and the start of the Devonian (419 Ma) marked when jawed fishes divided into three discrete groups including the placoderms (now extinct), early cartilaginous fishes, and bony fishes. This geological time period spanning several hundred million years included four of the Earth's five major mass extinction events: the Late Devonian extinction 375–360 Ma, the Permian Mass Extinction or "The Permian Crisis" 252 Ma, the Triassic-Jurassic Extinction 201.3 Ma, and the Cretaceous-Paleogene (K-Pg) Extinction or the "End Cretaceous" 66 Ma. Over this time period, the atmosphere also experienced dramatic changes in oxygen (O_2; declining below 15% at times), global cooling and heating events, and elevated CO_2 levels that, for an extended period of time, exceeded 4000 ppm (Fig. 1). Yet, also during this time, the ray-finned fishes—to which modern teleost fishes belong—diverged from the lobe-finned fishes, and success continued for the following 150 Myr while atmospheric O_2 levels were rising (nearing 30%, compared to today's 21%) and CO_2 levels were falling (from over 4000 ppm to below 500 ppm) (Fig. 1). Then, the Permian Mass Extinction marked a turning point in the evolution of the fishes. The lobe-finned fishes were, for the most part, eliminated from the water (Clack, 2007). Modern lineages moved onto land, leaving ray-finned fishes to expand and exploit the habitats left behind by the lobe-finned fishes (Clack, 2007). Even though the Permian Mass Extinction resulted in a loss of 96% of all marine fish species—of all animals for that matter—this transition signified one of the most profound radiation events among the teleost fishes (Randall et al., 2014). This radiation occurred despite the fact that volcanic activity was causing atmospheric CO_2 levels to rise again while O_2 levels were falling and global temperatures were rising (Fig. 1).

From the start of the cretaceous period 145 Ma, atmospheric O_2 levels rose and CO_2 levels steadily fell. As O_2 levels neared today's 21%, atmospheric CO_2 dropped to around 1000 ppm, and global temperatures were no longer in a warming phase. The K-Pg Extinction event occurred 66 Ma, potentially due to the impact of an asteroid or comet. This mass extinction resulted in a loss of more than 75% of all species on Earth, including the dinosaurs. Despite this, more than 80% of the cartilaginous fishes and more than 90% of teleost fishes survived (Patterson, 1993), even though some fish populations suffered high mortality (Zinsmeister, 1998). After the K-Pg Extinction 66 Ma, atmospheric CO_2 remained below 1000 ppm, falling below 400 ppm by 25 Ma, where it has remained to the current day (Masson-Delmotte et al., 2013). The Early Eocene Climatic Optimum 52–50 Ma was the last time atmospheric CO_2 may have reached 1000 ppm (Masson-Delmotte et al., 2013). Collectively, the dramatically changing atmospheric conditions over more than 400 Myr may have played a profound role in shaping the evolution and diversification of fishes (Fig. 1; Clack, 2007; Ward, 2006).

While the CO_2 content of the atmosphere and the ocean have changed dramatically over the 400 Myr evolutionary history of fishes, the rate of change has not been as fast as the contemporary rise in atmospheric CO_2 concentrations due to anthropogenic CO_2 emissions. On the current emissions trajectory, it is projected that atmospheric CO_2 will exceed 900 ppm by the end of this century (Collins et al., 2013), a level not seen for at least 50 Myr, increasing at a rate at least an order of magnitude faster than at any time in the past 66 Myr (Zeebe et al., 2016).

3. ADAPTATION TO HIGH AND VARIABLE CO_2 HABITATS

Among the approximately 34,000 fish species, ranging from primitive species (e.g., lampreys and hagfishes), cartilaginous fishes (approximately 1000 extant named species in the class Chondrichthyes), and modern and more derived teleost fishes (approximately 26,000 named species in the class Actinopterygii, infraclass Teleostei), there are numerous examples of species living in high/variable CO_2 habitats, perhaps making it possible to ascertain their adaptations to these habitats. Indeed, given the variable atmospheric and aquatic CO_2 conditions that fishes have experienced over their evolutionary history (described above), it is not surprising that some species have (pre) adaptations to compensate for low O_2 and/or high CO_2 conditions in some aquatic habitats that would normally preclude fish life. Changes in environmental O_2, pH, and/or temperature can dramatically affect O_2 uptake, transport, delivery, and CO_2 removal in fishes. There is an intimate interaction between O_2 and CO_2 transport at the gills, and in other tissues, due to their interactions with hemoglobin within the red blood cells (RBCs), which can vary by species (Brauner and Rummer, 2011; Jensen et al., 1993). Generally speaking, most cartilaginous fishes, such as sharks, skates, and rays, can efficiently compensate an acid-base disturbance due to the buffering capacity of their blood and plasma (Berenbrink et al., 2005). Moreover, most sharks, skates, and rays possess relatively pH-insensitive hemoglobins (Berenbrink et al., 2005; Wells et al., 1992), meaning that a pH disturbance associated with an acidosis, such as elevated PCO_2, may not compromise O_2 transport in the way we understand for teleost fishes. Modern teleost fishes have a different physiological response to an acidosis than the cartilaginous fishes. Teleosts possess extremely pH-sensitive hemoglobins (probably evolving nearly 400 Ma in basal Actinopterygians) and low buffering capacity at the blood and plasma. Adrenergically-activated transporters on the RBCs help to regulate pH, and plasma-accessible carbonic anhydrase in select locations enhances O_2 release from the tissues during an acidotic stress, such as elevated PCO_2 (Berenbrink et al., 2005; Randall et al., 2014; Rummer et al., 2013).

