



# Swimming performance of sharks and rays under climate change

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**Abstract** Climate change stressors (e.g., warming and ocean acidification) are an imminent challenge to the physiological performance of marine organisms. Several studies spanning the last decade have reported widespread effects of warming and acidification on marine fishes, especially teleosts, but more work is needed to elucidate the responses in marine elasmobranchs, i.e., sharks and rays. Dispersal capacity, as a result of locomotor performance, is a crucial trait that will determine which group of elasmobranchs will be more or less vulnerable to changes in the environment. In fact, efficient and high locomotor performance may determine the capacity for elasmobranchs to relocate to a more favorable area. In this review we integrate findings from work on locomotion of marine sharks and rays to identify characteristics that outline potential vulnerabilities and strength of sharks and rays under climate change. Traits such as intraspecific variability in response to climatic stressors, wide geographic range, thermotaxis, fast swimming or low energetic costs of locomotion are likely to enhance the capacity to disperse. Future studies may focus on understanding the interacting effect of climatic stressors on morphology, biomechanics and energetics of steady and unsteady swimming, across ontogeny and species.

**Keywords** Shark · Batoids · Ocean acidification · Global warming · Locomotion · Physiotype

## Introduction

Climate change is considered one of the biggest challenges for governments and managers as it may significantly accelerate loss of biodiversity (Intergovernmental Panel on Climate Change 2018; Arneth et al. 2020; Manes et al. 2021). Anthropogenic activity has increased atmospheric greenhouse gases concentration, particularly carbon dioxide ( $p\text{CO}_2$ ), causing the oceans to become warmer and more acidic (Dupont and Pörtner 2013; Intergovernmental Panel on Climate Change 2018). Climate models project a rise in  $p\text{CO}_2$  to levels of about 1000 ppm by the year 2100 (Raven et al. 2005). As a consequence, the ocean pH is expected to decline by up to 0.4 units by the end of the century (Gattuso et al. 2010; Riebesell et al. 2011). Even though ocean warming and acidification are considered to be some of the biggest threats to marine biodiversity, the individual and synergistic effects of these stressors on elasmobranch fishes (sharks and rays) are still clearly understudied (Rosa et al. 2017a; Di Santo 2019; Wheeler et al. 2020; Bouyoucos et al. 2020). Previous work on ocean acidification and warming has focused mostly on teleost fishes while the effect on elasmobranchs has been investigated to a much lesser degree (for example: Lauder and Di Santo 2015; Johnson et al. 2016; Rosa

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et al. 2017a, b; Di Santo 2019; Wheeler et al. 2020; Mirasole et al. 2020).

Marine organisms vary in their physiological and morphological characteristics and, as a result, their individual responses to ocean warming and ocean acidification differ significantly (Harvey et al. 2013). For this reason, efforts may be focused on identifying key traits that make “physiotypes”, i.e., organisms with similar physiological characteristics, more or less susceptible to climate-related stressors (Nelson 1970; Melzner et al. 2009; Di Santo et al. 2016). Responses to ocean warming and acidification may vary across the life history of organisms, with embryonic and juvenile stages being the most vulnerable (Lear et al. 2019), with acclimation (short vs. long term exposure), and across populations (Donelson et al. 2012; Frommel et al. 2012; Bignami et al. 2013; Harvey et al. 2013; Di Santo 2015; Downie et al. 2020; Gervais et al. 2021). Some long-lived organisms may experience a wide spectrum of environmental change, while others with faster generational turnover may only experience relatively stable conditions within their lifetime (Melzner et al. 2009; Somero 2010). As a consequence, some individuals may be able to acclimate over a relatively long period of time while some populations may rapidly adapt to the changes in their environment across generations favoring physiotypes that are resilient in the new conditions (Munday 2014; Ryu et al. 2018). Organisms can also employ other solutions, such as shifting their geographic range, to respond to environmental challenges (Harvey et al. 2013; Rosa et al. 2014; Browman 2017). Changes in locomotor performance, behavior and geographic range at large and small scale may have cascading and unexpected effects on biotic interactions, community structures and ecosystem functioning (Harvey et al. 2013; Di Santo et al. 2020). Thus, it is important to investigate how performance of different physiotypes may be affected under climate change to better forecast future shifts in marine ecosystems (Di Santo 2016).

Elasmobranchs are ecologically important as they fill many niches across a wide range of biota, from benthic, to coral reefs to open oceans (Wilga and Lauder 2004; Lauder and Di Santo 2015; Flowers et al. 2020). They typically occupy high trophic levels as top or meso-predators, thus playing a key role in the health of marine ecosystems (Rosa et al. 2014; Pisteveos et al. 2015). They are characterized by slow

growth and relatively long lifespans, and tend to have higher survival rates as juveniles when compared to teleost fishes (Wellington and Victor 1989; Chin et al. 2010). However, their relatively low generational turnover rate makes them particularly vulnerable to rapid changes in the environment (Chin et al. 2010; Rosa et al. 2014). Predictions of responses to climate change often involve modeling of geographic shifts (Parmesan et al. 1999; Saba et al. 2016). However, such projections of poleward movements need to consider swimming capacity and cost of transport. In fact, an efficient locomotor capacity would allow fishes to effectively relocate to environmental refugia (Lauder and Di Santo 2015). It is currently virtually unknown if elasmobranchs’ swimming performance levels may be maintained in response to climate change because only limited studies on relatively few, and especially benthic species have been conducted to date (Wilga and Lauder 2004; Aronson et al. 2007; Papastamatiou et al. 2015; Di Santo 2016; Payne et al. 2018; Lear et al. 2019).

