25 Climate Change and Sharks

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ABSTRACT

Globally, climate change is predicted to have unprecedented effects on ocean life, stemming from increasing trends of ocean warming, acidification, deoxygenation, and the frequency and severity of extreme climatic events (e.g., marine heatwaves, cold snaps, storms) well into the 21st century. These environmental changes are forecasted to impact marine organisms broadly and will likely change the structure of many marine ecosystems. Sharks and their relatives will not be immune to these shifts; yet, research has only just begun to elucidate how these rapid changes interact in this long-evolved, slowly reproducing group of fishes. Studying climate change in a group of often large, typically cryptic animals such as sharks is challenging; indeed, the majority of research to date has focused on 10 small, mostly benthic species that can be carefully exposed to future conditions in a laboratory setting. Nonetheless, findings indicate shifts at the molecular, physiological, and whole-organismal behavioral levels that have implications for larger ecological impacts. Moving forward, the impacts of climate

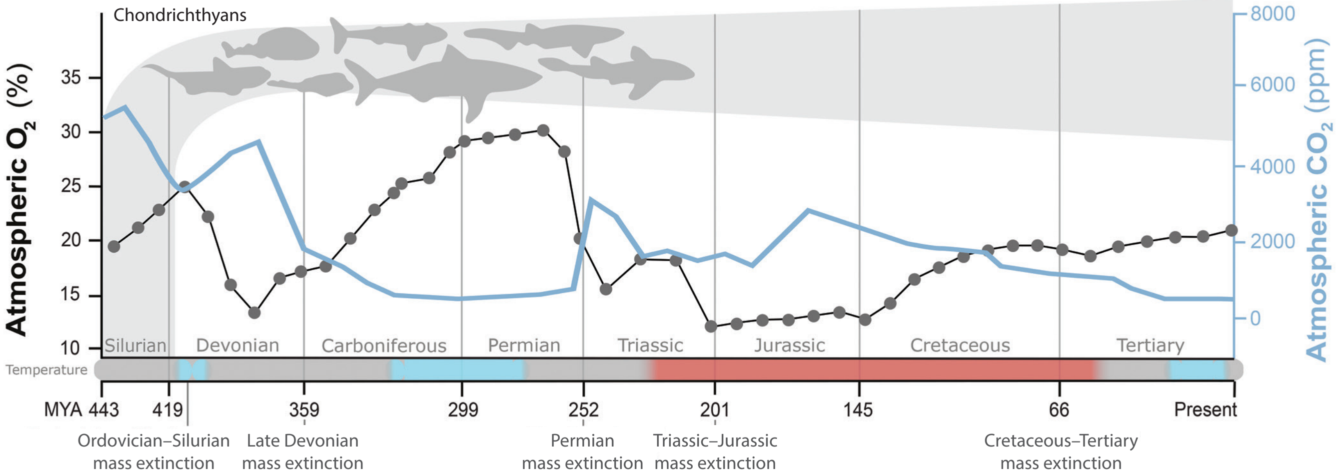

FIGURE 25.1 Geological timeline (MYA, million years ago) documenting the evolutionary history of Chondrichthyes (i.e., sharks, rays, skates, and chimeras) with corresponding atmospheric carbon dioxide (CO_2) concentrations in parts per million (ppm, right *y*-axis, blue); atmospheric oxygen (O_2) percentage (%, left *y*-axis, gray); and global warming and cooling periods noted by red and blue bars (*x*-axis). Also demarcated along the *x*-axis are the five major mass extinctions. (Adapted from Clack 2007, Munday *et al.* 2019, and Rummer and Munday 2017.)

change will be one of the most important areas of research, alongside other current-day issues (e.g., over-exploitation), to ensure effective conservation and management of this extraordinary group of marine megafauna.

25.1 INTRODUCTION

As a whole, climate change is among the greatest modern threats to marine organisms (Hoegh-Guldberg and Bruno 2010; Pörtner and Farrell 2008). Since the Industrial Revolution, anthropogenic gas emissions (i.e., greenhouse gases, including carbon dioxide [CO_2]) have contributed to warming of the Earth's atmosphere (IPCC 2019). The world's oceans act as a tremendous heat sink, resulting in a steady increase in the heat content and, therefore, temperatures of the oceans, aptly referred to as "ocean warming" (Hansen *et al.* 2006). The least optimistic projection, or Representative Concentrations Pathway (RCP), RCP 8.5 (i.e., an unabated greenhouse gas emission scenario), as per the Intergovernmental Panel on Climate Change, predicts increases in sea surface temperatures of 1°C to 5°C by the year 2100, depending on climatic region (IPCC 2019). In addition to absorbing heat, the oceans absorb CO_2, which acidifies water and reduces the saturation state of carbonate minerals (e.g., aragonite, calcite) in a process referred to as "ocean acidification" (Meinshausen *et al.* 2011). Present-day partial pressures of CO_2 (pCO_2) in the open ocean average 400 µatm and are expected to increase to approximately 1000 µatm by the year 2100, according to RCP 8.5 (IPCC 2019). Meanwhile, the increase in heat content of the oceans also reduces the solubility of gases in water, including oxygen (O_2), thereby contributing to a third global climate change phenomenon, referred to as "ocean deoxygenation" (Breitburg *et al.* 2018). Under RCP 8.5, oxygen content is expected to decline by up to approximately 5% (IPCC 2019). These three global climate change phenomena are collectively often referred to as the "deadly trio."

Critical to understanding the effects of these global change phenomena in marine organisms is an understanding of the physiological and behavioral effects of changes in temperature, CO_2, and O_2. Classic studies have investigated these factors on teleost fishes (Claireaux and Lefrançois 2007; Fry 1971; Randall and Brauner 1991), but only recently, during the early part of the 21st century, have these factors been heavily investigated within the context of global climate change (Sampaio *et al.* 2021).

Knowledge regarding the effects of global climate change phenomena on elasmobranch fishes (sharks, skates, and rays; hereinafter, sharks and their relatives) only started appearing in the literature within the first decade or so of the 21st century. Moreover, at the time this chapter was written only shark and skate (i.e., no ray or chimaera) species had been investigated within the context of climate change. Indeed, although the effects of temperature changes and low O_2 on various species of sharks and their relatives had been investigated for decades, the studies had not necessarily examined these factors within the context of climate change. Although the responses of sharks and their relatives to elevated pCO_2 and low pH were investigated in pure physiological studies (e.g., effects of hypercapnia, pH disturbances due to exercise) during the last several decades of the 20th century, evidence of the effects of elevated pCO_2 within the context of ocean acidification conditions was only first published in 2014. It was thought that, because sharks and their relatives evolved during periods of much higher atmospheric CO_2 than current day, they would be resilient to increases in ambient pCO_2, making such studies irrelevant (Figure 25.1) (Chin *et al.* 2010; Rummer and Munday 2017). However, since the second decade of the 21st century, studies have revealed mixed effects of elevated pCO_2 on biochemical, organismal, and behavioral aspects of sharks and skates (Di Santo 2019; Dixson *et al.* 2015; Green and Jutfelt 2014; Heinrich *et al.* 2014, 2015; Pegado *et al.* 2019a,b; Pistevos *et al.* 2015; Rosa *et al.* 2014, 2016a,b, 2017). Indeed, these findings have prompted an entire field of research investigating the effects of current and future climate change conditions, both in isolation and in combination, on sharks and their relatives.

The first study to holistically consider the vulnerability of sharks and their relatives to climate change stressors and global change phenomena was an ecological risk assessment for the Great Barrier Reef (Australia) that concluded that freshwater/estuarine species and coast-restricted species were most at risk but that most of the focal species had low relative vulnerability to climate change (Chin *et al.* 2010). Furthermore, managers and stakeholders in shark sanctuaries (i.e., marine protected areas specifically for sharks that usually span a country's entire jurisdiction) have suggested that, for some countries, ocean warming and acidification remain as "threats of least concern" to sharks and their relatives when compared to fishing-related threats such as targeted fishing, bycatch, or ghost fishing (Ward-Paige and Worm 2017). However, since this initial consideration of the effects of climate change on sharks and their relatives, studies have predicted changes in distribution patterns in response to ocean warming (Fuentes *et al.* 2016) and documented physiological and behavioral responses to simulated ocean warming, acidification, and deoxygenation conditions that suggest consequences for biological fitness (Rosa *et al.* 2017). Altogether, recently compiled evidence suggests that climate change is a more significant threat to sharks and their relatives than was previously considered (Chin *et al.* 2010; Rosa *et al.* 2017). Together, these global change stressors appear to have the potential to affect the distribution, physiology, behavior, and ultimately survival of sharks and their relatives.

25.2 PALEOCLIMATIC PERSPECTIVE

Sharks and their relatives survived all five major mass extinctions over the last ~450 million years (MY), making them arguably one of the most successful groups of marine organisms (Kriwet *et al.* 2008). Although the first reports of tesserate cartilage mineralization date back to only the Late Devonian, approximately 380 million years ago (MYA) (Long *et al.* 2015), the earliest, most explicit fossils, including scales and spines, date back to the early to mid-Silurian geological period (~427–444 MYA) (Grogan and Lund 2004; Märss and Gagnier 2001; Zhu 1998) and perhaps even the Late Ordovician (~455 MYA) (Janvier 1996; Turner 2004). Modern sharks and their relatives began their evolutionary history during a geological period (i.e., post Ordovician–Silurian mass extinction) when O_2 levels were on the rise (i.e., beyond current-day 21%), temperatures were in a cooling period, and atmospheric concentrations and aquatic $p\mathrm{CO}_2$ were much higher (i.e., atmospheric >4000 ppm) than today (>400 ppm) (Clack 2007; Munday *et al.* 2019; Rummer and Munday 2017) (Figure 25.1).

The evolutionary history of sharks and their relatives has likely helped to shape many of their defining physiological processes, especially as they relate to key traits relative to biological fitness, including respiration, acid–base regulation, calcification (Randall *et al.* 2014), development, and reproduction. Some experiments since the early part of the 21st century have revealed that various species are sensitive to the changes in temperature, CO_2, and O_2 levels that are predicted to occur in the oceans over the next 100 years due to ongoing anthropogenic CO_2 emissions into the atmosphere (Rosa *et al.* 2017). It is important to note, however, that, although extant species may have experienced challenging environmental conditions, including high CO_2 levels, in their deep evolutionary history, this does not necessarily mean that they will tolerate these conditions in the future. In order to reliably predict how populations will respond to climate change–relevant conditions over the next century due to accumulating anthropogenic CO_2 emissions, we must also consider their potential to geographically relocate or adapt over this time frame (Munday *et al.* 2013; Sunday *et al.* 2014).

25.3 CLIMATE CHANGE STRESSORS

25.3.1 Ocean Warming

Temperature is a key modulator of physiological performance, and marine ectotherms are particularly vulnerable to changes in external temperatures, given the relationship between temperature and, thus, ocean warming, and internal physiological and biochemical rate functions. Temperature is the most well-studied climate change–related stressor to date and is known to greatly influence the physiology of ectotherms such as the fishes, including sharks and their relatives (Fry 1971; Schulte 2015). As such, responses to temperature change can help explain trends in the abundance and distribution of species and populations (Payne *et al.* 2016; Pörtner and Knust 2007; Sunday *et al.* 2012).