These traits result in an enhanced capacity for O_2 transport, especially during conditions that would normally preclude efficient O_2 uptake. Indeed, these physiological traits may have facilitated the radiation of the teleosts throughout the Triassic and Jurassic periods, despite elevated PCO_2, low O_2, and warm temperatures (Fig. 1; Randall et al., 2014).

Ultimately, the adaptations that are in place to maintain O_2 transport and CO_2 removal, even under extreme conditions, may be responsible for the initial and continued (i.e., via modifications in swimming and feeding; Near et al., 2012) success of the fishes (Randall et al., 2014). Many of these adaptations have been investigated in both experimentally and naturally high CO_2 settings, and include over 200 studies to date (Hannan and Rummer, 2018). However, few studies have focused on the mechanisms required for maintaining O_2 transport under an acidosis, such as elevated PCO_2 (Hannan and Rummer, 2018).

Physiological responses to elevated PCO_2 have been investigated under laboratory conditions in an array of taxa, including primitive fishes, both freshwater and marine, and even air-breathing fishes (Chapter 2, Vol 37: Tresguerres et al., 2019; Chapter 3, Vol 37: Brauner et al., 2019; Chapter 8, Vol 37: Skov, 2019). For example, hagfish have been well studied to understand the evolution of O_2 and CO_2 transport and the relationship to acid-base balance and ion/water balance, as the hagfish retains several key ancestral traits associated with the most primitive vertebrates (Baker et al., 2015). In fact, it was the hagfish's superior capacity to tolerate and compensate for acidosis associated with elevated PCO_2 that gave concrete evidence that the gills first evolved to serve acid-base balance and then later for O_2 transport (Baker et al., 2015). While hagfish are known to create high CO_2 microhabitats due to their lifestyle and feeding habits that involve burrowing into sediment and/or rotting animal flesh, other fish species have been investigated due to their more obvious tendencies to inhabit elevated CO_2 environments. Highly productive lagoons and tide-pools as well as freshwater ponds and rivers (e.g., the Amazon) can diurnally and seasonally experience PCO_2 levels that are nearly 80-times what is predicted in the atmosphere by the end of the 21st century from anthropogenic CO_2 emissions (Ultsch, 1996). To tolerate and compensate for these conditions, species like swamp eel (*Synbranchus marmoratus*), armored catfish (*Pterygoplichthys pardalis*), and white sturgeon (*Acipenser transmontanus*) can preferentially regulate intracellular pH without added metabolic costs (Baker and Brauner, 2012; Brauner et al., 2004; Heisler, 1982). This strategy may be what allows such species that regularly encounter very high environmental PCO_2 to survive and thrive in such habitats. Some of the facultative and obligate air breathing fishes (e.g., *Arapaima gigas* and *Lipossarcus pardalis*) that inhabit diurnally and seasonally extreme habitats (e.g., the Amazon) have also been well studied, not only because of the elevated PCO_2 and often low O_2 of their environment, but also because of the division of tasks between the gill and the air breathing organ (e.g., swimbladder) for gas exchange and acid-base balance (Brauner and Val, 1996). These species use the characteristics of their hemoglobin to ensure O_2 uptake is not compromised for the sake of CO_2 removal (Brauner and Val, 1996), which would normally happen in other teleost fishes, because hemoglobin-O_2 binding requires the proton resulting from bicarbonate dehydration to form CO_2 for release via the gill, thus tightly coupling O_2 and CO_2 exchange (Brauner and Rummer, 2011). More derived species may either move to avoid daily or seasonal periods of high environmental PCO_2 or tolerate these episodic events through morphological adjustments (e.g. gill remodeling) and physiological compensation via exchanging bicarbonate from the environment for a counter-ion to correct extracellular pH (Deigweiher et al., 2008; Heuer and Grosell, 2014). But bicarbonate-mediated compensation is neither sustainable over the long term, nor under extreme hypercapnic conditions, as extracellular pH compensation is limited by the amount of bicarbonate that can be exchanged (Brauner and Baker, 2009; Heisler, 1986). Consequently, there are limits to the duration of exposure to extremely high CO_2 that teleosts can both tolerate and function effectively. Diverse teleost communities live around natural CO_2 seeps (e.g. Munday et al., 2014) in locations where PCO_2 is similar to that predicted for the end of the century (i.e., ~1000 μatm). However, fewer species occur near intense vents (P. L. Munday, personal observation) where PCO_2 ranges between 5000 and 10,000 μatm (Fabricius et al., 2011) and many that do enter these areas are mobile feeders on seagrass beds that dominate these extreme CO_2 locations. Therefore, they likely experience very high CO_2 for short periods of time but most species are not permanently exposed to extreme CO_2 levels.