Elasmobranch fishes display a great morphological diversity in body shapes that results in extraordinary locomotor diversity (Rosenberger 2001; Wilga and Lauder 2004; Lauder and Di Santo 2015; Porter et al. 2020). For instance, sharks exhibit an elongated body and swim using mostly their trunk and tail in an undulatory motion, while rays (i.e., skates and rays) have short, stiff head trunk regions forming a disc with slender tail and therefore swim using the pectoral fins (with a few exceptions) in undulatory (i.e., wave-like motion) or oscillatory (i.e., flapping up and down) motions (Rosenberger and Westneat 1999; Rosenberger 2001; Wilga and Lauder 2004). Morphological and kinematic characteristics of the body and fins explain how elasmobranch fishes move and provide cues on important adaptations that are involved with efficient locomotion (Lauder and Di Santo 2015; Di Santo et al. 2021). In this review, we examine the effects of ocean warming and acidification on locomotion in sharks and rays. We also briefly review major studies on the effect of warming and ocean acidification on locomotor performance of teleost fishes because of the paucity of work on elasmobranchs. We have based our review on studies where the effect of ocean warming and/or acidification was assessed on skeletal morphology, locomotor behavior and physiology of elasmobranch fishes. We also discuss features that characterize tolerant physiotypes

under the two major climate change stressors in relation to swimming performance.

### Locomotor performance

Locomotion is a key process in nearly all fishes, including elasmobranchs, that is involved in vital functions such as reproduction, migration, predator avoidance, ram ventilation, and small-scale movements (Daniel 1984; Sfakiotakis et al. 1999; Lauder and Di Santo 2015). Biomechanics, behavior and energetics of locomotion determine efficiency of movement and maximal performance (for instance, maximum speed during an escape response) under different conditions (Wilga and Lauder 2004; Lauder and Di Santo 2015), and, as such, these are the focus of the review. Two major locomotor behaviors are likely to increase survival rates in elasmobranchs: steady (or sustained) swimming and burst (or escape) performance. During steady swimming, fishes may modulate their speed and can often optimize energetic costs for large scale movements by selecting an optimal velocity (Webb 1994; Saadat et al. 2017; Di Santo et al. 2017b). On the other hand, fishes may undertake energetically costly movements such as fast-starts and bursts to escape a predator, or to capture a prey (Jayne and Lauder 1994; Johnson and Bennett 1995; Fernández et al. 2002; Wen et al. 2018).

#### Climate change and locomotor performance in teleost fishes

Locomotor performance has undoubtedly contributed significantly to the evolutionary success of fishes (Breder 1926; Lindsey 1978). In fact, fishes display a remarkable diversity of morphology and behaviors to achieve a variety of movements, from long-distance migrations, to fast swimming and escape responses (Lauder 2015). Fish locomotion is a well-studied topic (Bainbridge 1963; Sfakiotakis et al. 1999; Lauder 2015; Saadat et al. 2017; Di Santo et al. 2021), however studies on the single and combined effect of temperature and acidification on many traits that affect locomotor performance are often lacking within the same group of fishes. The scarcity of “full picture” data sets makes the identification of sensitive and tolerant phenotypes complicated. Swimming traits that are often analyzed are maximum speed,

metabolic rates, and escape mechanics, but rarely under ocean warming and acidification, and in the same organism (Melzner et al. 2009; Watson et al. 2018).

Temperature changes can affect skeletal morphology, swimming performance and behavior of fishes (von Herbing 2002; Eliason et al. 2011; Hein and Keirsted 2012). Thermal stress during embryonic development is a known teratogenic factor that produces skeletal deformities in teleost fishes (Takle et al. 2005). Warming results in severe malformations in the axial skeleton in species such as the mosquito fish (*Gambusia affinis*) and the Atlantic salmon (*Salmo salar*) where the proportion of fish with larger, fused and deformed vertebrae increases with temperature (Takle et al. 2005; Ytteborg et al. 2010; Sassi et al. 2010; Fraser et al. 2015). Likewise, ocean acidification is known to alter the morphology of the skeleton in teleost fishes (Powell et al. 2009; Baumann et al. 2012; Pimentel et al. 2014, 2016; DePasquale et al. 2015). In particular, acidification may lead to fusions, body malformation, and spinal curvatures (i.e., lordosis, scoliosis and kyphosis) (Baumann et al. 2012; Pimentel et al. 2014, 2016). Moreover, an increase in skeletal mineralization has been observed in site-attached fish (*Gobius bucchichi*) living near CO<sub>2</sub> seeps (Mirasole et al. 2020). Malformations of the axial skeleton can alter swimming performance, foraging and predator avoidance in teleosts (Powell et al. 2009). For instance, scoliotic teleost fishes achieve significantly lower swimming speed and are unable to recover quickly from exhaustive swimming when compared to control individuals (Powell et al. 2009).