The effects of temperature change occur at all levels of biological organization (Figure 25.2) (Schulte 2015). Changes in temperature invoke molecular responses (e.g., gene expression) (Bernal *et al.* 2020), biochemical responses (e.g., enzyme activity, substrate interactions) (Hochochka and Somero 2002), subcellular and cellular responses (e.g., membrane effects on mitochondrial respiration) (Chung *et al.* 2017), organ system responses (e.g., cardiovascular function) (Sandblom *et al.* 2016), and whole-organism responses (e.g., metabolic rate, growth) (Killen *et al.* 2010), all of which can have effects at the ecosystem level (Figure 25.2) (Hammerschlag *et al.* 2019). Biological rates (e.g., standard metabolic rate) increase exponentially with temperature, and performance traits (e.g., activity level, growth) are often modeled with thermal performance curves or reaction norms that are left skewed, exhibit an optimal temperature where the trait is maximized, and predict a critical upper thermal limit where the trait is zero (Figure 25.2) (Kellermann *et al.* 2019; Schulte *et al.* 2015). For example, metabolic rate typically doubles or triples (i.e., has a temperature quotient, Q_{10}, ranging from 2 to 3) with a 10°C increase in temperature (Figure 25.2) (Clarke *et al.* 1999; see also Chapter 10). The California Horn Shark (*Heterodontus francisci*), for example, has a $Q_{10} = 2.01$ (Luongo and Lowe 2018). Further, although teleost fish species have been found to exhibit a

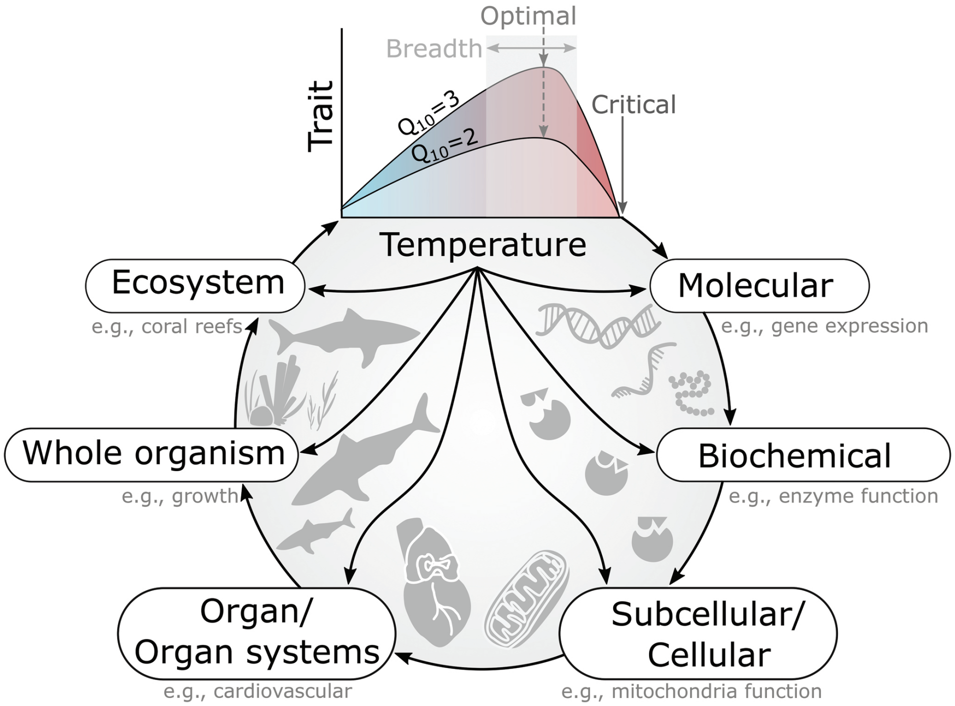

FIGURE 25.2 Schematic documenting the various levels of biological organization on which temperature can affect sharks and their relatives. A representative thermal performance curve is illustrated with two temperature quotient (Q_{10}) relationships, $Q_{10} = 3$ and $Q_{10} = 2$, such that rates triple or double, respectively, with a 10°C increase in temperature. Also shown are the optimal temperature for the arbitrary performance trait, the breadth of temperatures under which that trait operates, and the critical temperature beyond which that trait no longer functions. Cascading effects lie in molecular, biochemical, subcellular/cellular, organ/organ system, whole organism, and ecosystem levels with examples of each.

remarkable capacity for developmental, reversible, and transgenerational acclimation to temperature change (Donelson *et al.* 2012), this is not yet understood for chondrichthyan species. As such, there is much interest in quantifying thermal dependence of performance, thermal limits, and acclimation capacity in sharks and their relatives to predict population level responses to ocean warming.

25.3.2 OCEAN ACIDIFICATION

Changes in environmental or internal pCO_2 can markedly affect organismal physiology and behavior (Fry 1971). Species may already be experiencing or will be predicted to experience elevated pCO_2 in their environment into the future. This elevated pCO_2 can found be at naturally occurring CO_2 seeps (Munday *et al.* 2014); in low-O_2 environments (Gobler and Baumann 2016), where, for example, coastal upwellings bring CO_2-rich water from the O_2 minimum zone to the surface waters (Feely *et al.* 2008); in aquaculture; or as a result of ocean acidification (Ellis *et al.* 2017). Most water breathers are highly sensitive to increases in environmental pCO_2 when compared to air breathers because water breathers have inherently low arterial blood pCO_2 due to the high ventilation volume of gills, the high solubility of CO_2 in water, and the countercurrent nature of gas exchange across the gills (Evans *et al.* 2005). In addition, blood pCO_2 also increases internally as a metabolic waste product of aerobic cellular respiration (Hillman *et al.* 2013). When the CO_2 moves from the tissues into the blood, it hydrates to form carbonic acid (H_2CO_2) and then protons (H^+) and bicarbonate (HCO_3^-), resulting in an acid–base disturbance. Ventilation volume can be modulated (e.g., via swimming speed, ventilation rate) to reduce blood pCO_2 and potentially correct this acid–base disturbance (Esbaugh 2018), but CO_2 efflux is physically limited by the structural constraints of the respiratory system (Evans *et al.* 2005; Hillman *et al.* 2013). Instead, acid–base regulation occurs primarily through the exchange of H^+ and HCO_3^- with the environment but may also increase branchial ammonia excretion rates to ameliorate the acidosis further (Brauner *et al.* 2019). Thus, a typical (and simplified) response to an increase in environmental pCO_2—and the resulting increase in blood pCO_2 and decrease in pH—includes a net increase in [HCO_3^-] that can recover pH in a matter of hours (Wood 1991). Indeed, sharks and their relatives are thought to be resilient to acid–base disturbances largely due to their sophisticated acid excretion processes at the gill (Wood *et al.* 1995).

The consequences of an acid–base disturbance and subsequent regulation, however, can affect multiple physiological systems in fishes, including aerobic metabolism (e.g., cost of acid–base regulation reflected in standard metabolic rates), calcification processes (e.g., otolith formation in teleosts), and neurological function (e.g., hyperpolarization of inhibitory neurotransmitter receptors, reduced sensitivity of olfactory epithelia) and, therefore, behavior (reviewed in Heuer and Grosell 2014). Developmental, reversible, and transgenerational acclimation responses to elevated $p\mathrm{CO}_2$ may also be evident, as has been documented in teleost fishes. However, studies on sharks and their relatives are too few at this time to suggest this may be true in this group, as well. Developmental studies to date, however, have suggested little or no impact of ocean acidification–relevant $p\mathrm{CO}_2$ conditions on physiological performance, behavior, and survival (Johnson *et al.* 2016; Lopes *et al.* 2018; Pegado *et al.* 2018, 2019a, 2020b). Few of the studies (i.e., the 21 studies that are presented in this chapter) that have investigated ocean acidification–relevant $p\mathrm{CO}_2$ in isolation from other climate change stressors on sharks and their relatives have targeted reversible acclimation or plasticity (i.e., the ability of a single genotype to generate a variety of traits in response to environmental changes) and the resulting tolerance or intolerance.

Studies investigating transgenerational acclimation in elasmobranchs pose greater difficulties than studies on teleosts, because sharks and their relatives exhibit *K*-selected life-history strategies and therefore long generation times that prove difficult for such studies. Benthic oviparous species may be the best candidates for these types of studies, but to date no such study has been executed to completion such that conclusions can be drawn. It is also important to note that, despite their ability to compensate for levels of $p\mathrm{CO}_2$ exceeding those projected for ocean acidification into the near future (Ishimatsu *et al.* 2008), there is still mounting evidence, at least in teleost species so far, to suggest that exposure to ~900 to 1000 µatm $p\mathrm{CO}_2$ (i.e., RCP 8.5) has the potential for some level of physiological (reviewed in Hannan and Rummer 2018; Heuer and Grosell 2014) and behavioral (Tresguerres and Hamilton 2017) consequences, if not a combination of or trade-offs between both (Laubenstein *et al.* 2019). Therefore, future studies on sharks and their relatives should also aim to test the effects of simulated ocean acidification conditions on both physiological and behavioral endpoints.

25.3.3 OCEAN DEOXYGENATION

Oxygen is the greatest limiting factor for physiological performance in both bony and cartilaginous fishes (Fry 1971; Sampaio *et al.* 2021). Life is supported aerobically in fishes, and life without O_2 (i.e., anaerobic metabolism) is time limited. Because O_2 is the final electron acceptor in the electron transport chain, O_2 partial pressures ($p\mathrm{O}_2$) set the rates of aerobic cellular respiration. Aerobic metabolic rates are dependent on and independent of environmental $p\mathrm{O}_2$ along a continuum; species that regulate metabolic rate independent of environmental $p\mathrm{O}_2$ are referred to as "oxyregulators," and species whose metabolic rates conform to environmental $p\mathrm{O}_2$ are referred to as "oxyconformers" (Mueller and Seymour 2011). Most species are believed to be oxyregulators (Svendsen *et al.* 2019); however, maximum metabolic rates (MMRs), the upper limits of aerobic metabolic rates (see Chapter 10) in fishes (and ectotherms in general), are reduced by decreasing environmental $p\mathrm{O}_2$ but do not increase with environmental $p\mathrm{O}_2$ above saturation (Seibel and Deutsch 2020). Instead, the standard metabolic rate (SMR), the energetic cost of maintaining homeostasis, is regulated until $p\mathrm{O}_2$ is too low and fishes transition from oxyregulating to oxyconforming (see Figure 1 in Heinrich *et al.* 2014).

Ocean deoxygenation is another global syndrome—in conjunction with warming and acidification—but one that operates on different spatial and temporal scales; yet, this term was only first defined in 2009 (reviewed in Klein *et al.* 2020). The O_2 content of the oceans has decreased by more than 2% (−4.8 ± 2.1 pmol) since 1960. Although the causes are still not fully understood, it is agreed that this process involves decreased O_2 solubility and heightened biological consumption, which are worsened by enhanced stratification and induced by ocean warming, which will result in a further acceleration of reductions in ocean O_2 content with rising ocean temperatures throughout the 21st century (reviewed in Klein *et al.* 2020).

Although it should be clear that the term "hypoxia" is not interchangeable with ocean "deoxygenation" (Klein *et al.* 2020), quantifying hypoxia tolerance strategies and thresholds is key to defining the effects of ocean deoxygenation. Fishes can experience hypoxia in habitats with high rates of respiration, such as estuaries or tidal pools (Richards 2011), and in stratified waters, including O_2 minimum zones (Seibel 2011). Hypoxia is often defined in marine systems as a reduction in dissolved O_2 concentrations below 2.8 mg $\mathrm{O}_2\ \mathrm{L}^{-1}$ (Breitburg *et al.* 2018), although this is an arbitrary threshold. For example, 2 mg $\mathrm{O}_2\ \mathrm{L}^{-1}$ may be considered hypoxic for the Sandbar Shark (*Carcharhinus plumbeus*) (Crear *et al.* 2019) but not for the Clearnose Skate (*Rostroraja eglanteria*) (Schwieterman *et al.* 2019). Rather, hypoxia can be defined as the environmental (or internal) $p\mathrm{O}_2$ below which the function of a physiological system is altered. Hypoxia tolerance is often defined using various metrics that relate to the whole organism (Wood 2018), including the $p\mathrm{O}_2$ that reduces the SMR (Negrete and Esbaugh 2019), the MMR (Seibel and Deutsch 2020), or the $p\mathrm{O}_2$ that induces loss of equilibrium (Snyder *et al.* 2016). Exposure to hypoxia initiates a suite of physiological responses, including ventilatory depression (Chapman *et al.* 2011) and the expression of hypoxia-inducible factor proteins and heat-shock proteins (Renshaw *et al.* 2012). Some fishes can improve tolerance to low-$p\mathrm{O}_2$ environments via developmental and reversible acclimation (Gilmore *et al.* 2019; Wood *et al.* 2017). Yet, although several studies have investigated hypoxia and even anoxia tolerance in sharks and their relatives (e.g., Bouyoucos *et al.* 2020a; Butler and Tayler 1975; Carlson and Parsons 2001, 2003; Crear *et al.* 2019; Dabruzzi and Bennett 2013; Dabruzzi *et al.* 2013; Hickey *et al.* 2012; Morash *et al.* 2020; Musa *et al.* 2020; Perry and Gilmour 1996; Routley *et al.* 2002; Rytkönen *et al.* 2012; Short *et al.* 1979; Speers-Roesch *et al.* 2012; Wise *et al.* 1998), no study published before mid-2021 has done so within a climate change context (i.e., ocean deoxygenation). Investigating the effects of hypoxia is a start, but understanding and modeling the effects of deoxygenation on sharks and their relatives, identifying potential interactions with other climate change stressors, and determining impacts on ecosystem balance and fisheries (e.g., Vedor *et al.* 2021) will be research priorities as the 21st century progresses.