Beyond the mechanisms that more derived teleost fishes may use to compensate a pH disturbance under elevated CO_2 conditions, a mechanism by which O_2 delivery is maintained, if not enhanced, under such scenarios has been described, including in what would be considered a CO_2 sensitive species (i.e., rainbow trout; Alderman et al., 2016; Rummer and Brauner, 2011; Rummer et al., 2013). With pH sensitive hemoglobins, a reduction in pH not only reduces the affinity of hemoglobin for O_2 but also the carrying capacity (combined Bohr-Root effects). Under elevated CO_2 conditions, the ensuing acidosis often initiates an adrenergic response whereby catecholamines (e.g., adrenaline, noradrenaline) are released into circulation, and among other functions, also serve to activate ion exchangers (e.g., sodium/proton Na^+/H^+ exchange; βNHE) on the RBCs to protect intracellular pH and therefore O_2 transport (Rummer et al., 2013). Maintaining RBC pH increases hemoglobin-O_2 affinity and therefore safeguards O_2 uptake at the gill, despite an acidosis. However, at select locations (e.g., red muscle and heart), plasma-accessible carbonic anhydrase short-circuits this protective mechanism. The RBC is, therefore, reacidified, hemoglobin-O_2 affinity decreases, and O_2 is released to the tissue at those select locations (Rummer et al., 2013). In the species that have been investigated (i.e., salmonids) this mechanism may also be operating under a mild acidosis, not necessarily requiring catecholamine release to trigger the NHE. Moreover, this may be the mechanism by which some teleosts can maintain or even enhance aerobic metabolic scope under mildly elevated CO_2 conditions (Hannan and Rummer, 2018). However, this does not apply to cartilaginous fishes. As mentioned above, they have a relatively pH-insensitive hemoglobin and no adrenergically stimulated Na^+/H^+ transporters on their RBCs, precluding this mechanism from benefitting O_2 delivery. Despite the ability of most fishes to maintain O_2 delivery under elevated PCO_2 (reviewed in Hannan and Rummer, 2018; Lefevre, 2016; Chapter 6, Vol 37: Lefevre, 2019), effects on growth, survival and swimming performance have been observed in a range of species, especially in early life stages (Cattano et al., 2018; Heuer and Grosell, 2014; Chapter 9, Vol 37: Munday et al., 2019a), indicating that processes other than O_2 delivery become limiting at higher CO_2 levels. Regardless of the exact mechanism, understanding the link between the physiological performance of a diverse range of extant fishes in elevated CO_2 and their evolutionary history may help in predicting which species will respond to higher CO_2 conditions in the future.

4. PHENOTYPIC PLASTICITY AND GENETIC ADAPTATION TO FUTURE CO_2 LEVELS

Experiments have revealed that some fish species are evidently sensitive to predicted CO_2 levels over the next few hundred years (Cattano et al., 2018). These empirical assessments of CO_2 sensitivity are aptly viewed as an important first step, because they can distinguish CO_2-tolerant from potentially vulnerable species, affected from unaffected traits, and identify the most sensitive ontogenetic stages (Baumann, 2019). But a species' vulnerability to predicted future CO_2 levels is not just determined by its contemporary CO_2 sensitivity. Apart from indirect effects (i.e., altered food web or species interactions), the most important question is whether phenotypic plasticity and/or evolution can buffer the direct effects of elevated CO_2 over the timescale at which the environment is changing (Munday et al., 2013b; Reusch, 2014; Sunday et al., 2014). Therefore, the overall vulnerability to future elevated CO_2 levels might be thought of as the sensitivity to elevated CO_2 identified in experiments, less the adaptive potential from phenotypic plasticity and genetic adaptation.

$$\text{CO}_2\text{ vulnerability} = \text{CO}_2\text{ sensitivity} - (\text{phenotypic plasticity} + \text{genetic adaptation}) + \text{indirect effects}$$