Temperature also shapes the performance or aerobic scope of swimming (Fry 1947, 1967; Fry and Hart 1948). The concept of aerobic scope was introduced by Fry and Hart (1948) when they quantified the effects of temperature change on maximum and standard metabolic rates in goldfish (*Carassius auratus*). By subtracting the standard metabolic rate from the maximum, they put forward the idea of the scope for metabolic activity, i.e., the net energy beyond resting that organisms have to be active (Fry and Hart 1948; Farrell 2016). The aerobic scope is a measure of thermal dependence of physiological processes, and it has been used broadly by ecological physiologists to understand changes in performance as a consequence of thermal shifts (Farrell

2016). Performance curves often show that warming increases swimming metabolic rates, but that the peak of maximum oxygen consumption rates typically precedes the peak for resting rates, thus effectively showing a decline in performance at the highest temperatures an individual can tolerate (Fangue et al. 2008; Farrell 2016). Warming can also have a positive effect on swimming performance. In fact, higher temperatures increase muscle efficiency and contractility at high speeds, making swimming much more energetically efficient in teleost larvae (von Herbing 2002). Another study on herring and plaice larvae showed that an increase in muscle contraction performance during escape response leads to faster bursts (Batty and Blaxter 1992). On the other hand, the same study noted that other traits, such as tail amplitude and stride length, are not significantly affected by temperature (Batty and Blaxter 1992). Several studies have shown an increase in fast-start and burst swimming in adult fishes that resulted in enhanced escape performance with warming (Johnston et al. 1991; Wilson et al. 2001; Fernández et al. 2002; Lyon et al. 2008). The effect of temperature on oxygen consumption during steady swimming has been investigated using many species, from salmonids to Antarctic fishes (some examples: Brett 1967; Wilson et al. 2001; Jain and Farrell 2003; Fangue et al. 2008). In most studies warming increases swimming endurance and oxygen consumption up to the organism's thermal limit where performance rapidly declines (Brett 1964, 1967; Johnston et al. 1991; Steinhausen et al. 2008; Eliason et al. 2011; McDonnell and Chapman 2016). In some species temperature does not have a significant effect on swimming energetics or speed, unless the effect of low temperature was tested (Johnston et al. 1991; Fangue et al. 2008).

Ocean acidification has been shown to reduce swimming performance in some fish species but responses to ocean acidification are often complex (Munday 2014; Browman 2017; Clark et al. 2020). In fact, studies have reported an increase, a decrease, or no significant change in aerobic scope associated with swimming at high  $p\text{CO}_2$  (Munday et al. 2009; Couturier et al. 2013; Rummer et al. 2013; Esbaugh et al. 2016). High  $p\text{CO}_2$  levels decrease maximum speed during steady and burst swimming, and distance traveled (Allan et al. 2014; Watson et al. 2018). During escape responses, fishes bend their body into a "c", i.e., the first stage, and then produce a fast

burst to move away from the stimulus, i.e., the second stage (Jayne and Lauder 1994; Witt et al. 2015). Even though the bending angle during the first stage of the escape response may not be affected by acidification, fishes may be less responsive to stimuli that trigger the escape response (Wang et al. 2017).

To predict the long-term effects of ocean warming and acidification on swimming performance of fishes, it is important to consider whether physiological and behavioral traits associated with locomotion may adjust, or acclimate, within the time frame in which these changes are occurring in the environment, i.e., a few generations (Donelson et al. 2012). Although there is a dearth of studies that have evaluated the effects of warming and acidification across fish generations, metabolic rates and swimming kinematics are already known to be compensated during environmental shifts in some species (Schade et al. 2014; Shama et al. 2014; Munday 2014; Veilleux et al. 2015). Such transgenerational acclimation could be achieved via changes in the epigenetic state of parental generation that is transferred to next generation by producing offspring that maintain a similar performance in the new environment, or a maternal effect that provides, for example, different amount of nutrition to the offspring through the yolk (Shama et al. 2014; Veilleux et al. 2015; Ryu et al. 2018). However, there may be limitations to the traits that respond to transgenerational acclimation. Some biomechanical traits such as turning angle during escape response are affected by increase in  $p\text{CO}_2$  but do not seem to acclimate even when the parents are exposed to the same level of acidification (Munday 2014). On the other hand, exposure to acidification across generations might produce a carry-over effect thus further reducing performance and survival (Munday 2014). These early studies suggest that transgenerational acclimation may be inconsequential, reduce or exacerbate the effect of ocean acidification and warming on different morphological, physiological, and behavioral traits associated with swimming. Understanding the outcome of the single and combined effects of ocean warming and acidification on performance traits is a priority for studies that aim to realistically predict complex responses of organisms to changes in the environment. Even though just a few studies looked at transgenerational acclimation in teleost fishes, to our knowledge no study to date has quantified it on any elasmobranch species.