25.3.4 EXTREME EVENTS

Alongside gradual changes in long-term means of various environmental conditions, climate change is also manifested in the amplification of extreme events and their respective impacts (see Section 25.4.3.3). Marine heatwaves—transient periods of exceptionally high seawater temperatures (Hobday *et al.* 2016)—are becoming increasingly more severe, frequent, and widespread (Cai *et al.*, 2014a,b; Oliver *et al.* 2018, 2019) and are taking a toll on marine organisms (Bernal *et al.* 2020; Johansen *et al.* 2021; Nowicki *et al.* 2019), with consequent cascading effects to higher levels of biological organization (Smale *et al.* 2019). Somewhat counterintuitively, cold snaps are also predicted to increase in frequency and magnitude (Matich and Heithaus 2012; Matich *et al.* 2020). Likewise, the frequency, extent, and magnitude of both extreme acidification and hypoxic events (i.e., short-term episodes of abnormally low pH/calcium carbonate saturation and O_2 levels, respectively) are also expected to increase with rising CO_2 emissions (Breitburg *et al.* 2018; Burger *et al.* 2020). Importantly, although these extreme events may be quite devastating in isolation, common causal processes and interdependecies imply that these events are prone to overlap (Dzwonkowski *et al.* 2020; Lauvset *et al.* 2020; Melzner *et al.* 2013).

Given the swift onset of these phenomena, organisms may respond by seeking refuge or relocating to a temporarily more favorable area, or they may rely on their phenotypic plasticity to cope with the new conditions. Such strategies could entail important physiological and ecological trade-offs, particularly considering the energetic costs of physiological responses and relocation (Kroeker *et al.* 2020). Regardless, organisms must cope with both the direct effects of the rapidly changing and extreme conditions and the indirect effects of these events over other elements of marine communities, which may include changes in prey and habitat availability and predator pressure (Smale *et al.* 2019; Wild *et al.* 2019). Given the intrinsically low adaptation potential of sharks and their relatives in relation to the current rates of climate change (Chin *et al.* 2010; Rosa *et al.* 2017), understanding how they respond to current-day environmental extremes is particularly helpful to understand how they may respond to the future ocean conditions. Moreover, their high trophic position in marine food webs forecasts their potential to partially modulate the response of other species to these events (Nowicki *et al.* 2019; Wild *et al.* 2019). Nevertheless, targeted research into how sharks and their relatives will respond to extreme events is still scarce. Although only a few studies have expressly addressed the potential effects of such abrupt events on sharks and their relatives (Pegado *et al.* 2020b), it is worth noting that controlled experiments typically used in climate change–related experimental studies better align with responses to acute events than with long-term climate change, given their swift onset and duration of exposure (Sampaio *et al.* 2021).

25.3.5 CLIMATE CHANGE RESEARCH ON SHARKS AND THEIR RELATIVES

Ocean warming, acidification, and deoxygenation are predicted to affect sharks and their relatives across multiple physiological systems. However, as of mid-2021, only sharks and skates have been tested and only with respect to ocean warming and acidification conditions (i.e., not ocean deoxygenation). To date, no ray or chimaera species has been directly studied within the context of any of the three major climate change stressors. Moreover, very few studies (n = 30), of fewer species (n = 10), have investigated the effects of ocean warming (Gervais *et al.* 2016, 2018, 2021; Hume 2019; South and Dick 2017; Vila Pouca *et al.* 2018, 2019; Wheeler *et al.* 2021), ocean acidification (Bouyoucos and Rummer 2020; Dixson *et al.* 2015; Dziergwa *et al.* 2019; Green and Jutfelt 2014; Heinrich *et al.* 2014, 2015; Johnson *et al.* 2016; Lopes *et al.* 2018; Pegado *et al.* 2019b, 2020a; Rosa *et al.* 2016a,b; Rummer *et al.* 2020), or the combined global change stressors (Bouyoucos *et al.* 2020b; Di Santo 2015, 2016, 2019; Musa *et al.* 2020; Pistevos *et al.* 2015, 2017; Rosa *et al.* 2014, 2016b; Schwieterman *et al.* 2019) in sharks and skates using climate change–relevant experimental conditions (Table 25.1). It is important to note, however, that there exists a large body of relevant literature on the ecophysiology of sharks, skates, and rays, including the effects of temperature (Bernal *et al.* 2018; Dabruzzi *et al.* 2013; Miklos *et al.* 2003; Payne *et al.* 2018), CO_2 (Bouyoucos and Rummer 2020; Choe and Evans 2003; Graham *et al.* 1990; Heisler *et al.* 1988; Randall *et al.* 1976), and hypoxia (e.g., Bouyoucos *et al.* 2020a; Butler and Tayler 1975; Carlson and Parsons 2001, 2003; Crear *et al.* 2019; Dabruzzi and Bennett 2013; Dabruzzi *et al.* 2013; Hickey *et al.* 2012; Morash *et al.* 2020; Perry and Gilmour 1996; Routley *et al.* 2002; Rytkönen *et al.* 2012; Short *et al.* 1979; Speers-Roesch *et al.* 2012; Wise *et al.* 1998), but not necessarily under climate change–relevant conditions.

We conducted a meta-analysis to help summarize the current state of knowledge, including critical gaps, regarding the effects of climate change–relevant stressors and their interactions on sharks and their relatives (see Appendix for methodological details). It is evident that elasmobranchs have, indeed, been understudied. Tropical carpet sharks represent the most-studied group, with 11 studies across three species: Whitespotted Bamboo Shark (*Chiloscyllium plagiosum*), Brownbanded Bamboo Shark (*Chiloscyllium punctatum*), and Epaulette Shark (*Hemiscyllium ocellatum*). Temperate skates are the next most-studied group, with 11 studies across

TABLE 25.1
Climate Change Stressors

	Climate Change Stressor		
Species	**Ocean Warming**	**Ocean Acidification**	**Ref.**
Amblyraja radiata	✓	✓	Schwieterman *et al.* (2019)
Carcharhinus melanopterus		✓	Bouyoucos and Rummer (2020)
		✓	Rummer *et al.* (2020)
Chiloscyllium plagiosum		✓	Lopes *et al.* (2018)
		✓	Pegado *et al.* (2019a)
Chiloscyllium punctatum	✓	✓	Rosa *et al.* (2014)
	✓	✓	Rosa *et al.* (2016a)
	✓	✓	Rosa *et al.* (2016b)
Haploblepharus edwardsii		✓	Dziergwa *et al.* (2019)
Hemiscyllium ocellatum		✓	Heinrich *et al.* (2014)
		✓	Heinrich *et al.* (2015)
	✓		Gervais *et al.* (2016)
	✓	✓	Johnson *et al.* (2016)
	✓		Gervais *et al.* (2018)
	✓		Wheeler *et al.* (2021)
Heterodontus portusjacksoni	✓	✓	Pistevos *et al.* (2015)
	✓	✓	Pistevos *et al.* (2017)
	✓		Gervais *et al.* (2021)
	✓		Vila Pouca *et al.* (2018)
	✓		Vila Pouca *et al.* (2019)
Leucoraja erinacea	✓	✓	Di Santo (2015)
	✓	✓	Di Santo (2016)
	✓	✓	Di Santo (2019)
Mustelus canis		✓	Dixson *et al.* (2015)
Raja microocellata	✓		Hume (2019)
	✓	✓	Schwieterman *et al.* (2019)
		✓	Green and Jutfelt (2014)
	✓		South and Dick (2017)
		✓	Pegado *et al.* (2019b)
	✓		Musa *et al.* (2020)
		✓	Pegado *et al.* (2020a)

Note: A total of 10 species of sharks (six species) and skates (four species) have been investigated across 30 individual studies to assess the effects of climate change–relevant stressors (i.e., ocean warming and ocean acidification) and their interactions, in some cases, on various fitness-related traits. No studies to date have investigated ocean deoxygenation under climate change scenarios in any chondrichthyan species, so this stressor was accordingly omitted from this table.

three species: Thorny Skate (*Amblyraja radiata*), Little Skate (*Leucoraja erinacea*), and Smalleyed Skate (*Raja microocellata*). The temperate Port Jackson Shark (*Heterodontus portusjacksoni*) appears in five studies. The tropical Blacktip Reef Shark (*Carcharhinus melanopterus*) is represented in two individual studies, and the Shyshark (*Haploblepharus edwardsii*) and the Dusky Smoothhound (*Mustelus canis*) each has been studied only once within this context (Table 25.1). It is important to note that the majority of research effort has focused mostly on oviparous species with benthic, inactive lifestyles (Rosa *et al.* 2017), except for the viviparous, pelagic Dusky Smoothhound and the Blacktip Reef Shark. Although making up 40% of all chondrichthyans, oviparous species with benthic and inactive lifestyles may not be representative of all sharks and their relatives with regard to tolerance to climate change conditions (Wheeler *et al.* 2020).

Of the trait categories that have been examined under ocean warming conditions, studies assessing behavior have largely been on temperate species, whereas studies investigating cellular/molecular traits and survival have largely been on tropical species. Most of these traits have also mainly been examined in embryonic and neonate life stages (Figure 25.3). For nearly

TABLE 25.2
Meta-Analysis Modeling Outcomes of Ocean Warming, Acidification, and Combined Effects on 10 Species of Sharks and Skates Across 30 Studies

Ocean Warming

Log Likelihood	AIC	Studies, *n*	*K*	I^2 Total	Intra-Study I^2	Inter-Study I^2
–213.6539	445.3078	19	95	0.9175	0.0717	0.8458

Sublevel	Estimate	Standard Error	*z*	*P*	Lower CI	Upper CI
Behavior	–0.1719	0.5685	–0.3023	0.7624	–1.2862	0.9424
Body condition	0.3577	0.4559	0.7845	0.4327	–0.5359	1.2512
Cellular/biochemical	1.1308	0.606	1.866	0.062	–0.057	2.3185
Development	–0.7953	0.5741	–1.3853	0.166	–1.9205	0.3299
Hypoxia tolerance	0.5426	0.7819	0.6939	0.4877	–0.9899	2.075
Metabolism	1.53	0.3642	4.2003	<0.0001	0.816	2.2439
Survival	–0.3112	0.5589	–0.5568	0.5776	–1.4067	0.7843

Ocean Acidification

Log Likelihood	AIC	Studies, *n*	*K*	I^2 Total	Intra-Study I^2	Inter-Study I^2
–314.6599	647.3197	21	197	0.7270	0.1725	0.5545

Sublevel	Estimate	Standard Error	*z*	*P*	Lower CI	Upper CI
Behavior	–0.2332	0.2446	–0.9533	0.3404	–0.7125	0.2462
Body condition	–0.2097	0.2614	–0.8021	0.4225	–0.7220	0.3027
Cellular/biochemical	0.0020	0.1497	0.0135	0.9892	–0.2914	0.2954
Development	0.0221	0.3824	0.0579	0.9538	–0.7274	0.7717
Hypoxia tolerance	0.7848	0.5558	1.4118	0.1580	–0.3047	1.8742
Metabolism	0.1650	0.2497	0.6608	0.5087	–0.3244	0.6545
Survival	–0.2482	0.3443	–0.7208	0.4711	–0.9231	0.4267

Combination Effects

Log Likelihood	AIC	Studies, *n*	*K*	I^2 Total	Intra-Study I^2	Inter-Study I^2
–110.827	239.6541	11	62	0.8942429	0.0802584	0.8139845

Sublevel	Estimate	Standard Error	*z*	*P*	Lower CI	Upper CI
Behavior	0.40	0.6122	0.6544	0.5128	–0.7993	1.6006
Body condition	0.4508	0.5464	0.825	0.4093	–0.6201	1.5217
Cellular/biochemical	0.9227	0.4611	2.001	0.0454	0.0189	1.8265
Development	–0.4039	0.7522	–0.5369	0.5913	–1.8781	1.0704
Hypoxia tolerance	1.1699	1.1155	1.0488	0.2943	–1.0164	3.3562
Metabolism	0.9853	0.4681	2.1052	0.0353	0.068	1.9027
Survival	–0.5182	0.7359	–0.7042	0.4813	–1.9605	0.9242

Note: Model information includes the log likelihood, Akaike information criterion (AIC), number of studies, number of individual data points (*k*), and the coefficients of homogeneity (I^2).

all of these traits, with the exception of metabolism, no net effect of ocean warming has been detected across all studies, life stages, and species combined (Table 25.2). When assessing the traits examined under ocean acidification conditions, however, a more even distribution between temperate and tropical species is represented, although all studies that have examined developmental and survival traits under ocean acidification conditions to date have been on embryonic and neonate stages (Figure 25.3). When assessing all studies, life stages, and species combined, no net effect of ocean acidification conditions was detected for any trait category (Table 25.2).

