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# Sharks and their relatives: can their past help predict their future?

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Elasmobranchs (i.e., sharks, skates, and rays) have survived five mass extinction events and changed relatively little throughout their ~450-million-year evolutionary history. Therefore, elasmobranchs may provide critical evolutionary perspectives on how species and populations can elicit phenotypic plasticity and adaptation responses to climate change. Unfortunately, despite their roles as critical apex- and meso-predators, most elasmobranch species are considered to be highly vulnerable to the impacts of fisheries exploitation and climate change, which is compounded by their Kselected life history strategies. Furthermore, the future of elasmobranchs is uncertain at best in the face of anthropogenic climate change because there have only been a handful of studies that have directly investigated the effects of climate change related stressors. Phenotypic plasticity in response to climate change, specifically ocean warming, may be a species' best chance of resilience given the expedited rate of environmental change. However, despite extensive research on plasticity within and across generations in teleost fishes, there remains a knowledge gap for elasmobranch species, owing to their extended life spans and delayed sexual maturity. Here, we present four case studies on different elasmobranch species to lend perspectives on the capacity for phenotypic plasticity within the context of ocean warming. Furthermore, we discuss potential research avenues and modern technologies that may enable future investigations to empirically explore the capacity for phenotypic plasticity in elasmobranchs.

### KEYWORDS

plasticity, adaptation, elasmobranch, climate change, physiology

## **1** Introduction

Redistribution to optimal thermal habitats and phenotypic plasticity and/or adaptation to maintain performance and fitness have been documented as the primary means to circumvent climate change (Donelson et al., 2019; Vilmar and Di Santo, 2022). The ability of a species to employ these processes is often considered in relation to their ecology, with movement and

connectivity playing a substantial role. For example, some level of mobility will be required for species to take advantage of redistribution and range shifts (Bates et al., 2014). Furthermore, movement of individuals may allow rapid response to environmental change and even maintain stable internal conditions (i.e., behavioral thermoregulation; Papastamatiou et al., 2015). For site-attached species, the capacity for physiological plasticity is key to responding to environmental change (Fox et al., 2019). Whereas phenotypic plasticity is the ability of individual genotypes to produce various phenotypes (Ghalambor et al., 2007), adaptation is a population level process by which a species increases its fitness and is the result of natural selection acting upon heritable variation over two or more generations (Fraser et al., 2011). How adaptation has occurred in the past can help predict future responses. For example, whether local adaptation to historical conditions has occurred, as determined by selective forces and connectivity between diverse habitats, may influence the capacity for future adaptation.

Elasmobranch fishes (i.e., sharks, skates, and rays) have changed relatively little throughout their ~450-million-year evolutionary history and have survived the world's five mass extinction events (Kriwet et al., 2008); consequently, using the past to predict the future may be highly relevant for these species. Unfortunately, there have been only a few studies on elasmobranchs within a climate change context (Rummer et al., 2022), and even fewer have directly assessed phenotypic plasticity of physiological traits within these species (Tullis and Baillie, 2005; Rytkönen et al., 2012; Devaux et al., 2019). This paucity of information highlights critical knowledge gaps in understanding how elasmobranchs will respond to future climate change. This is particularly concerning, considering the vital roles that elasmobranchs fulfill as apex- and meso-predators within the world's marine ecosystems. To lend perspective, we first lay the theoretical foundation for phenotypic plasticity as a response to environmental change, outline types of plasticity, and discuss conditions under which they are expected. We then explore how the expectations of plasticity types relate to elasmobranch ecology, utilizing a series of case studies to highlight species that may fit various plasticity expectations under ocean warming. Following this, we utilize the knowledge base of physiological plasticity from teleost fish studies to lend perspective on how physiological plasticity may occur within elasmobranchs and suggest future research initiatives for this taxon.