## Effect of ocean warming on locomotor performance in elasmobranchs

Temperature is known to have a profound effect on nearly every physiological process, including metabolic rates (for example, Hawkins and Day 1996; Rosa et al. 2014; Gervais et al. 2018), but there is a paucity of data on the effect of temperature on morphology of elasmobranchs, beyond body size, and swimming performance (Di Santo 2015, 2019). In one study, Di Santo (2019) investigated the effect of ocean warming on skeletal mineralization in a batoid fish. Little skate (*Leucoraja erinacea*) embryos were exposed to temperature projected for the year 2100 (Di Santo 2019). Warming had a negative effect on the mineralization of the pectoral fins as the density of apatite decreased (Di Santo 2019). One of the possible causes of a reduction in mineralization in the pectoral fins of skates may be attributed to a mismatch between high growth in juveniles at higher temperatures and mineralization processes that might proceed at lower rates (Di Santo 2019). High stiffness of the cartilage provides an efficient energy transfer during locomotion (Dean and Summers 2006; Porter and Long 2010). A decrease in mineralization of the cartilage in the pectoral fins produces higher flexibility during movement but the fish needs to actively stiffen the fins to achieve higher swimming speeds, thus increasing metabolic costs during swimming (Di Santo et al. 2017a).

Warming also correlates with a smaller body size, a phenomenon so widespread across terrestrial and aquatic organisms that it is known as one of the universal responses to climate change (Gardner et al. 2011; Forster et al. 2012; Baudron et al. 2014). A smaller body size has been observed in juvenile epaulette shark, *Hemiscyllium ocellatum*, (Gervais et al. 2018) while juvenile little skates showed a lower body condition when exposed to higher temperatures (Di Santo 2015). In little skates, local adaptation seems to have a strong effect on the temperature-size relationship. Skates from the areas where temperature fluctuates frequently seem to be less affected by warming than conspecific living in more stable environments (Di Santo 2015, 2016). Populations of Port Jackson sharks (*Heterodontus portusjacksoni*) also exhibit differences in metabolic rates in response to temperature, even though swimming performance was not different (Gervais et al. 2021). Smaller elasmobranch

and teleosts fishes tend to be more tolerant to high temperatures and are assumed to perform better at higher temperatures than their larger conspecifics (Di Santo 2016; McKenzie et al. 2020). In particular, smaller skates escape more intensely (burst/min) and can recover faster after a chasing experiment when compared to larger conspecifics at the same temperatures (Di Santo 2016). Even though smaller fishes are known to perform better under increasing temperatures, a small body size can significantly impair long-distance locomotor capacity by increasing cost of transport in skates (Dulvy et al. 2014; Lauder and Di Santo 2015; Di Santo and Kenaley 2016; Di Santo et al. 2017b) and sharks (Carlson et al. 2004).

Warming is associated with a reduced aerobic scope for activity and increased stress (Schwieterman et al. 2019). It has been suggested that some fish species that live close to their thermal optimum may experience a reduction in the amount of available energy for aerobic activities, such as locomotion, with warming (Rummer et al. 2014). Elasmobranch species that are fast swimmers and obligate ram ventilators have the highest measures of routine metabolic rates to maintain, for example, higher digestion rates and, in some cases, heterothermy, and therefore are expected to have limited amount of energy to cope with environmental challenges than less active species (Carlson et al. 2004). On the other hand, even though locomotor efficiency per se may be reduced, these elasmobranchs may be more likely to relocate to a more suitable area by swimming faster (Wilga and Lauder 2004; Chin et al. 2010; Lauder and Di Santo 2015). However, it is difficult to establish the effect of temperature on aerobic scope as many studies have now shown that the maximum metabolic rates in fishes are affected by digestion, swimming capacity, stress, and other masked abiotic factors such as oxygen levels (Roche et al. 2013; Di Santo and Lobel 2016; Rummer et al. 2016; Esbaugh et al. 2021; Pauly 2021). In a previous study, Di Santo (2015) argued that an increase in active metabolic rate as a consequence of warming, should not be always considered an advantage. In fact, determining the actual maximum metabolic rate is difficult and it relies heavily on the technique used to test swimming performance (Roche et al. 2013; Rummer et al. 2016), so it is possible that researchers have been routinely measuring the elevated costs of activity with climate stressors rather than an increase in aerobic scope. Conclusions

on the effect of temperature and other stressors on aerobic scope should therefore be cautious.