Among the studies to date that have examined the combined effects of ocean warming and acidification, those that have examined cellular and molecular traits have done so using tropical species (Heinrich *et al.* 2014; Lopes *et al.* 2018; Rosa *et al.* 2016a,b), whereas body condition traits have largely been examined in temperate species (Di Santo 2015, 2019; Hume 2019; Musa *et al.* 2020; Pistevos *et al.* 2015). Most studies have only investigated the combined effects of ocean warming and acidification on embryonic and neonate life stages (Figure 25.3), and the net effects of combined ocean warming and acidification on various traits are likely largely driven by the influence of temperature, which is evident in the net effect on metabolic traits (Table 25.2). Interestingly, however, net effects of ocean warming and acidification can also be detected in cellular and molecular traits, where net effects were not obviously (i.e., not statistically significant) affected by ocean warming conditions alone (Table 25.2). Indeed, past

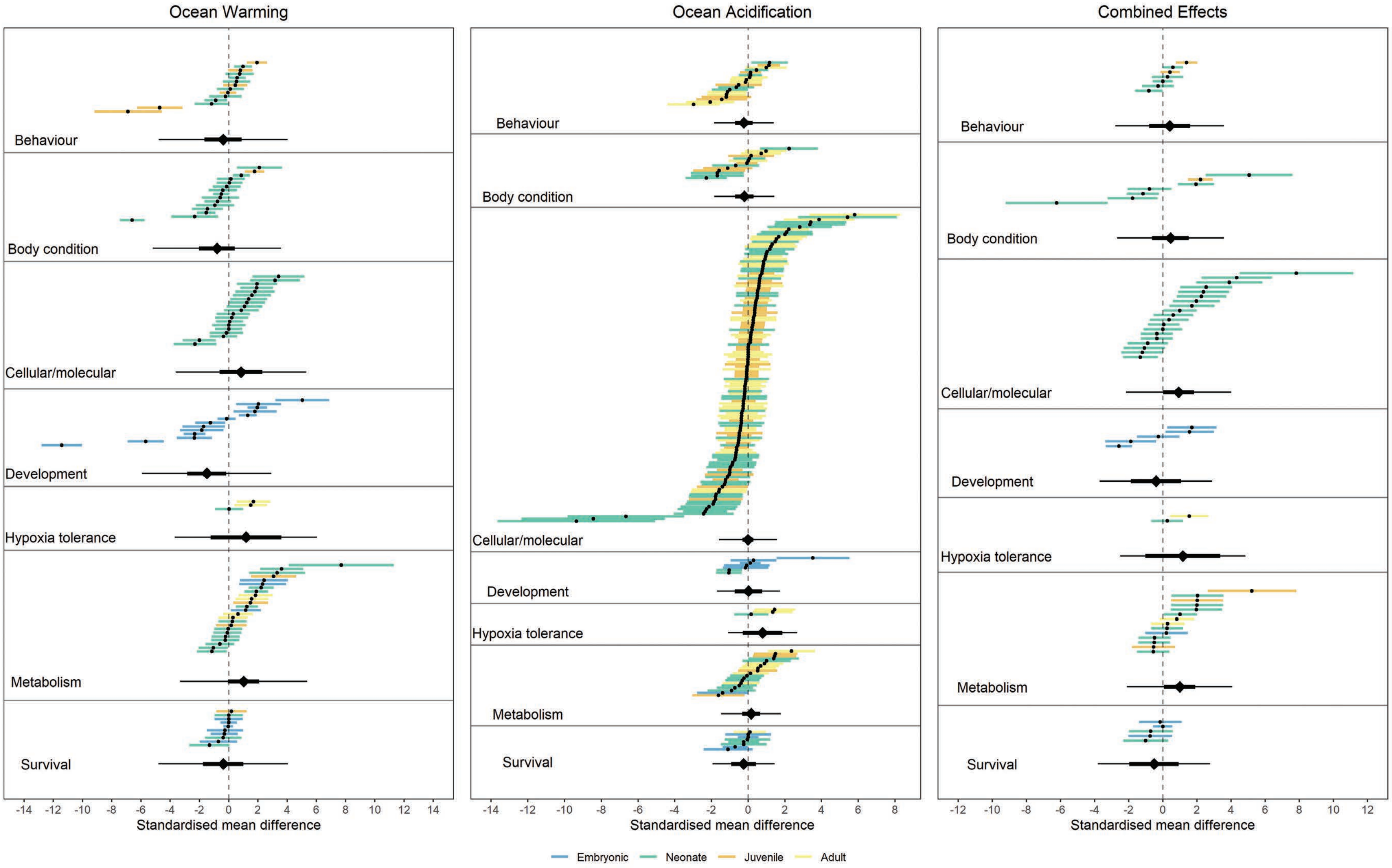

FIGURE 25.3 Caterpillar plots as per outputs from mixed effects models demonstrating an array of effects of ocean warming (left panel), ocean acidification (middle panel), and the combined effects (right panel) on seven categories of traits on embryonic (blue), neonate (green), juvenile (orange), and adult (yellow) life stages of species of sharks and their relatives. Small black points and horizontal color segments represent the individual trait effect sizes and confidence intervals, respectively. The large black diamonds and the thick and thin shaded black horizontal bars represent the overall effect estimates, confidence intervals, and prediction intervals, respectively, for each category. The direction of the standardised mean difference represents the direction of change for a trait (e.g., metabolic rate), not necessarily the direction of the impact on the organism. For example, an increase in metabolism from ocean warming (positive effect) could have overall negative consequences for an individual.

studies have observed greater effects under the combination of the two stressors than under either in isolation (Di Santo 2015; Rosa *et al.* 2014), although antagonistic interactions have also been reported (Pistevos *et al.* 2017), a topic requiring further investigation.

25.4 IMPACTS OF CLIMATE CHANGE AT DIFFERENT LEVELS OF BIOLOGICAL ORGANIZATION

A whole-body response is required to cope with new environmental conditions, from the acquisition and integration of environmental cues that elicit behavioral responses to the shifts in metabolic pathways that allow acclimation, but all adaptive responses ultimately start at the subcellular level. Literature on the effects of the "deadly trio" on sharks and their relatives has been steadily growing over the past decade; yet, most studies have focused on whole organisms and behavior. Only a few studies have focused on the lower levels of biological organization within a climate change context.

25.4.1 Molecular and Cellular Levels

25.4.1.1 Energy Metabolism

As discussed earlier in this chapter, O_2 consumption or, more accurately, O_2 uptake rates are often used as broad proxies for aerobic metabolism—the complex series of biochemical reactions tasked with making cellular energy via the use of O_2. Studies that measure O_2 uptake rates of organisms under resting, unfed states aim to estimate SMRs, or the basic maintenance costs of the organism under various conditions, across life stages, by sex, etc. This metric can help predict how basic maintenance costs of the animal can change under various conditions, including those related to climate change. The effects of climate change stressors, particularly temperature, on SMRs are relatively well understood (e.g., the Q_{10} relationship between temperature and metabolic rate and potentially increased metabolic costs due to acid–base regulation under ocean acidification conditions) (Deutsch *et al.* 2015; Lefevre 2016; see also Chapter 10). More specifically, the O_2 uptake rates of sharks and their relatives typically trail environmental temperature trends (e.g., Gervais *et al.* 2021; Rosa *et al.* 2014; Tullis and Baillie 2005; Wheeler *et al.* 2021). However, it is not enough to just examine resting physiological functions (e.g., SMR), and there is still no general consensus as to how temperature, let alone other climate change stressors, affects maximum whole organism traits. Exercise protocols can be used to estimate MMRs, defined as the highest rate of O_2 uptake during aerobic activity. Indeed, the effects of a stressor on a species or population may be underestimated if both the SMR and MMR are not examined, which is highlighted in studies investigating "plastic floors and concrete ceilings" (Sandblom *et al.* 2016). One or both metabolic traits could be driving changes in aerobic scope, which is calculated as the difference between the two metrics (i.e., MMR – SMR) and defines the total amount of O_2 available to the organism (i.e., under said conditions) to devote to all aerobic activities beyond basic maintenance (e.g., movement, feeding, reproduction) (Clark *et al.*, 2013). Aerobic scope is a commonly used metric and is predicted to decrease under some climate change scenarios (Lefevre 2016). Beyond aerobic metabolism, many studies have investigated metrics of anaerobic metabolism by challenging the study species beyond their aerobic capacity and then monitoring recovery, which can be calculated as excess post-exercise O_2 consumption. The amount of O_2 and the time required to recover from anaerobic activity (e.g., burst swimming, simulated fishing encounters, air exposure) will vary under different conditions and can therefore be another relevant metric to communicate how an organism will respond, metabolically, to stressors such as those related to climate change. Yet, the challenge still remains when extrapolating responses to short-term changes in conditions to long-term effects that will occur over generations. Indeed, these are still just broad metrics and may not capture the hundreds if not thousands of processes that are being affected by one stressor or another and therefore key to phenotypic plasticity and/or adaptation to future climate conditions.

At the biochemical level, no changes (Rosa *et al.* 2016a) and even a decrease (Tullis and Baillie 2005) in the activity levels of citrate synthase (CS), a key enzyme involved in aerobic production of cellular energy (i.e., adenosine triphosphate), have been observed in two species within the genus *Chiloscyllium* under warming conditions. Meanwhile, a decline in CS activity observed under acidification conditions is reflected in the decline in O_2 uptake rates observed in juveniles of the Brownbanded Bamboo Shark (Rosa *et al.* 2014; 2016b). These results contrast with those from Heinrich *et al.* (2014), where no changes in CS activity were reported in the Epaulette Shark in response to elevated pCO_2. Although the two are closely related species, they occupy different niches; yet, both are known for their exceptional tolerance to environmental extremes that appear to extend to hypercapnic conditions. However, individuals of the Brownbanded Bamboo Shark were exposed to more extreme levels of elevated pCO_2 (1400 μatm) than the Epaulette Shark (880 μatm) and over a longer period, throughout embryogenesis. Contrasting findings between the two species may suggest differences between developmental effects (i.e., Brownbanded Bamboo Shark) and reversible effects (Epaulette Shark) and between different levels of elevated pCO_2. In addition, upon exposure to elevated pCO_2, the Brownbanded Bamboo Shark increased activity of lactate dehydrogenase, an enzyme that mediates the inter-conversion of pyruvate and lactate within the context of anaerobic respiration (Rosa *et al.* 2016a). This indicates an increased reliance on anaerobic pathways to uphold energetic demands, which may not be sustainable over the long term (Pörtner *et al.* 2017).