## 2 Phenotypic plasticity

For many species, plasticity is expected to play a significant role in persistence, because the rate of environmental change is likely to surpass the rate at which many species may be able to adapt (Visser, 2008). The nature of environmental heterogeneity and predictability influences whether and what type of plasticity occurs, including the magnitude, duration, and thresholds of environmental cues that elicit plastic responses. There are three primary forms of phenotypic plasticity: reversible plasticity (RP), developmental plasticity (DP), and transgenerational plasticity (TGP) (Leimar and McNamara, 2015; Donelson et al., 2019); however, these forms are not mutually exclusive. Here, we define TGP as an inclusive term (including carryover effects and parental effects) that does not require the interaction between past and current generation conditions (Bonduriansky et al., 2012). RP is a shift of performance within a relatively rapid temporal period in response to environmental variability (Beaman et al., 2016). Most RP responses reflect acclimation processes that occur from seasonal and/or diel variation and indicate the organism's capacity to revert to previously experienced environmental conditions (Angilletta, 2009). RP is likely to be important in longer-lived species where environmental cues in early life or past generations may not be relevant for current environmental conditions (Munday et al., 2013). DP generally occurs in response to environmental conditions experienced during prezygotic to early juvenile developmental periods (Beaman et al., 2016). Moreover, DP is often expected when thermal environments are heterogenous, intergenerationally (Angilletta, 2009). TGP is expected to occur when conditions also vary intergenerationally but requires environmental predictability between generations. Methods of transfer can include nutrients, hormones, and mRNA (Angilletta, 2009), and TGP can occur in response to conditions experienced in the parent and previous generations. This need for predictability between generations can result in TGP being highly sensitive to the timing, duration, and magnitude of environmental influences experienced by past generations to establish beneficial phenotypes for the offspring's environment (Munday et al., 2013; Donelson et al., 2018). Two crucial ontogenetic stages to facilitate TGP are the periods from fertilization to early development and the period centered around reproduction, because embryonic cells are more sensitive to environmental factors and have higher rates of epigenetic changes during these time periods (Burton and Metcalfe, 2014; Fawcett and Frankenhuis, 2015).

## 3 Plasticity for elasmobranchs

Previous studies on the potential for phenotypic plasticity in elasmobranchs have mainly focused on small, benthic species (e.g., Hemiscyllium ocellatum), particularly in relation to hypoxia/anoxia (Dowd et al., 2010; Hickey et al., 2012; Devaux et al., 2019); however, studies related to how these species compensate physiological traits to thermal changes in the context of climate change context are lacking. The thermal sensitivity of elasmobranchs and, consequently, the potential need for plasticity were reviewed by Pereira-Santos and colleagues (2021) and provided an overview of responses and knowledge gaps. This synthesis suggests that ocean warming will negatively affect elasmobranchs, regardless of climatic region, taxonomic order, lifestyle, or reproductive mode (Pereira-Santos et al., 2021). Some traits exhibit consistent patterns with warming, such as reductions in development time or increases in feeding, digestion, and metabolic rates (Papastamatiou et al., 2015; Wheeler et al., 2021). However, the eclectic range of effect size responses indicates that substantial diversity in thermal sensitivity exists (Pereira-Santos et al., 2021), and, for many species, plasticity will be critical.

Elasmobranchs are generally K-selected life history strategists and thus long-lived, slow-growing, sexually mature at a late age; have long reproductive cycles; and produce few, high-quality offspring (Conrath and Musick, 2012). As the oldest living vertebrates on Earth (Edwards et al., 2019), RP would seemingly be beneficial as individuals are likely to experience environmental change within their lifetime (Beaman et al., 2016). In addition, many species exhibit large home-ranges and migrations resulting in high potential for behavioral plasticity to optimize performance (Payne et al., 2018). This can arise in the form of behavioral thermoregulation, such as for whale sharks Rhincodon typus partitioning their time between the surface and deep water to allow behavioral warming at the surface (Thums et al., 2013). Alternatively, frequent movements can coincide with physiological capacity to thrive across a range of environmental conditions (e.g., bull shark Carcharhinus leucas; Huepel and Simpfendorfer, 2008). For species that exhibit site fidelity, environmental variation (i.e., range and stochasticity) relative to thermal performance will dictate whether physiological plasticity is necessary. Although most elasmobranchs are long-lived, some species have a maximum life expectancy of <20 years, similar to teleosts in which DP and TGP occur (Mejía-Falla et al., 2014). The key consideration is whether intergenerational shifts in environmental conditions are predictable to yield TGP or DP, but high levels of environmental stochasticity could instead result in bet-hedging (Shama, 2015). In the following, we outline four examples of species' characteristics and expected plasticity outcomes in response to ocean warming.