Predictions of future responses to climate change often include shifts in geographic ranges, while small scale alterations in habitat use have received less attention. Elasmobranchs can utilize the diel abiotic and geographical variability in their environment to decrease costs of locomotion (Papastamatiou et al. 2021). Sharks and rays are known to exploit the thermal heterogeneity in their environment by selecting different temperatures throughout the day, a behavior known as thermotaxis (Fangue and Bennett 2003; Wallman and Bennett 2006; DiGirolamo et al. 2012; Speed et al. 2012). Elasmobranchs may select specific temperatures to enhance physiological processes, from swimming performance to digestion to reproduction (Wallman and Bennett 2006; Di Santo and Bennett 2011a; Papastamatiou et al. 2015), while others do not seem to adjust to changes in the environment by thermoregulation (Nay et al. 2021). One example of thermoregulation is the trade-off between optimal foraging and thermal habitats (Sims et al. 2006; Sims 2010), where sharks and rays hunt in warmer waters, to maximize muscle performance, and rest in cool waters, to slow down the passage of food across the absorptive surfaces and increase nutrient uptake, thus reducing the daily energy costs (Sims et al. 2006; Sims 2010) and increasing digestive efficiency (Di Santo and Bennett 2011a, b). It is possible therefore that elasmobranchs may not shift their latitudinal range with warming, but rather select deeper cooler waters to enhance physiological processes. These small scale movements may be just as significant to the survival of sharks and rays to ocean warming than poleward relocations. Seasonal shifts towards deeper water are already occurring for batoids at high latitudes (Stebbing et al. 2002; Perry et al. 2005; Dulvy et al. 2008b; Lauder and Di Santo 2015). Perry et al. (2005) quantified a higher mean depth in the distribution of the ray *Leucoraja naevus* that correlates with warming trends. In this multi-species study, fishes that shifted their geographic range tended to have faster life history compared to non-shifting species (Perry et al. 2005). Dulvy et al. (2008b) suggested that there is evidence for coherent deepening of fish in response to climate change and found that the shift in depth was more pronounced than the latitudinal shift in benthic elasmobranchs. Although a shift in distribution is possible,

bathymetry (deep waters), the expansion of oxygen minimum zones (Di Santo et al. 2016; Vedor et al. 2021), potential decoupling of current predator–prey dynamics and trophic structure (Deutsch et al. 2015), and behavioral characteristics of movement (philopatry, restricted home ranges) may hinder the capacity to relocate to more favorable refugia (Aronson et al. 2007; Dulvy et al. 2014).

#### Effect of ocean acidification on locomotor performance in elasmobranchs

Elasmobranch fishes evolved during the Devonian Period when atmospheric CO<sub>2</sub> was greater than today's levels (Johnson et al. 2016; Rosa et al. 2017a). This has led to the hypothesis that elasmobranch fishes may be able to tolerate ocean acidification, and it was not until recently that experimental data showed that high levels of pCO<sub>2</sub> can affect elasmobranch fishes directly by causing morphological, behavioral and physiological anomalies (Pistevos et al. 2015; Rosa et al. 2017a). Di Santo (2019) evaluated the effect of ocean acidification on mineralization of the skeleton of little skates that were developmentally acclimated to pH levels expected by year 2100. Levels of pCO<sub>2</sub> ~ 1100 µatm increased mineralization of the crura (modified pelvic fins that some rays use to walk underwater) and jaws in little skates (Di Santo 2019). Skates might even gain an advantage as high mineralization of the crura is a good predictor of the ability of batoids to walk underwater (Koester and Spirito 2003; Macesic and Summers 2012; Bilecenoglu and Ekstrom 2013). Apatite in the crura increased with pCO<sub>2</sub> with no significant effect of temperature, implying that future ocean acidification may favor walking in benthic batoids regardless of warming (Di Santo 2019). On the other hand, a denser skeleton increases the weight of the skeleton thus reducing buoyancy which, in turn, increases energetic costs of swimming (Di Santo 2019). Elasmobranch do not have a swim bladder and need to swim in order to create hydrodynamic lift and even hover in the water column. Therefore, a heavier skeleton is expected to increase costs of locomotion at any speed (Di Santo et al. 2017b). While external features such as teeth and denticles are not affected by pCO<sub>2</sub> levels expected by the end of the century (Green and Jutfelt 2014; Di Santo 2019), higher levels projected for the year 2300 are known to cause corrosion of

denticles in sharks (Dziergwa et al. 2019). Denticle size and morphology are important during locomotion as these features may increase efficiency by reducing the friction between the skin and the water (Oeffner and Lauder 2012; Wen et al. 2014; Domel et al. 2018). Studies have not reported any body malformation linked to acidification in elasmobranchs yet, and it has been suggested that elasmobranch embryos might be protected from acidification during the earliest stages of development while inside their mothers or in a closed eggcase (Leonard et al. 1999; Di Santo 2015). Additionally, elasmobranchs have direct development, while many teleosts go through a larval phase that is considered vulnerable to acidification (Frommel et al. 2012; Bignami et al. 2013).