Studies assessing the effects of oxygen loss on metabolic traits in sharks and their relatives are sparse and mostly restricted to acute exposures to hypoxic and anoxic conditions, often focusing on rather tolerant species (Dowd *et al.* 2010; Hickey *et al.* 2012; Morash *et al.* 2020; Speers-Roesch *et al.* 2012). Even so, the strategies employed to cope with oxygen deprivation vary widely. Indeed, although the two sharks are closely related, the Epaulette Shark has been shown to respond to hypoxia with metabolic depression and increased reliance on anaerobic pathways, whereas the Brownbanded Bamboo Shark appears to increase O_2 carrying capacity in response to anoxia (Chapman and Renshaw 2009; Routley *et al.* 2002). Different species appear to implement different strategies or combinations of strategies that likely depend on the duration and magnitude of exposure (Dabruzzi and Bennett 2013; Morash *et al.* 2020). In fact, following short-term hypoxia exposure and accompanying the accumulation of lactate (suggesting the activation of anaerobic pathways), a significant increase in CS activity in the liver was observed in the Maugean Skate (*Zearaja maugeana*). This was an intriguing result under O_2-stressed conditions, because there was no evidence of metabolic depression in this species (Morash *et al.* 2020). Biochemical adjustments in response to hypoxia also exhibit a strong tissue specificity (Speers-Roesch *et al.* 2012), as well as species and habitat specificity. Although the subcellular mechanisms underpinning these responses have been the target of research (Rytkönen *et al.* 2012), further investigation (with more ecologically relevant conditions in a climate change context) could provide important clues regarding how this group may cope with increasingly lower oxygen levels and more frequent hypoxic conditions.

25.4.1.2 Oxygen Transport and Hematological Parameters

Along with an increase in O_2 demand and a decrease in O_2 content in seawater with elevated temperatures, most fishes respond, counterintuitively, by reducing blood O_2 affinity (Nikinmaa *et al.* 2019). Most sharks and their relatives possess high blood O_2 affinity when compared to teleost fishes (Morrison *et al.* 2015), but this same pattern, whereby blood O_2 affinity is reduced with elevated temperatures, is still typically observed (Bernal *et al.* 2018; Bouyoucos *et al.* 2020a; Morrison *et al.* 2015). Nonetheless, and similarly to some tuna species, a reduced or even reversed temperature effect has been reported, specifically in regionally endothermic, highly active sharks (Bernal *et al.* 2018; Larsen *et al.* 2003), thus highlighting the potentially steep interspecific differences in sharks and their relatives that may be related to species ecology and potentially result in distinct responses toward environmental stressors. It is important to emphasize, however, that the way these organisms respond to decreases in O_2 intertwines with the response to rising temperatures (Bouyoucos *et al.* 2020a; Butler and Taylor 1975); therefore, it is important to consider both stressors in concert, especially when designing future studies to understand the effects of ocean deoxygenation.

Hemoglobin is the primary protein in the blood of most organisms that is responsible for transporting O_2, but sharks and their relatives lack the extensive responsiveness of teleost fishes (Schwieterman *et al.* 2021). Yet, studies indicate that several species can adjust their hematological profile in response to environmental challenges. In this context, the hematocrit (i.e., the ratio of packed red blood cells to total blood volume) of several species has been shown to increase with rising temperatures (Bouyoucos *et al.* 2020c; Butler and Taylor 1975; Neale *et al.* 1977), possibly resulting in increased O_2 carrying capacity and mitigating the effects of a lower blood O_2 affinity inherent with elevated temperatures (Bernal *et al.* 2018; Bouyoucos *et al.* 2020a). With no changes in hemoglobin concentrations or mean corpuscular hemoglobin content (MCHC) (Bouyoucos *et al.* 2020c), increased hematocrit may be related to changes in the numbers, maturity, and morphometric properties of these red blood cells (Neale *et al.* 1977; Pegado *et al.* 2020b). Exposure to a 10°C temperature elevation over 30 days largely surpasses the long-term mean projections for end-of-century climate change conditions but potentially aligns with extreme marine heatwave conditions. Such an exposure results in a decline in red blood cell numbers, an increase in red blood cell size, an increase in hemoglobin concentrations, and a concomitant increase in hematocrit and MCHC in Horn Sharks (*Heterodontus francisci*) (Neale *et al.* 1977), which may be suggestive of an acute stress response. Following 48 hours of exposure to hypoxic conditions, a hypoxia-tolerant skate has been found to decrease its MCHC, which the authors suggest could be potentially associated with increasing red blood cell volume (Morash *et al.* 2020), but no effects of acute hypoxia have been observed with respect to hematocrit and hemoglobin concentrations across the several species tested so far (Carlson and Parsons 2003; Dabruzzi and Bennett 2013; Morash *et al.* 2020; Perry and Gilmour 1996; Routley *et al.* 2002; Short *et al.* 1979; Speers-Roesch *et al.* 2012). However, it is important to note that some species may ramp up their O_2 carrying capacity more obviously in response to low O_2 levels and in ways not directly reflected in hematological parameters (Chapman and Renshaw 2009; Morrison *et al.* 2015). As climate change–relevant studies evolve, this is an area worthy of future emphasis.

In studies simulating future ocean acidification conditions, acute exposure (i.e., 72 hours) to elevated $p\mathrm{CO}_2$ results in an increased hematocrit in juveniles of the Blacktip Reef Shark (*C. melanopterus*) (Rummer *et al.* 2020), but no changes were observed in the same population and life stage following a more extended exposure (i.e., 17 days) to elevated $p\mathrm{CO}_2$ (Bouyoucos *et al.* 2020c). This highlights the importance of considering exposure duration and that there is potential for distinct responses to long-term changes in ocean conditions that may be different than responses to acute events. Indeed, no other study to date has observed significant effects of ocean acidification conditions on hematocrit (Dziergwa *et al.* 2019; Green and Jutfelt 2014; Heinrich *et al.* 2014; Pegado *et al.* 2020c), but all of these previous studies featured longer exposures to treatment conditions. Although the changes reported by Rummer *et al.* (2020) may represent transient responses to acute events, the highly tolerant Epaulette Shark (*H. ocellatum*) has shown an increase in MCHC and hemoglobin concentrations after 60 days of exposure to higher $p\mathrm{CO}_2$ conditions (Heinrich *et al.* 2014), in what appears to be a sustained physiological adjustment to ocean acidification conditions. Species that are in direct contact with the coral reef matrix, which we know fluctuates in $p\mathrm{CO_2}$ substantially over diel cycles and with other hydrodynamic properties (Hannan *et al.* 2020), may already possess adaptations to cope with elevated $p\mathrm{CO_2}$ on a transient basis but may need to initiate other strategies when $p\mathrm{CO_2}$ remains elevated for extended periods of time. Therefore, it is important to consider not only the species and life-history strategies but also the habitat conditions when predicting responses to these fluctuating conditions.

Finally, an endpoint severely understudied but also directly related to hematological parameters is the effects of climate change–related stressors on the rather unique immune system of sharks and their relatives (Neale *et al.* 1977; Pegado *et al.* 2019b, 2020b). Changes in the ratio of leucocytes—namely, heterophils and neutrophils (i.e., granulocytes)—relative to lymphocytes under warming conditions should foster further research (Neale *et al.* 1977; Pegado *et al.* 2020b). Meanwhile, it is also worth noting that no changes in the prevalence of red blood cell abnormalities have been observed following exposure to moderate warming (+3°C) or acidification (−0.3 pH units) in Small-Spotted Catshark (*S. canicula*) (Pegado *et al.* 2019b, 2020b); however, more extreme conditions (+6°C) have been shown to elicit an increase in both nuclear and cellular abnormalities in the red blood cells of a teleost species (Ashaf-Ud-Doulah *et al.* 2019).

25.4.1.3 Acid–Base Balance

Previous studies indicate that sharks and their relatives possess a remarkable capacity to counter generalized acidosis by relying on an accumulation of plasma $\mathrm{HCO_3^-}$ through active ion transport and the inherently high buffering capacity of their hemoglobin to changes in $p\mathrm{CO_2}$ (Morrison *et al.* 2015; Nikinmaa *et al.* 2019). This has been reviewed extensively for the fishes in general (see Hannan and Rummer 2018; Heuer and Grosell 2014) and has been found to be the case in the Epaulette Shark in response to mid- and end-of-century $p\mathrm{CO_2}$ conditions (Heinrich *et al.* 2014). Although studies on $p\mathrm{CO_2}$ conditions relevant to ocean acidification have increased (Dziergwa *et al.* 2019; Green and Jutfelt 2014; Heinrich *et al.* 2014; Rummer *et al.* 2020), past studies focused on the mechanistic basis of acid–base balance in sharks and their relatives (e.g., Choe and Evans 2003; Claiborne and Evans 1992; Graham *et al.* 1990). Meanwhile, little is known regarding the potential effects of ocean warming or deoxygenation on acid–base regulation (Heisler *et al.* 1988). Although the active upkeep of acid–base homeostasis may constitute an additional energetic constraint, potentially reallocating energetic resources away from other important life-history and fitness-related processes, when placed within a climate change context the energetic costs are likely to be mild (Lefevre 2016).

25.4.1.4 Neuroendocrine Responses

Shifts in shark behavioral patterns have been detected following simulated conditions of both ocean warming (Pistevos *et al.* 2017; South and Dick 2017; Vila Pouca *et al.* 2018, 2019) and acidification (Dixson *et al.* 2015; Green and Jutfelt 2014; Pegado *et al.* 2018; Pistevos *et al.* 2015); however, the neuroendocrine pathways underpinning these findings remain largely unaddressed. Behavioral changes in the context of experiments with teleost species related to ocean acidification have been mostly attributed to perturbations in the γ-aminobutyric acid type A ($\mathrm{GABA_A}$) receptor function, resulting from the acid–base disturbance and subsequent compensatory mechanisms (Nilsson *et al.* 2012). However, although this hypothesis has been used to tentatively explain the effects of elevated $p\mathrm{CO_2}$ on shark behavior, the role of $\mathrm{GABA_A}$ receptors with respect to such behavioral shifts remains to be tested (Dixson *et al.* 2015; Green and Jutfelt 2014). Other mechanisms and neuroendocrine pathways may underlie some of the changes in behavioral patterns that have been observed to date. Indeed, reductions in acetylcholinesterase activity have been observed in the telencephalon and optic lobe of juveniles of the Whitespotted Bamboo Shark after they had been exposed to simulated ocean acidification conditions after hatching (Pegado *et al.* 2018). Interestingly, the closely related Brownbanded Bamboo Shark exhibited no significant changes in acetylcholinesterase activity at the whole-brain level upon exposure to elevated $p\mathrm{CO_2}$ (under control temperatures) since early embryogenesis, but subsequent exposure to warming alone and in combination with elevated $p\mathrm{CO_2}$ resulted in an increase in acetylcholinesterase activity (Rosa *et al.* 2016a). These results indicate that both ocean warming and acidification stressors have the potential to interfere with cholinergic pathways, with possible behavioral implications. Further research is warranted.

Climate change stressors are also known to influence endocrine pathways (Servili *et al.* 2020); however, this topic has been severely understudied in sharks and their relatives. Research by Mull and colleagues (2008) revealed a negative relationship between warming and testosterone levels of male Round Stingray (*Urobatis halleri*), whereas an opposite trend was observed for Horn Shark (*Heterodontus francisci*) (Neale *et al.* 1977). Field research and seasonal time series can showcase the role of temperature in regulating circulating sex steroid hormones (Elisio *et al.* 2019; Heupel *et al.* 1999; Mull *et al.* 2008, 2010; Nozu *et al.* 2018), but controlled laboratory experiments are key to disentangling these effects from potential cofounding factors.