### 3.1 Expected reversible behavioral plasticity

The tiger shark (Galeocerdo cuvier; Figure 1A) is a highly mobile species that is globally distributed throughout tropical and temperate latitudes (Papastamatiou et al., 2013). As such, temperature drives their movement patterns and abundance (Ferreira et al., 2015; Dicken et al., 2016). Indeed, mechanistic distribution models based on abundance, performance and movement data suggest 22°C as a persistent thermal optimum (Pavne et al., 2018). Data from two satellite-tagged individuals lends further evidence of long-term behavioral thermoregulation in this species, given that they maintained 22°C year-round across 14° of latitude (Holmes et al., 2014; Payne et al., 2018). G. cuvier occasionally inhabit temperatures outside this thermal optimum in exchange for increased access to preferred prey, such as green sea turtles (Fitzpatrick et al., 2012). As the oceans warm, G. cuvier represents an example of behavioral plasticity, given that movements coincide with thermal gradients that optimize performance. Many elasmobranchs behaviorally thermoregulate to similar extents, and future expectation for such species would be poleward shifts and exploitation of thermal depth or current refuges (Papastamatiou et al., 2015). The risk for these species is if the environment shifts beyond their capacity to use behavior to maintain optimum body temperatures, as they likely lack capacity for physiological plasticity (Logan et al., 2019).

# 3.2 Expected reversible physiological plasticity

The epaulette shark (Hemiscyllium ocellatum; Figure 1B) is endemic to the Great Barrier Reef and coastal waters of northern Australia (Wise et al., 1998). This species is physiologically robust to low oxygen conditions (1.55 mg O<sub>2</sub> L<sup>-1</sup>; Wise et al., 1998), elevated carbon dioxide (880 µatm; Heinrich et al., 2014; Heinrich et al., 2016), and thermal variation (Gervais et al., 2018; Wheeler et al., 2022), likely because of the environmental fluctuations that it routinely experiences in the shallow reef flats it inhabits. H. ocellatum encounters dramatic daily temperature fluctuations on a diurnal and seasonal basis (12°C; Potts and Swart, 1984). The lack of long-distance locomotor capabilities to pursue optimal thermal habitats and the relatively extreme environmental variability experienced would suggest high thermal tolerance and capacity for physiological plasticity as adults, which can be utilized in response to ocean warming (Nay et al., 2021). Some of these plastic responses may include compensation of metabolic traits, blood-oxygen carrying capacity, and mitigation of reactive oxygen species. Indeed, H. ocellatum has previously been observed to exhibit RP outcomes through compensatory mitochondrial and metabolic adjustments in response to hypoxic and/or anoxic stress (Dowd et al., 2010; Hickey et al., 2012; Rytkönen et al., 2012). The potential for DP within this species seems less likely, as acute warming conditions of 31°C during embryonic development resulted in reduced embryonic growth, decreased metabolic performance, and reduced size and body mass post-hatching (Wheeler et al., 2021). However, this sensitivity might also indicate that embryonic development occurs under more stable thermal conditions (e.g., reef crest, deeper depths) during the austral summer months (Huepel and Bennett, 1998; Wheeler et al., 2021).

### 3.3 Expected reversible behavioral plasticity and/or transgenerational plasticity

The blacktip reef shark (Carcharhinus melanopterus; Figure 1C) inhabits shallow coral reefs, sand flats of atolls, and high islands, and, occasionally, non-reef environments throughout the western Indo-Pacific (Mourier et al., 2013). Whereas C. melanopterus regularly exhibits site fidelity (8-12 km<sup>2</sup>; Papastamatiou et al., 2010), some coastal populations undergo larger movements to adjacent coastal habitats including offshore reefs (Chin et al., 2013; Mourier et al., 2013). This level of mobility allows some behavioral thermoregulation (Papastamatiou et al., 2015) but is not expected to result in perfect thermoregulation due to relatively high thermal safety margin in neonates (~6°C) above the summer average conditions (Bouyoucos et al., 2018; Bouyoucos et al., 2021). Species that entirely rely on behavioral thermoregulation are expected to maintain a relatively narrow thermal window; consequently, such species would likely be living close to their upper thermal limits.