4.1. Within and Between Generation Plasticity to High CO_2

While exposure to elevated CO_2 may have negative effects in the short-term, individuals may be able to adjust to these conditions over the longer term as a result of plasticity in physiological processes that underpin growth, survival, reproduction, and behavior. In general, there is limited evidence for within-generation acclimation of fish to elevated CO_2. Instead, most experimental studies that conduct sampling at varying time points tend to find that the species or trait of interest is either affected or unaffected by elevated CO_2 and remains that way through time (e.g. Davis et al., 2018; Munday et al., 2013a; Sundin et al., 2017). In other words, most studies report either tolerance or sensitivity to elevated CO_2 (Hamilton et al., 2017; Schmidt et al., 2017), not an initial high sensitivity that is then buffered by phenotypic plasticity. In one of the few clear exceptions, Lopes et al. (2016) found that exposure to elevated CO_2 for 7 days affected group cohesion in larval sand smelt (*Atherina presbyter*), but it was no longer affected after 21 days of exposure. One reason for the paucity of studies showing within-generation plasticity to elevated CO_2 is that few studies have compared the same traits over short vs long exposure durations. It is possible that more examples of within-generation plasticity and acclimation to elevated CO_2 will emerge if greater attention is given to repeat sampling of CO_2-sensitive traits over relevant timeframes. Indeed, in the only study of its type to date, Schunter et al. (2018) found 184 genes were differentially expressed in spiny damselfish that had been exposed to elevated CO_2 for 4 days vs 5 month before sampling. The differentially expressed genes in the fish exposed to elevated CO_2 for 4 days were significantly enriched in ATPase-related processes, indicating an initial physiological cost to high CO_2 exposure, which does not persist over the longer term.

In contrast to the limited evidence for within-generation plasticity and acclimation to elevated CO_2, there is ample evidence that exposure to elevated CO_2 in one generation can affect the performance of future generations. Miller et al. (2012) were the first to show that parental effects can improve the performance of fish early life stages under elevated CO_2. Juvenile cinnamon anemonefish (*Amphiprion melanopus*) had a higher metabolic rate, slower growth rate, and higher mortality when reared in elevated CO_2 compared to controls. However, these negative effects of elevated CO_2 were completely ameliorated in offspring whose parents had been exposed to elevated CO_2 for several months prior to the start of the breeding season. This result was recently repeated by Jarrold and Munday (2019), who showed that beneficial parental effects on offspring growth and survival were of similar magnitude to the beneficial effects arising from diel cycles in the CO_2 treatment (Chapter 9, Vol 37: Munday et al., 2019a). More efficient acid-base regulatory processes and/or mitochondrial function when both parents and offspring experienced the same high CO_2 conditions could potentially explain the restoration of juvenile resting metabolic rate to control levels and the corresponding improvement in growth and survival of juveniles from high CO_2 parents (Miller et al., 2012). Murray et al. (2014) found similar beneficial parental effects in a wild population of Atlantic silversides (*Menidia menidia*). Offspring produced from wild spawners repeatedly throughout the spawning season became progressively more tolerant to elevated CO_2, which coincided with the natural pH decline (CO_2 increase) in the adult's habitat during the spawning season. Here again, matching environmental conditions experienced by parents and offspring appeared to improve performance of the offspring in high CO_2.

Baumann et al. (2018) took the Atlantic silverside story a step further. By combining results of experiments conducted at various times throughout the season they showed that juvenile tolerance to high CO_2 first climbs in conjunction with rising CO_2 in the parental spawning habitat, but then declines again late in the season, most likely due to reduced maternal egg provisioning and thus reduced egg quality late in the season. This additional knowledge is important, because it illustrates that parental effects are not a "magic bullet" and can interact with energetic constraints and other environmental factors. Indeed, in an experimental demonstration of this issue, Stiasny et al. (2018) showed that the presence of beneficial parental effects may depend on the energy supply available to the offspring. Reduced survival of larval Atlantic cod (*Gadus morhua*) in elevated CO_2 was partly compensated by parental exposure to high CO_2 exposure, but only when ample food was available for the larvae. This interaction with food supply suggests that surplus metabolic resources may be needed to elicit beneficial transgenerational effects. In contrast to these positive parental effects, parental exposure to elevated CO_2 had a negative effect on the survival and growth of juvenile threespine stickleback (*Gasterosteus aculeatus*) (Schade et al., 2014), demonstrating that not all parental effects are beneficial, and that stressful conditions in one generation can have negative carryover effects to future generations. Overall, these studies highlight the importance of considering parental and transgenerational effects when attempting to determine how fish early life stages will respond to rising CO_2 levels.