25.4.1.5 Heat Shock Responses

Environmental disturbances can lead to loss of function and denaturation of proteins, to which animals can respond through the induction of molecular chaperones, such as the heat shock proteins (HSPs), to help maintain and restore misfolded proteins (Hochachka and Somero 2002; Iwama *et al.* 1998). The onset of the heat shock response has the potential to increase an organism's thermal tolerance and is typically triggered near the organism's thermal limits (Chen *et al.* 2018; Pörtner 2001). In this context, the levels of HSP70 have been addressed in the context of acute temperature increases (6°C) in both the Spiny Dogfish (*Squalus acanthias*) and the Smooth Dogfish (*Mustelus canis*), with a marked increase detected in the former but no changes in the latter, despite both species being naturally exposed to the temperatures tested (Bockus *et al.* 2020). This suggests that some species may already be pushing their thermal tolerance limits under current-day conditions, which is an important consideration, given the energetic costs associated with the heat shock response, which may become increasingly difficult to sustain as temperatures continue to rise. The same study also investigated the effects of increased temperatures on trimethylamine *N*-oxide (TMAO) levels, an osmolyte implicated in osmoregulation in sharks and their relatives that can also act as a "chemical chaperone" and a potentially less expensive alternative to HSPs (Kolhatkar *et al.* 2014). However, no changes were observed in TMAO levels in relation to control temperatures (Bockus *et al.* 2020). Although these responses appear far from widespread (Pegado *et al.* 2020a), exposure to ocean acidification conditions resulted in a reduction in HSP in the gills of the Whitespotted Bamboo Shark, along with increased levels of ubiquitin, suggesting an increase in irreversibly damaged proteins (Hanna *et al.* 2007; Lopes *et al.* 2018). However, Morash and colleagues (2020) found no significant changes in HSP70 activity in response to acute hypoxia, despite the close association between thermal and hypoxia tolerance recently described in sharks (Bouyoucos *et al.* 2020a, 2021). Studies have also found protective roles for HSPs under both hypo- and hyperosmotic conditions in species such as the Spiny Dogfish Shark (*Squalus acanthias*), juvenile Gummy Sharks (*Mustelus antarcticus*), and School Sharks (*Galeorhinus galeus*) (MacLellan *et al.* 2015; Morash *et al.* 2016; Tunnah *et al.* 2016). Further research regarding the processes of cross-tolerance is certainly warranted.

25.4.1.6 Oxidative Stress

Oxidative stress ensues when an organism's antioxidant machinery is overwhelmed by high levels of reactive oxygen species (ROS) and can be triggered by a wide range of environmental disturbances (Lesser 2006). Given sharks and their relatives' basal position in the vertebrate branch of the tree of life, they possess a remarkable antioxidant arsenal, featuring relatively highly active enzymatic antioxidants thought to be further supplemented by abundant non-enzymatic ROS scavengers, such as urea and glutathione (Lopes *et al.* 2018; Vélez-Alavez *et al.* 2015). Nonetheless, ocean warming has been shown to trigger lipid damage across tissues in the Brownbanded Bamboo Shark and, although there is little evidence of oxidative damage in response to ocean acidification in isolation (Lopes *et al.* 2018; Pegado *et al.* 2020a; Rosa *et al.* 2016a), the combined stress of elevated temperatures and elevated $p\text{CO}_2$ exacerbates neurooxidative damage, despite upregulation of antioxidant machinery (Rosa *et al.* 2016a). This highlights the importance of experimental designs that incorporate multiple stressors.

25.4.2 WHOLE ORGANISM LEVEL

25.4.2.1 Embryonic Development

Research on the effects of climate change on embryonic development of sharks and their relatives is limited to oviparous species. Development time, *in ovo*, is reduced under elevated temperatures, with effects documented across 28 species of temperate and tropical sharks, skates, and chimaeras to date (Wheeler *et al.* 2020). For example, when individuals of the Port Jackson Shark are reared at 3°C above ambient temperatures, they develop faster but still exhibit 100% survival rates to hatching (Pistevos *et al.* 2015). Faster growth rates and yolk consumption rates drive these faster hatching rates (Rosa *et al.* 2014; Wheeler *et al.* 2021). However, there is an upper critical temperature for development, where survival to hatching is greatly reduced by 30% to 60%; this temperature ranges from 3°C to 5°C above current-day water temperatures, and effects have been documented in Brownbanded Bamboo Shark, Epaulette Shark, and Little Skate (Di Santo 2015; Gervais *et al.* 2016; Rosa *et al.* 2014; Vila Pouca *et al.* 2019). Furthermore, embryonic metabolic rates initially increase under elevated temperatures (i.e., between 26°C and 30°C) (Rosa *et al.* 2014), but then significantly decrease when rearing temperatures are higher—between 18°C and 20°C (Di Santo 2015) or between 29°C and 31°C (Wheeler *et al.* 2021)—indicating a reduction in physiological performance with elevated temperatures. Studies investigating the effects of ocean acidification conditions on embryonic development report mixed effects (Di Santo 2015; Johnson *et al.* 2016; Pistevos *et al.* 2015; Rosa *et al.* 2014). Elevated $p\text{CO}_2$ does not impact development time or survival to hatching in Brownbanded Bamboo Shark, Epaulette Shark, or Port Jackson Shark (Johnson *et al.* 2016; Rosa *et al.* 2014). However, metabolic rates during the late stages of development and survival for 30 days post-hatch are reduced in Brownbanded Bamboo Shark reared under elevated $p\text{CO}_2$ conditions (Rosa *et al.* 2014). Synergistic effects of elevated temperature and $p\text{CO}_2$ have also been documented in Brownbanded Bamboo Shark and Little Skate during this vulnerable life stage, where elevated $p\text{CO}_2$ further exacerbates the impact that temperature has on growth, development, and survival (Di Santo 2015; Rosa *et al.* 2014). These profound effects across several species from both temperate and tropical latitudes highlight the impact that climate stressors have, especially during early life stages where individuals are already vulnerable (Dahlke *et al.* 2020) but also emphasizes the need to consider the role of developmental and transgenerational acclimation in future studies.

25.4.2.2 Neonates and Juveniles

When reared under future climate change conditions, the survival rates of neonates from various species continue to decline for 30 days post-hatch (Di Santo 2015; Gervais *et al.* 2016; Rosa *et al.* 2014). Neonates reared under future climate change conditions also hatch at smaller sizes (Di Santo 2015; Hume 2019; Rosa *et al.* 2014; Wheeler *et al.* 2021), feed exogenously more quickly, and consume more food (Di Santo 2015; Rosa *et al.* 2014; Wheeler *et al.* 2021) than their control condition counterparts. Specifically, when individuals of the Epaulette Shark are reared at 32°C, which is 4.0°C above ambient conditions, hatchlings exhibit a visible coloration and pattern disruption that does not reverse when hatchlings are returned to control temperatures (Gervais *et al.* 2016). Studies on neonate and juvenile stages of viviparous species, especially those that are larger bodied and occupy higher trophic levels within an ecosystem, are not usually able to rear animals under various climate change scenarios for entire life-history stages, as is possible with most oviparous species that have been investigated thus far. Indeed, studies of large-bodied carcharhinid sharks (e.g., Blacktip Reef Shark, Sandbar Shark) have focused only on neonates or juveniles that are amenable to captivity and experimental apparatuses such as respirometers. However, the Blacktip Reef Shark and Sandbar Shark have exhibited disparate responses to temperature. For example, neonates of the Blacktip Reef Shark did not exhibit measurable differences in metabolic rates when acclimated to 3°C above ambient conditions for 2 to 4 weeks (Bouyoucos *et al.* 2020a, 2020c); yet, the combination of end-of-century $p\text{CO}_2$ and elevated temperatures resulted in increased SMRs in some, but not all, individuals (Bouyoucos *et al.* 2020c). Conversely, metabolic rates were elevated and hypoxia tolerance decreased at temperatures associated with ocean warming in the Chesapeake Bay in juveniles of the Sandbar Shark (Crear *et al.* 2019). Metabolic responses to temperature increases differed between these studies, but neither species' activity, as measured by dynamic body acceleration, was affected by the elevated temperatures (Bouyoucos *et al.* 2020c; Crear *et al.* 2019). For viviparous species, only neonates of the Blacktip Reef Shark have been examined in the context of ocean-acidification–relevant (~1000 μatm) elevated $p\text{CO}_2$ conditions. Neonates of the Blacktip Reef Shark exhibit acute hematological responses to elevated $p\text{CO}_2$ (Rummer *et al.* 2020) but do not appear to exhibit behavioral (e.g., lateralization, foraging, activity levels) or physiological (e.g., hematology, metabolic rates, hypoxia tolerance) responses following 2 to 4 weeks of exposure to elevated $p\text{CO}_2$ (Bouyoucos and Rummer 2020; Bouyoucos *et al.* 2020c). Additional studies are clearly warranted to define responses of ram ventilating, viviparous, and large-bodied sharks to climate change stressors.

25.4.2.3 Adults

At the time of this analysis, no studies had yet assessed the effects of any climate change stressor on reproduction for any chondrichthyan species. Because of the large, mobile/migratory nature of the taxa, most species, particularly those using viviparous strategies, do not thrive and reproduce in captivity without large holding facilities and long durations. These logistical constraints make controlled laboratory experiments assessing the effects of future climate change conditions challenging. A limited number of studies indicate that environmental temperature, as in many other classes of vertebrates, is partially responsible for cueing and regulating reproduction in sharks and their relatives, as well (Elisio *et al.* 2019). The onset of the reproductive season and changes in reproductive morphology and physiology coincide with changes in water temperatures (Elisio *et al.* 2019; Heupel *et al.* 1999), and ocean warming could very well shift these processes. Viviparous females can behaviorally thermoregulate to occupy warmer areas to reduce gestation durations (Hight and Lowe 2007; Speed *et al.* 2012; Sulikowski *et al.* 2016; Wallman and Bennett 2006), and oviparous species have been documented depositing egg capsules in warmer areas to shorten development time *in ovo* (Salinas-De-León *et al.* 2018; Wheeler *et al.* 2020). These temperature-dependent traits could indicate that sharks and their relatives will be vulnerable to ocean warming; however, directed studies are lacking. Other climate change stressors, such as ocean acidification and hypoxia, and the synergistic effects on reproduction have not been studied. The exact implications climate change will have on reproduction in sharks and their relatives is still largely unclear, although it is hypothesized that demersal and/or oviparous species that typically do not undertake large movement patterns will be unevenly affected because they are unlikely to relocate to more favorable environments (Wheeler *et al.* 2020).

25.4.2.4 Behavior, All Life Stages

Changes in behavioral patterns in response to climate change stressors have been documented across several species of sharks and their relatives and across all life stages (Figure 25.3). When Small-Spotted Catsharks were exposed to elevated $p\text{CO}_2$ (993 μatm), they changed their nocturnal swimming from bursts to more continuous patterns and increased their lateralization (a metric commonly assessed in fishes with a T-maze to test changes in asymmetric behavior that is common in vertebrates) (Green and Jutfelt 2014). Odor tracking behaviors in the Dusky Smoothhound have been found to decrease under high $p\text{CO}_2$ scenarios (Dixson *et al.* 2015), and Port Jackson Sharks require more time to find food (Pistevos *et al.* 2015). On the other hand, elevated $p\text{CO}_2$ conditions do not result in changes in activity levels or foraging behaviors in the Epaulette Shark (Heinrich *et al.* 2015). Similarly, neonates of the Blacktip Reef Shark do not change their behavioral responses when exposed to an odor cue following 20 days of exposure to ~600 and 1000 μatm $p\text{CO}_2$ at ambient (~29°C) temperatures (Bouyoucos and Rummer 2020) or activity levels or lateralization following 7 to 13 days of exposure to ~600 and 1000 μatm $p\text{CO}_2$ at ambient (~28°C) and elevated (~31°C) temperatures (Bouyoucos *et al.* 2020c). Warming and acidification scenarios have been found to result in antagonistic effects on juveniles of the Port Jackson Shark, however, where increased temperature alone increases activity and feeding, but the addition of elevated $p\text{CO}_2$ negates this effect (Pistevos *et al.* 2017). Furthermore, juveniles learn to discriminate between two numbers to receive a positive stimulus more quickly and exhibit a higher proportion of correct choices under warming conditions when compared to their control counterparts, indicating that behavioral changes could alleviate some of the other negative climate change related impacts (Vila Pouca *et al.* 2019). The authors cite potential metabolic trade-offs (i.e., increased metabolic requirements increase the value of rewards) or changes in endocrine pathways that may underpin these results on the Port Jackson Shark (Vila Pouca *et al.* 2019). As mentioned earlier, the mechanistic underpinnings for these behavioral effects are still not well understood for each isolated stressor, let alone how they may be working synergistically, which is an area warranting further investigation.