The combined effect of ocean warming and acidification on locomotor performance in elasmobranchs

Ocean warming and ocean acidification will occur simultaneously in oceans, and organisms, including elasmobranchs, may be negatively impacted by the interactive effects of these stressors (Byrne and Przeslawski 2013; Boyd et al. 2015; Di Santo 2015; Pistevo et al. 2017). Di Santo (2015, 2016, 2019) provides the only series of studies that have looked at single and combined effects of ocean warming and acidification on different performance traits for the same elasmobranch species across ontogeny. First, ocean warming and acidification interacted during mineralization of the skeleton of skates. Acidification increased density of the crura and the jaws at control temperature; however, when combined with warming, acidification had no significant effect on the mineralization of the jaws (Di Santo 2019). On the other hand, warming did not reduce the effect of acidification on the mineralization of the crura (Di Santo 2019). Complex and non-directional results are becoming common in studies of ocean acidification and warming across organisms (Kroeker et al. 2010, 2013; Schlegel et al. 2012).

Denser skeletal parts as a consequence of acidification and less mineralized pectoral fins as a consequence of warming can have a profound effect on locomotor performance. In fact, both a heavier skeleton that reduces buoyancy and less stiff pectoral fins that need to be actively stiffened using muscles, increase the costs of locomotion in skates (Di Santo

2016; Di Santo et al. 2017a, b). During a chasing experiment, combined warming and acidification prolonged the time to recover from intense exercise (Di Santo 2016). A longer recovery time and higher energetic costs to escape may make skates vulnerable to predators as they need to pay off the oxygen debt accumulated during intense sequential bursts, and they may need to explore the environment to seek additional food (Di Santo 2015, 2016). Moreover, a few studies have shown that hunting efficacy in sharks may be impaired by the effect of ocean acidification and warming, while other studies found no effect (Pistevo et al. 2015, 2017; Heinrich et al. 2016; Rosa et al. 2017b; Gervais et al. 2018). Elevated temperature increased swimming activity while searching for food and reduced the time used by elasmobranchs to digest (Di Santo and Bennett 2011a; Pistevo et al. 2017), but acidification can reduce elasmobranchs' ability to use olfactory cues and increased the time to find food even in combination with elevated temperature (Pistevo et al. 2017). Port Jackson sharks under warming scenarios increased the time spent near chemical cues for prey but pCO<sub>2</sub> reduced the attraction to food (Pistevo et al. 2017). Pistevo et al. (2015) reported that it took four times longer for sharks to detect prey under elevated pCO<sub>2</sub>. When combined with elevated temperature, sharks reduced the time to locate the prey by a third but was still significantly longer than the time needed by control individuals (Pistevo et al. 2015). High pCO<sub>2</sub> may reduce elasmobranchs' ability to detect prey perhaps because of a dysfunction of the GABAA receptor (Hamilton et al. 2014), thus making some elasmobranch species slower and less successful hunters. These studies suggest that ocean warming and acidification may have the potential to reduce hunting abilities in some elasmobranchs by disrupting olfactory capacity, thus requiring them to rely more on vision and electroreception to find prey (Pistevo et al. 2015).

The effect of ocean warming and acidification can be modulated by the local environment a population or individual has experienced. For instance, when comparing the escape performance of little skate from two adjacent locations, the Gulf of Maine and the Georges Bank, under simulated warming and acidification conditions, the smaller skates from the Georges Bank were able to escape for a longer period of time and recovered faster from exercise (Di Santo 2016). It is unclear however, whether there was a

maternal effect given by the periodic exposure of egg-laying females to low-pH upwelling waters in the Georges Bank (Mavor and Bisagni 2001; Raven et al. 2005) or a smaller body size favored locomotor performance in that particular population of skates (Di Santo 2016). Additional studies are needed to understand the role of local adaptation and size on locomotor performance in elasmobranchs under climate change scenarios.

### Consequences of alterations in locomotion efficiency on geographic shifts

Low locomotor efficiency is associated with a reduced capacity for migrating, hunting, and effectively utilizing the environment through small-scale movements (Lauder 2015; Lauder and Di Santo 2015). At a global scale, fishes migrate to relocate to more favorable conditions and find thermal refugia (Stebbing et al. 2002; Perry et al. 2005; Dulvy et al. 2008b). Even though there are no apparent geographic barriers to marine dispersal (Aronson et al. 2007), a reduction in locomotion efficiency can limit elasmobranch movement and the capacity to relocate.

Large scale migrations to find thermal refugia occur as a poleward expansion or towards deeper waters (Stebbing et al. 2002; Perry et al. 2005; Dulvy et al. 2008b; Lauder and Di Santo 2015). Range expansions and poleward shifts assume that (1) species are able to migrate and (2) species are able to find new suitable habitats. Some elasmobranchs show strong philopatry or are geographically restricted, making it hard for them to colonize new habitat (Dulvy et al. 2008b; Lauder and Di Santo 2015; Kneebone et al. 2020). In particular, skate populations show high philopatry, and even when a nearby population is locally extirpated, they are unlikely to expand their range and repopulate that area (Dulvy et al. 2014). In some cases long distance relocations might be hindered in deep waters as benthic elasmobranchs cannot stop and rest on the bottom of the oceans to recover (Dulvy et al. 2008a, b). In fact, high hydrostatic pressure increases the concentration of trimethylamine-*N*-oxide (TMAO) in the body fluids of elasmobranchs (Priede et al. 2006; Laxson et al. 2011; Yancey et al. 2014, 2018). TMAO is a naturally occurring osmolyte that stabilizes the three-dimensional structure of proteins (Yancey et al. 1982). In

deep waters high pressure causes muscle TMAO to increase and urea to decrease. TMAO amplifies the inward osmotic gradient which becomes fatal as the kidneys are unable to compensate (Aronson et al. 2007). On the other hand, TMAO production plateaus at depths of around 3000 m, hence elasmobranchs may be unable to accumulate sufficient TMAO to counteract pressure (Laxson et al. 2011).