Only a handful of studies have tested for beneficial parental effects on behavior in elevated CO_2. Welch et al. (2014) found no evidence for parental effects in behavioral responses to elevated CO_2 in juvenile spiny damselfish. Juveniles exhibited impaired responses to alarm cues and altered behavioral lateralization, irrespective of whether their parents had been exposed to high CO_2 or not. Similar results were observed in clownfish, where elevated CO_2 impaired antipredator behavior of juveniles, regardless of the CO_2 treatment of their parents (McMahon et al., 2018). By contrast, Allan et al. (2014) found that parental exposure to elevated CO_2 reduced the negative effects of high CO_2 on the escape performance of juvenile fish, especially the proportion of fish that responded to the threat stimulus, indicating that beneficial parental effects may occur in some traits and in some contexts, but not others.

The parental effects described above could occur through a number of different mechanisms. Parents can influence the phenotype of their offspring by differences in nutritional provisions of eggs (Snyder et al., 2018), the transmission of hormones, proteins and other somatic factors, and potentially by the transfer of epigenetic marks, including DNA methylation and histones (Munday, 2014). As yet, the mechanisms by which parental exposure to elevated CO_2 influences the performance of offspring under high CO_2 have not been identified, although new molecular approaches could help answer this question. For example, Schunter et al. (2018) found that patterns of gene expression altered by within-generation exposure to elevated CO_2 returned to baseline levels following parental exposure to elevated CO_2. This suggests a fundamental resetting of developmental pathways when offspring experience the same high CO_2 condition as their parents. Epigenetic mechanisms could be involved, and this will be a fruitful area for further research.

4.2. Heritability and Selection to High CO_2 in Fishes

It is possible that fishes could adapt to future higher CO_2 levels. To illustrate this point, consider an experiment where exposure to elevated CO_2 reduced the survival of an experimental population by half. This doubling in mortality would be concerning to an ecologist, but an evolutionary biologist would point out that 50% of the population appeared to be CO_2 tolerant and would therefore have a fitness advantage in future environments. Thus we might observe a gradual increase in the frequency of the alleles conferring CO_2 tolerance, registering as an adaptive evolutionary response of the population. In theory, CO_2 resistant genotypes could also arise randomly from new mutations (*de novo*), but this pathway is likely limited to single cell organisms with generation times of days to weeks (Lohbeck et al., 2012; Reusch, 2014). For fish and other metazoans with generations of months to decades, it is the genetic variation that currently exists in natural populations that may or may not allow them to adapt to high CO_2 (Sunday et al., 2014). Generation length and standing genetic diversity are important parameters, but to predict the potential, strength and direction of evolutionary responses to high CO_2 oceans, we still need to know more.

To approach the task, we can start with the *breeders equation* (Falconer and Mackay, 1996).

$$\Delta Z_i = {h^2}_i \times S_i$$

This equation calculates the change in trait i from one generation to the next (ΔZ) as the traits heritability (h^2) multiplied by the strength of selection (selection differential, S). Heritability measures the proportion of phenotypic variation in a trait that is attributed to additive genetic variance; hence, strongly heritable traits can potentially evolve quickly under selection, whereas nonheritable traits will not respond. Fortunately, estimating the heritability part of the breeders equation is relatively straightforward. It has routinely been done using cross-breeding designs, parent-offspring regressions or other approaches as long as they allowed tracking genetic relatedness in experimental populations (Mousseau and Roff, 1987). Unfortunately, published trait heritabilities specific to high CO_2 environments are still rare (Sunday et al., 2014) and remain scarcer still for fish.

One pioneering experiment subjected newly fertilized Atlantic silverside embryos from a large number of wild spawners to high CO_2 ($\sim$2300 μatm) and then quantitatively sampled all perished and surviving individuals for 15 days posthatch (Malvezzi et al., 2015). Afterward, all parents and offspring were genotyped using microsatellite markers, which allowed reconstructing parent–offspring pedigrees and thereby revealed that genetically related individuals were more similar in their survival than unrelated ones. Because the additive genetic variance comprised a fifth of the total phenotypic variance, the heritability of survival at high CO_2 was estimated to be 0.20. This value is remarkable only for being utterly common in complex, polygenic traits like survival, growth or fecundity across taxa and irrespective of the agents of selection (Mousseau and Roff, 1987).

Similar heritabilities of larval mortality and growth under contrasting CO_2 conditions were recently estimated for California grunion (*Leuresthes tenuis*) (Tasoff and Johnson, 2019). Here, the authors used a classic cross-breeding design to produce 31 offspring families with different degrees of relatedness, which were reared for 14 days post hatch under control (650 μatm) vs high (1630 μatm) CO_2 conditions. As in the first experiment, a multivariate animal model (Johnson et al., 2010; Kruuk, 2004; Wilson et al., 2007) allowed partitioning phenotypic variances of larval mortality and growth, thereby estimating heritability and maternal effects in these traits. Again, heritabilities for larval mortality were small but significant (0.12–0.18) and even lower for larval growth (0.09–0.10). As is commonly observed in marine species (Marshall et al., 2008), nongenetic maternal effects explained a considerable proportion (26–36%) of the variability in larval mortality.