25.4.3 Population and Ecosystem Levels

25.4.3.1 Persistence of Species and Populations

Understanding the patterns of within-species genetic diversity represents a priority to forecast which species and populations are more likely to be challenged by rapidly changing climate (Bennett *et al.* 2019). Although the genetic diversity of sharks and their relatives remains understudied (Domingues *et al.* 2018; Stein *et al.* 2018), the importance of intraspecific variation in climate change response has been underscored by controlled laboratory experiments, revealing varying responses to climate change conditions between locally adapted populations of both sharks and their relatives (Di Santo 2016; Gervais *et al.* 2021). Gervais *et al.* (2021) found that a cool-water population (Adelaide, Australia) of the Port Jackson Shark was more thermally sensitive, in terms of energetics, than a warmer water population (Jervis Bay, Australia). Di Santo (2016) found that juveniles of the Little Skate from southern locations (Georges Bank) exhibited a lower sensitivity to climatic stressors in terms of metabolic costs than their more northern counterparts (i.e., Gulf of Maine). These two findings alone suggest that there could be profound impacts associated with thermal history and highlight the importance of considering intraspecific variation in terms of thermal sensitivity.

Given the timeframe of human-induced climate change and cumulative action of other anthropogenic pressures, however, the *K*-selected life-history strategy typical of sharks and their relatives, with low fecundity and late maturation, limits their potential for gradual genetic adaptation (Chin *et al.* 2010; Rosa *et al.* 2017). In this context, the ability for sharks and their relatives to cope with a rapidly changing environment may greatly depend on their phenotypic plasticity. This shortcoming may, nonetheless, be buffered by epigenetic reprogramming and transgenerational acclimation (Ryu *et al.* 2018). Indeed, a case of rapid local adaptation in skates (namely, to regions with distinct temperature regimes) has been mostly attributed to changes in gene expression patterns rather than changes in allele frequencies (Lighten *et al.* 2016). As suggested by Lighten *et al.* (2016), this process may play an important role in the evolutionary success of this group, particularly in the context of their modest potential for adaptation, emphasizing the relevance of further research into the epigenetic processes underpinning phenotypic plasticity in chondrichthyans. Likewise, the potential for transgenerational acclimation, with or without an epigenetic basis, remains to be investigated in this taxonomic group and represents a challenging endeavor due to the logistics associated with reproduction and maintenance under laboratory conditions, yet it is a key avenue for future research.

25.4.3.2 Species and Populations on the Move

Patterns of habitat suitability and biodiversity distribution are predicted to change alongside ocean warming. In general, a poleward shift in species distribution limits is expected to occur in response to ocean warming, with mounting evidence indicating that this is already taking place across taxa, including some shark species (Bangley *et al.* 2018; Bennett *et al.* 2021; Hastings *et al.* 2020). Accordingly, several modeling studies forecast a poleward shift in habitat suitability for some pelagic sharks (Birkmanis *et al.* 2020a,b; Hobday 2010; Robinson *et al.* 2015). Overall range size is expected to disproportionally decrease for sharks and their relatives by the end of the century (Davies *et al.* 2017); however, effects are likely to differ across regions and species (Birkmanis *et al.* 2020a; Hazen *et al.* 2013). Nonetheless, even species bestowed with the potential for range expansion may have to cope with increased energetic costs associated with higher temperatures and shifts in prey availability (Birkmanis *et al.* 2020a,b; Sunday *et al.* 2015). It is also worth considering that, in addition or alternative to latitudinal shifts in distribution, sharks and their relatives may also exploit vertical temperature gradients, seeking refuge in deeper waters (Andrzejaczek *et al.* 2018; Beaugrand and Kirby 2018; Birkmanis *et al.* 2020b). Although temperature represents one of the most influential factors, many other abiotic factors influence movement in sharks and their relatives, including pH and O_2, and are expected to change in response to climate change (Bindoff *et al.* 2019; Schlaff *et al.* 2014). Indeed, the expansion and shoaling of O_2 minimum zones is expected to result in a compression of vertical habitat for pelagic species, including large and already vulnerable sharks, with consequences for predator–prey dynamics and susceptibility to fisheries (Gilly *et al.* 2013; Stramma *et al.* 2012; Vedor *et al.* 2021).

Climate change may further influence shark distribution patterns indirectly through its influence on biotic factors—namely, prey availability, competition, and predator pressure (Schlaff *et al.* 2014). As typically high-ranking predators, sharks and their relatives may also be indirectly impacted by climate change, regardless of their own physiological capacity, because of the effects on lower trophic levels. In other words, it may not just be the predator that is affected, but the prey may also be affected; yet, the effects may be asymmetrical. Accordingly, ecosystem models suggest that the effects that factors related to climate change have over lower trophic levels may trickle into effects over sharks and their relatives. For example, under climate change, models suggest that primary production of lower trophic levels (e.g., phytoplankton and benthic producers) can affect fisheries catch and value, the biomass of animals that are of conservation interest, and community composition (Booth *et al*., 2019; Brown *et al.* 2010). In another study modeling the potential future (i.e., 2040) impacts of fishing and ocean acidification, additive, synergistic, and antagonistic effects were determined (Griffith *et al.* 2011). The greatest impacts were predicted to be on the demersal food web, with fishing impacting predation and acidification affecting benthic production, but ultimately also an overall restructuring of both pelagic and demersal food webs as a result (Bascompte *et al.* 2005; Griffith *et al.* 2011). Other studies modeling the effects of decreases in pH related to ocean acidification (e.g., 0.2-unit drop in pH) found wide-ranging magnitudes of effects, with the most dramatic direct effects being found on epibenthic invertebrates (e.g., crabs, shrimps, benthic grazers, benthic detritivores, bivalves) and strong indirect effects on demersal fishes, including sharks, and epibenthic invertebrates (e.g., dungeness crab, *Metacarcinus magister*), likely because they consume pH-sensitive species (Marshall *et al.* 2017). Indeed, the presence and direction of change vary across models, study regions, and factors at play (Brown *et al.* 2010; Griffith *et al.* 2011; Marshall *et al.* 2017).

At a smaller but crucial scale, suitable habitat for juveniles of the Sandbar Shark in a nursery area has been projected to decrease horizontally, but increase vertically (Crear *et al.* 2020). Meanwhile, field observations have also documented the Bull Shark (*Carcharhinus leucas*) expanding its nursery range over the first couple decades of the 21st century in association with increasing temperatures and salinity, with potential consequences for community structure and human-shark interactions (Bangley *et al.* 2018). Similar trends may, nonetheless, not hold true across species and locations. In fact, often located in coastal shallow waters and estuaries, these critical nursery habitats are particularly vulnerable to extreme climate change impacts (Chin *et al.* 2010; Heupel *et al.* 2007; Matich and Heithaus 2012; Matich *et al.* 2020). Hence, targeted research regarding the effects of climate change over nursery areas represents a research priority.

Phenological cycles and seasonal patterns of distribution are also likely to be affected by climate change (Anderson *et al.* 2013; Cohen *et al.* 2018). Poleward shifts in distribution mean that animals will experience different light and temperature cycles (Servili *et al.* 2020), both known to play a central role in phenological processes, with potential consequences for the onset of migrations and reproduction (Grubbs *et al.* 2007; Hazen *et al.* 2018; Mull *et al.* 2008).

25.4.3.3 Coping with Extremes

In addition to persistent trends in abiotic and biotic drivers, extreme events also have a strong influence on movement in sharks and their relatives. Flight responses have been documented in the context of tropical storms (Gutowskey *et al.* 2021; Heupel *et al.* 2003; Strickland *et al.* 2020; Udyawer *et al.* 2013), possibly in response to changes in barometric pressure (Heupel *et al.* 2003). The onset of this response appears to be species specific, likely related to depth use and tolerance levels of the species (Udyawer *et al.* 2013). Moreover, this aversion behavior appears to be innate (Heupel *et al.* 2003; Udyawer *et al.* 2013); however, the time until response appears to vary considerably between individuals, with late responses possibly associated with mortality (Strickland *et al.* 2020), which is of considerable importance as tropical storms become more pervasive (Cai *et al.* 2015; Collins *et al.* 2019; Kossin *et al.* 2014, 2016; Krauss *et al.* 2020). Flight responses have also been reported in response to temperature extremes (Matich and Heithaus 2012), and observations beyond species' typical ranges have been reported in the context of marine heatwaves (Pearce *et al.* 2011; Pearce and Feng 2013). In the study by Matich and Heithaus (2012), later analyses suggested that the flight responses were almost ubiquitously unsuccessful, perhaps resulting in 100% mortality and a near complete reset in the nursery area (Matich *et al.* 2020). Although responses to extreme acidification and hypoxic events have not been specifically studied in sharks and their relatives, these phenomena are likely to influence behavior and movement patterns (Schlaff *et al.* 2014; Vedor *et al.* 2021). Temporary relocation may allow them to escape the adverse conditions, but this response should become increasingly more expensive as climate change advances and these events become more ubiquitous, particularly in species and ontogenetic stages strongly bound to specific coastal habitats (Chin *et al.* 2010; Heithaus 2007; Schlaff *et al.* 2014). However, given that the magnitude of these events is expected to increase, the overall risk associated with keeping position also increases, placing more pressure on this ecological trade-off (Schlaff *et al.* 2014). Indeed, there have been circumstantial reports of mortality in the context of hurricanes (Strickland *et al.* 2020), marine heatwaves (Roberts *et al.* 2019), cold snaps (Matich and Heithaus 2012; Matich *et al.* 2020), and hypoxic events (Hernández-Miranda *et al.* 2010). On the other hand, relatively stable catches have been reported for Tiger Sharks (*Galeocerdo cuvier*) in a marine heatwave context (Nowicki *et al.* 2019). The latter study further highlighted the trophic level and diet flexibility dependency of species' responses to these events, a finding that should lead to further *in situ* research into how extreme events may affect sharks and their relatives. Moreover, controlled studies with more targeted designs, considering the regional specificities of these events in terms of magnitude, natural fluctuations, and overall timeframe, are key to understanding the processes behind the real-world impacts of these events and in improving mitigation potential of management measures.

25.5 IMPLICATIONS FOR ECOSYSTEM SERVICES AND CONSERVATION

Although not the most imminent threat to chondrichthyans and only recognized as a threat in the first decade of the 21st century, climate change has the potential to amplify the effects of fisheries and habitat degradation (Dulvy *et al.* 2014; Vedor *et al.* 2021; Ward-Paige *et al.* 2012). Moreover, the efficacy of conservation measures may also be undermined under climate change. For example, sharks and their relatives are expected to lose coverage under the current set of large marine protected areas (Davies *et al.* 2017). Likewise, shifts in distribution patterns and range retractions may impact the revenue obtained through fisheries and tourism directly, given this group's economic value (Gallagher and Hammerschlag 2011; Hammerschlag *et al.*, 2019; Kendrick *et al.* 2019), and indirectly, given their potential to modulate community response through top–down pressure (Estes *et al.* 2016; Ferretti *et al.* 2010; Heithaus *et al.* 2010; Nowicki *et al.* 2019, 2021; Wild *et al.* 2019; see also Chapter 15). On the other hand, climate change may also potentiate negative interactions with humans, as species historically perceived as "dangerous" move into new areas (Bangley *et al.* 2018; Chapman and McPhee 2016).