Future warming is forecasted to be most pronounced in the Southern ocean (Intergovernmental Panel on Climate Change 2015) and elevated temperatures are expected to facilitate the introduction and establishment of new species (Aronson et al. 2007). Thus, a significant latitudinal shifting of elasmobranchs is expected to be towards shallow waters in Antarctica in the southern hemisphere (Aronson et al. 2007). The continental shelf around Antarctica is deeper than 3000 m and when migrating to Antarctica, elasmobranchs must swim continuously to cross the deep ocean (Aronson et al. 2007). Fast swimming pelagic sharks have the ability to swim continuously and have a high probability of crossing the depths to reach Antarctica, while benthic sharks, skates and most rays lack the capacity to swim continuously thus facing physiological challenges while crossing the continental shelf (Aronson et al. 2007). Additionally, benthic elasmobranchs tend to have small body size (Carrier et al. 2004) which corresponds to high cost of transport regardless of swimming metabolic rates, thus limiting large scale migrations (Lauder and Di Santo 2015). With ocean acidification increasing skeletal mineralization, we might expect that benthic elasmobranchs will develop an even more sluggish behavior, making their migrations paths less likely to occur. Therefore, we suggest that morphological and physiological traits that contribute to swimming ability may be considered important factors when modeling future large-scale shifts in elasmobranch fishes.

### Identifying tolerant elasmobranch physiotypes under climate change

Elasmobranch fishes have survived all five major mass extinction events that have occurred over their evolution (last 400 million years), making them one of the most resilient marine groups (Rosa et al. 2017a). However, because they have relatively long generation time and many of them are currently

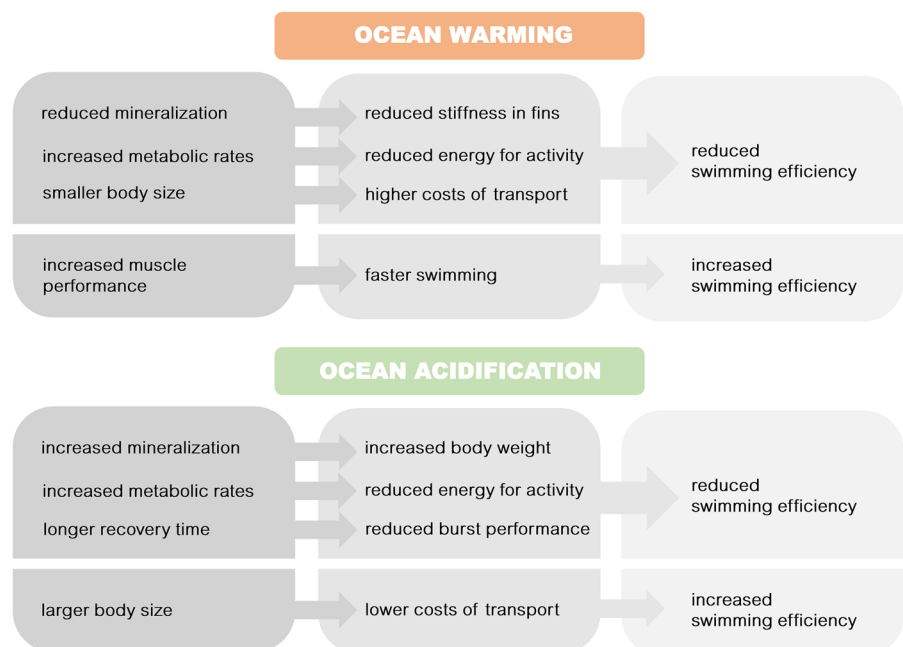


overfished, they are considered one of the most threatened marine groups (Field et al. 2009; Chin et al. 2010). Current rates of change in temperature and pH are much faster than those they experienced during previous climatic shifts (Hoffmann and Sgrò 2011). Specifically, the rate of warming and acidification combined with other stressors (e.g., habitat destruction, prey availability, exploitation) may render their management and protection difficult (Baum et al. 2003; Dulvy et al. 2008a, 2014; Dawson et al. 2011; Birkmanis et al. 2020). As it is unlikely that elasmobranchs may be able to adapt to rapid changes in the environment through evolutionary processes, many species may adjust to these synergistic changes through alterations in behavior (such as shifts in habitat utilization) or distribution. To be able to forecast future outcomes and strategize on different measures to implement to manage wild populations, it is important to identify key traits that impact swimming performance under climate change scenarios (Fig. 1).