Ontogenetic movements of C. melanopterus generally consist of heavily localized males and females mating during the summer and early autumn months, presumably within deeper fore reef environments (Chin et al., 2013) after which adult females shift to lagoons and remain for the 8-to 11-month gestation period (Mourier and Planes, 2013; Mourier et al., 2013). Upon parturition, neonates remain in the warmer, thermally variable lagoon nursery areas for the first years of development before moving to cooler, deeper fore reefs (Mourier et al., 2013). Shifts due to ontogeny or environmental conditions make DP less likely. Neonates and juveniles endure challenging habitat conditions in exchange for protection from predators (Knip et al., 2010; Bouyoucos et al., 2018; Bouyoucos et al., 2020; Bouyoucos et al., 2022). However, the high site fidelity and extended exposure of mother, embryos, and neonates to the same environmental conditions could create predictability between generations, thus promoting potential for TGP (Mourier and Planes, 2013; Beaman et al., 2016).

# 3.4 Expected reversible behavioral plasticity, possibly developmental, and/or transgenerational physiological plasticity

The Atlantic stingray (*Hypanus sabinus*; Figure 1D) is a euryhaline, viviparous species that resides predominately within western Atlantic inshore estuaries (Snelson et al., 1988). Adults and juveniles can inhabit inshore estuaries year-round and have profound physiological thermal tolerance, enduring temperatures from 0.7°C to 43°C (Fangue and Bennett, 2003; Wallman and Bennett, 2006). Pregnant females behaviorally thermoregulate during gestation to expedite embryonic development, preferring warmer temperatures (~26.1°C) than their non-pregnant counterparts that prefer 0.8°C cooler (Wallman and Bennett, 2006). Mating occurs during the spring, and parturition occurs during late summer (Snelson et al., 1988). Occasionally, *H. sabinus* may seasonally migrate to deeper, offshore waters during winter months (Snelson et al., 1988), likely indicating sub-optimal coastal temperatures during these time frames. Although *H. sabinus* has some capacity for behavioral thermal plasticity, it is unlikely sufficient to keep pace with the rate of climate change, especially given these highly variable shallow habitats can fluctuate  $\sim 10^{\circ}$ C daily. Because *H. sabinus* can either reside in the same estuaries, creating predictability between generations, or migrate offshore, creating possible variation between generations if not returning to the same estuaries, TGP and DP may be possible as thermal conditions shift beyond optimal.

# 4 Mechanisms of physiological plasticity

Behavioral thermal plasticity influences environmental conditions experienced by individuals and thus acts upon lower levels of biological organization. Under future circumstances where behavior can no longer keep pace with environmental change or for less mobile species, physiological plasticity becomes critical. For elasmobranchs that employ physiological plasticity, preliminary studies investigating phenotypic plasticity in response to other environmental stressors as well as knowledge accumulated on potential mechanisms from teleost fishes can direct future research. At the organismal level, metabolic rates represent all processes encompassing the acquisition of energetic resources from the environment, assimilation, and utilization for fitness-enhancing processes, ultimately forming the mechanistic link between an organism's fitness and environmental resources (Brown et al., 2004). Despite intrinsic links to the functional energetic capacity of organisms, high degrees of intraspecific phenotypic flexibility of metabolic rates in response to the environment remain (Norin and Metcalfe, 2019). For example, when exposed to warming, barramundi (Lates calcarifer) individuals with originally depressed metabolic attributes at control temperatures elicited greater reversible thermal plasticity at elevated temperature when compared to individuals initially exhibiting elevated metabolic attributes (Norin et al., 2016). Multi-generational research on a coral reef damselfish, Acanthochromis polyacanthus with limited dispersal ability, and thus possibly high environmental predictability between generations, suggests high capacity for TGP and mild DP of aerobic metabolism (Donelson and Munday, 2012). It is worth noting that the capacity for plasticity can differ between populations of the same species, likely due to differences in environmental heterogeneity (Donelson and Munday, 2012). Multigenerational experiments are exceptionally challenging for elasmobranchs, given their prolonged life histories, and TGP and DP are not likely if strong RP outcomes exist. Metabolic performance in elasmobranchs is expected to be thermally sensitive, as ATP production and blood-oxygen carrying capacity becomes inefficient (Bouyoucos et al., 2019).