Apart from mortality and growth, physiological and behavioral traits could affect fitness, too, and therefore respond to selection. In tropical reef fish, high CO_2 exposure is known to elicit abnormal behavior (e.g., loss of predator avoidance or orientation) in many but not all individuals of an experimental population. The fitness relevance of these effects was demonstrated in a combined laboratory and field study, showing that CO_2 affected damselfish juveniles (*Pomacentrus wardi*) suffered higher predation mortalities when transplanted to the field (44%) than their CO_2 tolerant conspecifics (32%) (Munday et al., 2012). The heritability of predator avoidance behavior (response to chemical alarm cues) was subsequently estimated in a different damselfish model, the spiny chromis (*Acanthochromis polyacanthus*) (Welch and Munday, 2017). Here, the additive genetic component of the phenotypic trait variance was determined via father-offspring regressions, an alternative to unworkable cross-breeding designs in species with parental offspring care. Intriguingly, avoidance behavior had a high heritability ($h^2 = 0.56$–0.65) in both wild and laboratory reared populations only when estimated after acute exposures (4 days) to elevated CO_2 (750 µatm). After prolonged high CO_2 exposure (42 days), however, behavioral responses appeared non-heritable ($h^2 = -0.01$–0.02). This result came about because variation in phenotypic responses to elevated CO_2 that were present after 4 days exposure to elevated CO_2 were absent after 42 days. Thus, it seems that nonadaptive plasticity acted to obscure genetic variance in the trait and thereby reduce its heritability. The reality of continuous high CO_2 exposure in the future may be that reduced phenotypic variation could constrain the evolutionary potential in fitness-relevant traits.

Estimating trait heritabilities under high CO_2 conditions is a required first step toward anticipating evolutionary responses. Appropriate experimental approaches exist (Munday et al., 2013b; Sunday et al., 2014), but have been applied in just a handful of cases. So far, the sparse empirical evidence for fish suggests that fitness relevant survival and growth responses to high CO_2 conditions have a small but significant genetic basis on which selection could act. It is the other half of the breeders equation—estimating selection—where the knowledge gap is widest and available tools are most wanting.

4.3. Selection Differentials

Almost by definition, today's laboratory experiments determine species sensitivities to average CO_2 levels as they may occur decades to centuries from now. Where responses occur, selection differentials could be calculated (Malvezzi et al., 2015; Munday et al., 2012), but these could still be unrealistic because average CO_2 levels are rising in a gradual process spanning dozens of generations. Consider that current models predict a maximum rise in atmospheric CO_2 levels to ~2000 µatm by the year 2300 (Caldeira and Wickett, 2003), i.e., a ΔCO_2 of 1600 µatm in 280 years. For a hypothetical fish species with a generation span of 3 years this amounts to a 17 µatm increase in average CO_2 level from one generation to the next. Yet, individuals within each generation will also be exposed to PCO_2 variation on daily, seasonal and periodic (e.g. upwelling) timescales that will be far greater than the year-by-year increase in average PCO_2. It is possible that the gradual nature of the rise in average CO_2 levels may thus impose very small selection differentials, and in combination with small trait heritabilities, result in little to no evolutionary change for many decades, until the average PCO_2 or the PCO_2 peaks associated with natural variation rise to levels that have a meaningful effect on fish fitness. Moreover, beneficial phenotypic plasticity (as discussed in Section 4.1) will conceivably weaken the impetus for genetic adaptation further. The concern here is that eventually environmental changes will exceed the acclimation threshold, which could trigger unexpected and severe productivity losses in the short term, until adaptation finally catches up over the long term (Bell, 2013).

The generation times of fish and the incremental nature of rising CO_2 levels render real-time experiments largely useless for quantifying realistic selection. Computer models could be an alternative and if appropriately parameterized offer scenarios for how specific combinations of trait heritabilities × selection differentials may play out over dozens to hundreds of fish generations. Some insights may also come from examining intraspecific local adaptations in species distributed across spatial CO_2 gradients (Calosi et al., 2017; Sunday et al., 2011). Such gradients are abundant in nature and exist with depth or between regions that differ in upwelling intensity (Kelly et al., 2013; Vargas et al., 2017), at natural CO_2 seeps (Fabricius et al., 2011) or across the general nearshore–offshore axis of diminishing natural CO_2 variability (Baumann, 2019). The value of these so-called "space-for-time" approaches is a long-standing topic of scientific debate, as these approaches may elucidate whether evolution can occur and what adapted traits look like, while leaving the question how long this adaptive process takes unanswered (Baumann and Conover, 2011). Furthermore, the small spatial extent of some CO_2 gradients, such as CO_2 seeps, means that the very populations under selection are also constantly being swamped with genotypes from the surrounding low CO_2 environment, thus overriding the potential for genetic change (Munday et al., 2013b).