Sharks and their relatives may also play an important role in the fight against the looming threat of climate change. One up-and-coming topic is blue carbon ecosystems. Both understanding the threats that sharks and their relatives face with climate change and determining appropriate conservation strategies for sharks and their relatives contribute to preserving coastal ecosystems and the larges stores of carbon in the soils that might otherwise be released as CO_2. For example, the delicate balance between sea turtles and seagrass communities that is necessary to avoid ecosystem collapse relies on intact shark populations (Heithaus *et al.* 2014). The study by Heithaus *et al.* (2014) and other studies suggest that marine predators help to protect carbon stocks in blue carbon ecosystems, such as coastal communities and coral reefs (Atwood *et al.* 2015, 2018). Indeed, as charismatic organisms, with an underlying societal and cultural value, and concrete evidence of impacts related to climate change factors (Atwood *et al.* 2015, 2018; Heithaus *et al.* 2014; Nowicki *et al.* 2021; Pistevos *et al.* 2015; Rosa *et al.* 2014, 2017; Vedor *et al.* 2021), this group represents a great flagship for public engagement in the climate change crisis and an umbrella for the conservation of marine biodiversity in a rapidly changing future (Jepson and Barua 2015).

25.6 SUMMARY AND CONCLUSIONS

The evolutionary history of sharks and their relatives spans a geological time frame extending back roughly 450 million years. Over the course of their evolutionary history, species have experienced warming and cooling periods. Species have experienced atmospheric and therefore ocean CO_2 levels by far exceeding current-day conditions, as well as periods where O_2 levels exceeded current-day (>21%) conditions and periods of hypoxia, not to mention five major mass extinctions. This would collectively suggest a robust evolutionary history that would also be robust to future environmental change as well. However, as a scientific community, and as has been demonstrated here via meta-analysis and literature synthesis, it is clear that the rate at which various habitat conditions are changing today, and have since pre-Industrial times, as well as the increased frequency and severity of extreme environmental events, keep sharks and their relatives at a heightened risk when it comes to climate change, especially when other stressors, such as fishing pressure and habitat loss, are considered (Hyatt *et al*., 2018). However, it is also clear that some species (e.g., Epaulette Shark) and life stages (e.g., neonate reef sharks) already occupy habitats that exhibit challenging conditions. Although not necessarily analogous to future climate scenarios, findings from controlled laboratory studies on these species and life stages can help elucidate which traits may be most important in sustaining species and populations over the long term. Indeed, creating robust, trait-based models is likely the best approach to predicting the responses of sharks and their relatives to the no-analog future conditions caused by climate change. Responses of individuals can also be scaled up using current models to provide population- and community-level predictions; yet, elucidating community consequences related to changes in shark populations remains challenging outside of a small number of taxa and conditions.

25.6.1 ASSESSING CHANGES IN THE CONTEXT OF UNCERTAINTY

Research into the effects of climate change on sharks and their relatives is challenging on multiple fronts (e.g., logistical constraints to controlled experiments, challenging field research, paucity of genetic information, limited data availability for modeling), and timely assessments of species' vulnerability may be achieved through assumptions based on relatively broad life-history traits reasoned to moderate species' responses to climate changes (Albouy *et al.* 2020; Chin *et al.* 2010; O'Brien *et al.* 2013). Indeed, biological and ecological parameters have been used to predict patterns of extant genetic diversity across species against a context of past climate changes (O'Brien *et al.* 2013; Stein *et al.* 2018). Hence, traits associated with a species' ability to move or rebound from perturbations, along with their degree of environmental specialization, regarding both diet and habitat, should allow us to gauge a species' intrinsic sensitivity to future environmental change. Also, information on habitat use and projections regarding factors related to climate change provide the grounds to assess exposure at regional and global scales (Albouy *et al.* 2020).

As mentioned earlier, the only risk assessment of sharks and their relatives' vulnerability to climate change was conducted in the first decade of the 21st century and was restricted to the Great Barrier Reef (Chin *et al.* 2010). Considering the available literature, those authors identified and integrated species-specific traits that influence species' sensitivity or adaptive capacity regarding near-future conditions, along with factors related to climate change with the potential to impact sharks and their relatives, evaluating the exposure of key ecological groups across the different factors. Under the proposed framework, 30 of the 133 species evaluated were categorized as "Vulnerable." Species associated with freshwater or estuaries, along with coastal and reef systems, rank higher with respect to climate change risk; however, acknowledging the challenges associated with quantifying large-scale impacts of each driver, current advances in the literature suggest that the effects of ocean acidification may have been underestimated (Marshall *et al.* 2017; Rosa *et al.* 2017). Moreover, deoxygenation, in the form of either long-term O_2 depletion or an increase in hypoxic events, was not included as a stress driver, despite its potential to greatly impact biological responses (Sampaio *et al.* 2021). Nevertheless, the study by Chin *et al.* (2010) provided the early grounds for management and research priorities and represents a precious steppingstone toward the scalable assessment of chondrichthyan vulnerability in a climate change context. Moreover, the interplay between climate change drivers and the importance of a species' ecological context was highlighted. Given the current rate of climate change and the massive parallel pressures that challenge the conservation of sharks and their relatives, the application of similar frameworks at both regional and global scales represents a priority in informing assertive conservation measures.

25.6.2 HORIZON SCANNING, MOVING FORWARD

What is clear from the analyses to date is that, although climate change stressors must first be understood in isolation, conclusions as to how species, populations, and ecosystems will be affected by climate change can only be drawn if multiple climate change stressors are investigated together. Great efforts have been made to determine the effects of elevated temperatures, elevated $p\mathrm{CO}_2$, and deoxygenation on sharks and their relatives, but most studies have indeed focused on a single stressor. Granted, this becomes complicated when investigating an array of species with diverse life-history strategies, across an array of life-history stages where some stages may be inherently more vulnerable than others, and across an array of traits spanning various levels of biological organization where trade-offs may exist between, for example, one performance trait in order to safeguard another (Boyd *et al*., 2018). Effects of multiple climate change stressors can be synergistic or antagonistic; therefore, if extrapolations are made based on the effects of just one stressor, then whole organismal, species, populations, and even ecosystem-level responses can be grossly underestimated or misrepresented. Multiple-stressor experiments are the next step in predicting the impact of future climate change on the performance and therefore survival of sharks and their relatives.

Also perhaps overlooked in studies investigating the effects of climate change stressors on multiple traits and/or levels of organization is the variation in responses among individuals (Sunday *et al.* 2011). Many overarching predictions are based on the average response of a population, which can often mask the sometimes extreme variability in how individuals respond. This is even evident in the outcome of our meta-analysis, where at a glance it would appear that there is no net effect of any climate change stressor or the combination of ocean warming and acidification on traits from nearly all seven categories across all life-history stages of species that have been investigated to date, but that is simply not true. Identifying winners and losers and determining a species' capacity for adaptation in the face of global change are crucial but, especially in the case of winners, can be detrimental to climate change abatement by giving a false sense that species will thrive despite adverse conditions. Indeed, without basic information on genetic variation in fitness-associated traits, it is not possible to make informed decisions about the impacts of climate change stressors on populations of sharks and their relatives over the timeframes in which environmental conditions in their habitats are changing. Between-generation studies are not as feasible in chondrichthyans when compared to studies on teleost fishes, largely due to the long generation times of most species of sharks and their relatives. This makes it difficult to determine parental and transgenerational effects, but developmental plasticity is still possible to assess for many species, especially the well-studied, benthic oviparous species. Yet, more studies are needed to truly disentangle transgenerational effects from developmental plasticity, and modern molecular methods will help in identifying the mechanistic basis for within and between generation plasticity, as well.

It is also key to understand how selection acts on variation in traits. Which traits and which variations among traits are heritable? This has been well studied with respect to fitness-related traits that are influenced by elevated temperatures (Rummer and Munday 2017) and elevated CO_2 (Munday *et al.* 2019), but not in combination and not necessarily under climate change–relevant conditions in sharks and their relatives. Correlations between, for example, behavioral traits and those more closely aligned with physiological traits can play a role in facilitating or limiting adaptive potential. The importance of investigating multiple traits simultaneously was highlighted earlier in this chapter, but here, within the context of selection, it is ever more important. For example, if two traits are positively correlated, then selection can act unimpeded on the population by acting in the same direction as the most variation in the population (Munday *et al.* 2013). However, if two traits are negatively correlated, then selection may act orthogonally in the direction of the most variation in the population, which may result in limited influence on a population. This is because selection for one trait will decrease performance in the other and vice versa (Sunday *et al.* 2014). Describing this relationship between traits can therefore aid in predicting whether selection can act freely on a population or will be constrained, thus limiting species' ability to adapt to future conditions. Thus, identifying correlations among key traits is an important step in predicting species persistence in the face of climate change (Munday *et al.* 2019; Sunday *et al.* 2014). Sensitivity analyses and evolutionary rescue models have been used exhaustively for terrestrial species and populations, but they have not yet been used for chondrichthyan populations; yet, incorporating such evolutionary and environmental parameters may prove useful in predicting how populations will respond to global climate change and is an area worthy of more thorough investigation.

Finally, and perhaps especially for chondrichthyan species specifically, because it is not reasonable to investigate a wide range of species, life-history strategies, habitat preferences, and geographic distributions to make generalizations as to how sharks and their relatives will respond to global climate change, candidate and bioindicator species will be key. Such species, including many that have been discussed in this chapter and especially those that are not precluded by logistics (e.g., large size, migratory patterns) and are amendable to controlled laboratory conditions, will be important in moving forward in understanding the effects of climate change on this important vertebrate taxon. Candidate species will also be key for developing new molecular tools and testing some of the important evolutionary questions that will be crucial to answer in order to make better predictions as to the winners and losers and the species with and without adaptive capacity under future climate change conditions.

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APPENDIX. APPROACH AND METHODOLOGY

This chapter considered mixed-effects model outputs upon testing the effects of ocean warming, ocean acidification, or the combination for seven different response categories. A meta-analysis was performed on ocean warming, acidification, and the combined effects on sharks and their relatives. Data were collected until February 2021 from all studies that specifically investigated climate change effects (ocean warming, ocean acidification, and combination effects) on sharks and their relatives. At the time of this analysis, no study had investigated ocean deoxygenation within the context of climate change, so this climate change stressor was omitted from the meta-analysis. Moreover, studies that assessed temperature or $p\mathrm{CO}_2$ effects, but not specifically climate change–relevant scenarios (i.e., IPCC), were also excluded. Within each study that was selected for the meta-analysis, the mean, variance, and sample size for each trait examined were extracted for the control and highest treatment groups. For example, if a study used 27°C as a control and both 29°C and 31°C for climate change–relevant experimental conditions, only data from the 27°C and 31°C treatments were used.

Individual traits were grouped into seven categories: (1) behavior (e.g., lateralization, changes in swimming and feeding behavior); (2) body condition (length, mass, condition factor); (3) cellular/molecular (e.g., blood parameters, tissue enzyme activities); (4) development (for oviparous species within egg cases, such as time developing *in ovo*, time to hatch, growth rates); (5) hypoxia tolerance (e.g., critical O_2 tensions, critical saturation minima); (6) metabolism (e.g., estimates of standard, routine, and maximum metabolic rates; aerobic scope; recovery from exercise; ventilation rates); and (7) survival (upon acute and chronic exposure). Reported variances from studies (standard errors of the mean, 95% confidence intervals, and interquartile ranges) were standardized to standard deviation. If the mean and variance were not specifically reported in a study, values were extrapolated from figures using ImageJ (Schneider *et al.* 2012).

Data were first analyzed using the escalc function in the metafor package (Viechtbauer 2010) in R (R Foundation for Statistical Computing, Vienna, Austria) to calculate the standardized mean difference and variance between the control and elevated treatment for each trait. Then, the multivariate/multilevel linear (mixed-effects) model function (rma.mv) was applied. Trait category (the seven listed above) was included as a moderator. Study number and individual data point number were both included as random effects to account for variation in methodologies and treatments between studies and pseudo-replication from using multiple traits within a study. Caterpillar plots were produced from modifications of the caterpillar plot function in the package OrchaRd (Nakagawa *et al.* 2020). The coefficients of heterogeneity (I^2) indicate high heterogeneity within each overall model and between studies, which likely represents differences among study methodologies, species, respiratory styles, and life histories (Senior *et al.* 2016). However, the intra-study I^2 values were low, indicating low heterogeneity within individual studies.