The metabolic responses at the cellular level are largely influenced by the thermal sensitivities of mitochondria and the kinetic properties of metabolic enzymatic reactions (Pörtner, 2001; Pörtner, 2002; Pörtner et al., 2017; Chung and Schulte, 2020; Illing et al., 2020). Mitochondrial plasticity in response to temperature stress has been well documented, with studies identifying modified morphology, densities, and feedback functions of critical enzymes involved in cellular respiration (Tyler and Sidell, 1984; Blier et al., 2013; Pichaud et al., 2019). Conserved performance through compensation of cytochrome-c-oxidase and citrate synthase activities occurred when zebrafish (Danio rerio) embryos were warm-acclimated and then subsequently exposed to this same temperature as adults, indicating beneficial DP (Schnurr et al., 2014). RP of mitochondrial function was demonstrated in the tilapia (Oreochromis mossambicus), where fish acclimated to warmer conditions exhibited increased oxidative capacity (Schnell and Seebacher, 2008). Citrate synthase enzyme activities, which suggest a degree of biochemical compensation through RP, have been observed in white spotted bamboo sharks (Chiloscyllium plagiosum) acclimated to 30°C (Tullis and Baillie, 2005). In response to hypoxia, mitochondrial plasticity in H. ocellatum has been shown to reduce free radical production by decreasing succinate metabolism (Devaux et al., 2019). This could potentially serve to prevent reactive oxygen species production at elevated temperatures. Such ex situ techniques offer a means to explore thermal tolerance in species that are challenging to maintain in aquaria and/or for whole-organism testing. However, some enzymatic and mitochondrial function results may overestimate thermal tolerance in cases were the cardiovascular system fails (Pörtner et al., 2017).

Gene regulation has been shown to be a primary mechanism underpinning phenotypic plasticity (Bonduriansky et al., 2012; Duncan et al., 2014; Ryu et al., 2020). Elucidating the epigenetic states that drive resultant phenotypes can reveal the critical mechanistic nexus for understanding how ocean warming may contribute to the emergence of novel physiological phenotypes (Salinas et al., 2013; Fanter et al., 2022). For example, in A. polyacanthus, Veilleux et al. (2015) observed upregulation of genes related to metabolic function, stress, and immune responses with thermal DP and TGP, with the same genes differentially expressed. Further investigation determined that genes affiliated with metabolism, development, cardiovascular function, and heat shock responses also exhibited differentially methylated regions (Ryu et al., 2020). In H. ocellatum, exposure to hypoxia or anoxia leads to compensatory changes in the proteome, involving both structural and metabolic reorganization (Dowd et al., 2010). In addition, transcriptional responses have been observed (Rytkönen et al., 2012), implying a level of phenotypic flexibility that allows for compensation in the face of environmental stressors. Linking gene expression changes to levels of higher biological function is crucial for understanding phenotypic plasticity, as not all changes in gene expression necessarily lead to significant phenotypic changes. Currently, there are no molecular investigations into thermal plasticity in elasmobranchs, highlighting for future research in this area.

### **5** Future directions

Despite the vast knowledge gap regarding the necessity and capacity for thermal plasticity in elasmobranchs, given their long-life histories and logistical constraints for field and captive studies technologies are emerging such that theoretical predictions for this

TABLE 1	Future research initiatives and technological advances that may help fill knowledge gaps regarding elasmobr	anchs' potential for phe	enotypic
plasticity	and adaptation to environmental change.		