4.4. Genetic Correlations

Estimating the evolutionary potential of a single trait to a single environmental stressor is challenging enough, but realistic predictions for multiple traits and stressors are still more complicated. For one, fish will not adapt to high CO_2 in isolation, but to future high CO_2 environments that will also be warmer, less oxygenated, and likely exhibit altered food webs and habitats (Enochs et al., 2015, Chapter 9, Vol 37: Munday et al., 2019a). For example, some tropical reef fish may be capable of acclimating and adapting to warming (Donelson et al., 2012; Munday et al., 2017), but could still fail to overcome rapid climate degradation of their coral reef habitats (Jones et al., 2004; Pratchett et al., 2008). For multiple stressors acting on a single trait (e.g., survival), exploring underlying genetic correlations will be crucial. Genetic variance among individuals in a population could vary such that CO_2 tolerant genotypes also survive better at higher temperatures (positive genetic correlation), thus leading to an accelerated adaptive response. However, negative genetic correlations are equally plausible, which would dampen or impede adaptation in a multistressor environment (Munday et al., 2013b; Sunday et al., 2014).

Related but separate from genetic correlations are evolutionary trade-offs between multiple traits. Darwinian fitness measures an individual's contribution of progeny to the next generation, and this overall outcome is the product of many fitness-related traits. These traits are likely not free to evolve independently, but involve trade-offs that lead to evolutionary constraints. A textbook analogue from fish life history is the strong negative coupling between annual mortality rate and maturation age, where combinations of (i) late maturation/high mortality or (ii) early maturation/low mortality simply cannot arise due to evolutionary trade-offs in reproduction (Charnov and Berrigan, 1991). A new study by Laubenstein et al. (2019) has demonstrated such a trade-off between fitness-related traits in reef fishes under the combined climate change conditions of elevated CO_2 and warming. In the spiny damselfish there was a negative correlation between physiological performance (aerobic scope) and behavioral performance (appropriate response to a predation-risk cue), but only in fish reared in the combined elevated CO_2 and high temperature treatment. This negative correlation means that individuals with high aerobic scope (a measure of aerobic performance) exhibit the most impaired response to a predation-risk cue, and visa-versa. There is a trade-off because individuals can have high performance in one trait, but not both. If this trade-off has a corresponding genetic correlation, it would be expected to constrain the evolution of one trait or both under future climate change conditions.

5. SELECTION IN AQUACULTURE

Before the term "ocean acidification" was even coined, aquaculturists had already been studying fish sensitivities to high CO_2 for decades (Ishimatsu et al., 2008), recognizing that extreme CO_2 environments ($>$10,000 μatm) are a frequent metabolic byproduct of maintaining fish in high densities in confined enclosures (Ellis et al., 2017, Chapter 8, Vol 37: Skov, 2019). In fact, the apparent CO_2 tolerance of fish juveniles and adults likely contributed to an early—but now outdated—notion that rising CO_2 levels from anthropogenic emissions will not affect fish. It is now recognized that aquaculture conditions provide a unique opportunity to better understand the effects of high CO_2 on fishes (Ellis et al., 2017), and few areas are as ripe for discovery as the physiological and genomic underpinnings of acclimation and adaptation to high CO_2 environments. In farmed species with closed life cycles artificial selection to high CO_2 is likely, thereby presenting opportunities to quantify how selection decreases genetic diversity and how trait and genetic correlations may accelerate or impede adaptive change. For example, a recent study examined quantitative trait loci (QTL) in the genome of wild, farmed, and wild × farmed Atlantic salmon (*Salmo salar*), finding that six QTLs explained 10–15% of the phenotypic variation in length, weight, and condition factor, while a seventh QTL was significantly related to survival (Besnier et al., 2015). Interestingly, within one of the QTL regions of the genome the analyses revealed strong allelic correlations (linked genomic variants) most likely caused by strong artificial selection "sweeping" (removing) large parts of the genetic diversity in farmed animals. For salmon, this is a recognized conservation concern, given the well-documented accidental interbreeding between farmed and wild strains. There is good evidence for increased CO_2 tolerance in farmed populations of Sydney rock oysters compared with their wild counterparts (Parker et al., 2011), but whether there is similar selection for high CO_2 tolerance in farmed fishes is currently unknown.

Domestication and loss of genetic diversity in aquaculture populations also has profound yet often unacknowledged implications for experimental research on the effects of high CO_2 in general. For practical reasons, many experimental research groups obtain specimens (particularly embryos and larvae) from commercial and laboratory brood stocks to conduct sensitivity assessments of these organisms to climate stressors (e.g. Baumann et al., 2012; Bromhead et al., 2015; Chambers et al., 2014; Stiasny et al., 2018). While these studies are valuable, they are likely not accurate representations of the genetic diversity and thus evolutionary potential of species and populations as they currently exist in the wild. The widespread potential of marine fish to precondition offspring to parental environments (i.e., Section 4.1 above) compounds the problem, because brood stocks are not only genetically altered, but also often experience constant temperature, CO_2, light, and feeding conditions that do not resemble conditions in the wild (Baumann, 2019). This additional uncertainty needs to be more clearly communicated and accounted for in an attempt to assess the sensitivity of fish to future CO_2 levels, and their adaptive potential.

6. KNOWLEDGE GAPS AND FUTURE DIRECTIONS

The evolutionary history of fishes spans periods of geological time where atmospheric CO_2 was much higher than today, and some fishes continue to occupy habitats that can experience very high PCO_2 (>10,000 μatm). By contrast, other extant fishes appear to be adapted to the low atmospheric CO_2 conditions (<400 μatm) that have persisted for the last 25 Ma. The physiological processes that make some species sensitive and others tolerant to projected future CO_2 levels (~1000–2000 μatm) are still not well understood. Phylogenetically controlled comparative studies could be especially useful in establishing what processes and mechanisms are responsible for these differences in CO_2 tolerance among fishes and how they are related to the evolutionary history of modern fishes.

The greatest knowledge gap in predicting the effects of future higher CO_2 levels on marine and freshwater fishes is the limited understanding of their adaptive potential to the rapid rise in PCO_2 that will occur over coming decades. An increasing number of studies are testing for adaptive plasticity to higher CO_2 levels in fish populations, both within and between generations. These studies illustrate the importance of considering parental effects, because negative effects of elevated CO_2 observed in offspring may be mitigated when parents experience the same environmental conditions. Nevertheless, parental effects must not be viewed as a "magic bullet", because not all traits exhibit improved performance, and there are also examples of negative carry-over effects from parental exposure to high CO_2. One issue in studying parental and transgenerational effects is that most experimental designs used to date cannot adequately separate apparent transgenerational effects from developmental plasticity (Donelson et al., 2018). More complex experimental designs are needed if future studies are to disentangle true transgenerational effects from developmental plasticity induced by exposure of critical early life stages (e.g. eggs and embryos) to high CO_2 (Donelson et al., 2018). We also have limited understanding of the physiological mechanisms underpinning most examples of parental and transgenerational effects, although modern molecular methods are being used to address this issues (Ryu et al., 2018; Schunter et al., 2018) and could provide unprecedented insight into the mechanisms of within and between generation plasticity.

Despite a rich theory and well-developed experimental methods in quantitative genetics (e.g. Lynch and Walsh, 1998), only a handful of studies have tested for genetic variation in CO_2 sensitive traits, which might enable fish to adapt to projected future CO_2 levels. This is a serious knowledge gap that needs a concerted research effort to overcome. Without basic information on genetic variation in fitness-associated traits and the strength of selection, it is not possible to make informed decisions about the impacts of elevated CO_2 on fish populations over the timeframes that CO_2 is changing. Most fish populations will experience dozens of generations before PCO_2 reaches levels that cause negative populations effects. Moreover, higher CO_2 levels will be accompanied by higher temperatures, and even less is known about genetic correlations of traits in response to different environmental stressors that could either constrain or facilitate the pace of adaptive responses.

Meaningful estimates of some important evolutionary parameters, such as selection gradients to intergenerational increases in PCO_2 will be difficult to measure. Sensitivity analyses will be useful to modeling adaptive responses under a range of selection scenarios. So-called evolutionary rescue models (see Bell, 2013 and associated papers) are likely to be especially powerful in assessing population level responses to high CO_2 and warming because they can explicitly incorporate both the negative demographic effects of these stressors on the population, and the population genetic response to selection, to predict population trajectories under a range of environmental conditions and evolutionary parameters. While this approach has been used in terrestrial ecosystems, to our knowledge, it has not yet been used to model the trajectory of fish populations in response to global climate change.

Finally, it is simply impossible to assess the evolutionary potential in every fish species, or even a tiny percentage of all species. Therefore, to gain traction it will be important to focus on a few species that are amenable to experimental manipulation in an evolutionary context. Species such as the spiny damselfish, clownfish, Atlantic silverside and salmon that have already been a mainstay of plasticity and adaption research, and for which good molecular resources have been developed, are good candidates. The yellowtail kingfish is emerging as a representative for large pelagic fishes (Munday et al., 2019b). Representative species from polar, deep sea and rocky temperate habitats are needed. Model species have proven enormously successful in testing evolutionary questions in terrestrial biology and are likely to be similarly successful in aquatic ecosystems.

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