Research Area	Method/Study Design/Technology	Example
Determination of the relative capacity for behavioral versus physiological reversible plasticity.	Use of modern biologgers and tracking technologies to determine body temperature in nature. Complimentary laboratory studies using <i>in situ</i> thermal knowledge to investigate physiological performance and plasticity.	(Wilmers et al., 2015)
Baseline understanding of physiological thermal sensitivity of species.	For species amenable to aquariums, whole organism physiological testing is possible. For other species, cellular level determination of thermal sensitivities (e.g., enzymes) is more practical.	(Tullis and Baillie, 2005; Schnurr et al., 2014)
Investigating how plasticity is linked to genomic markers.	Utilizing modern day biologging technologies (i.e., accelerometers) or non-lethal whole organismal traits (e.g., metabolism) in conjunction with epigenome and genome wide association analyses from eDNA/eRNA, single nucleotide polymorphisms, etc. Allowing for understanding of the relationship between gene responses and physiological or behavioral plasticity.	(Barnes and Turner, 2016; Fanter et al., 2022)
Determining environmental thresholds for plasticity (e.g., magnitude and duration). Intraspecific between populations and interspecific comparisons are ideal.	Experimental and molecular studies: genomics, transcriptomics, and epigenomics; environment-trait correlation analyses.	(Crozier et al., 2011; Schunter et al., 2016; Veilleux et al., 2018)
Determine sensitivity of life stages and ontogenetic timing for within generational plasticity (DP or RP) and explore the mechanistic link of these two plasticity types.	Experimental and molecular studies: genomics, transcriptomics, and epigenomics. Modeling developmental and reversible plasticity modifiers and comparing how they influence performance between life stages.	(Seebacher et al., 2014)
In cases, where RP cannot keep pace with environmental change determine the potential for TGP and the timing sensitivity of previous generations (i.e., developmental and reproductive conditions).	Split family/brood experimental designs that allow tracking of genetic backgrounds.	(Donelson et al., 2018
Distinguish genetic selection from plastic responses.	Animal model analyses, common garden studies, space for time substitutions, fine-grained population responses, and quantitative genetics approaches.	Reale et al., 2003; Franks et al., 2007; Crozier and Hutchings, 2014; Merila and Hendry, 2014)
Determining the molecular mechanisms that drive genetic selection and phenotypic plasticity.	Comparative analyses of whole genome or epigenome methylation patterns.	(Rytkönen et al., 2012; Ryu et al., 2018; Ryu et al., 2020)
Determining how genetic selection and plasticity underpin performance markers.	Genome-wide and epigenome association analyses coupled with physiological experimentation of species relevant performance biomarkers.	(Wang and Zhang, 2021; Fanter et al., 2022)
For mobile species, investigation into how genetic variation and phenotypic plasticity are involved with range expansion.	Measure genetic and phenotypic distinctions of new invaders versus those of native individuals.	(Wellband and Heath, 2017; Kelly, 2019)

Examples are primarily from teleost literature.

taxon can be tested. A candidate species approach to represent the diverse life histories, movement ecology, ontogeny, and reproductive modes would be ideal moving forward. Determining the level at which species rely on either behavior and physiology within a generation is a critical first step. This is especially important as behavior and physiology are intrinsically linked, and the reliance on one or the other influences the need for other forms of plasticity and the sensitivity to future climate change (Table 1). Species such as the Atlantic stingray, epaulette shark, and blacktip reef shark might be ideal candidates for experimental ideas outlined in Table 1, as they are amenable to captivity and ecologically, differing capacities and types of plasticity would be expected (Figure 1). Ultimately, evolutionary insights require empowering future studies through integrative, multidisciplinary approaches that utilize modern

technological advances in genetics to bridge this gap (Donelson et al., 2023). It should be noted that this perspective has been written largely from the viewpoint of beneficial plasticity to respond adaptively to environmental change, focusing on warming. As climate change threatens ecosystems worldwide, it is critical to identify and understand the capacity for elasmobranchs to acclimate and adapt to shifting environmental conditions.

# Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

### Author contributions

AH: Conceptualization, Writing – original draft, Writing – review & editing. JD: Conceptualization, Writing – original draft, Writing – review & editing. JR: Conceptualization, Writing – original draft, Writing – review & editing. TR: Conceptualization, Writing – review & editing.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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