Physiotypes that are able to swim fast have an advantage when shifting their geographic distribution and exploiting new thermal gradients and areas. These are for example heterothermic (lamnid) sharks that can usually swim faster and for longer periods than poikilothermic species (Carrier et al. 2004; Sims 2010). Morphological features such as tapered fins and streamlined bodies also favor swimming

efficiency, and are characteristic of elasmobranch physiotypes that already show wide geographic distribution (Lauder and Di Santo 2015). Warmer habitat physiotypes from lower latitudes may be more likely to fare well in future climate change, as they may experience a smaller increase in temperature compared to species at higher latitudes (Perry et al. 2005; Gervais et al. 2018), however hypoxic events in these areas could reduce performance (Parsons and Carlson 1998; Carlson and Parsons 2001; Di Santo et al. 2016; Crear et al. 2019; Esbaugh et al. 2021). Species experiencing fluctuating environments across their geographic range might be better able to adjust to climate change (Hoffmann and Sgrò 2011; Seibel et al. 2012; Di Santo 2016; Johnson and Hofmann 2020). Such species can either exhibit locally adapted populations that respond differently to stressors (species with reduced dispersal capacity) or global distribution (high swimming and dispersal capacity) (Dulvy et al. 2008b; Field et al. 2009; Booth et al. 2011; Lauder and Di Santo 2015). Physiotypes with widespread distribution usually have a higher tolerance to novel environments because they have already experienced a variety of climate and habitat conditions within their home range (Field et al. 2009). Furthermore, a wide geographic range usually correlates positively with body size (Dulvy et al. 2014). Bigger elasmobranchs exhibit lower costs of transport compared to

**Fig. 1** Four major consequences of ocean warming and acidification on traits that affect swimming performance in elasmobranchs



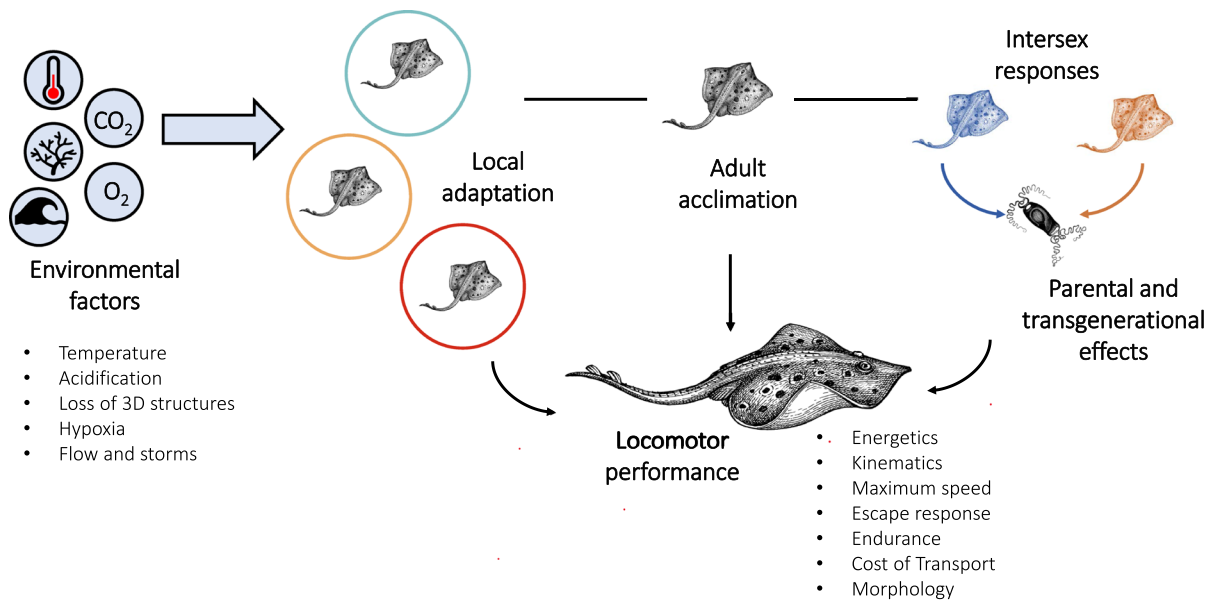
smaller ones (Lauder and Di Santo 2015), and have the potential to effectively respond to environmental stressors through changes in distribution. Yet, phenotypes characterized by smaller body size could have an advantage, even if not during migrations. In fact, smaller fishes tend to be more tolerant to changes in temperature compared to bigger ones (Di Santo and Lobel 2017; McKenzie et al. 2020), and are less sensitive to warming and ocean acidification (Wittmann and Pörtner 2013; Di Santo and Lobel 2016; Di Santo 2016). Smaller and benthic elasmobranchs typically show low metabolic rates during swimming, and are known to exploit the variation in their habitats by shuttling across thermal gradients (Wallman and Bennett 2006; Di Santo and Bennett 2011a; Papastamatiou et al. 2015; Flowers et al. 2020). Small scale movements may be important for the survival of many benthic species that could not otherwise relocate to more suitable areas. For instance, elasmobranchs that live in thermally variable environments may continue to select specific temperatures to enhance different physiological processes, for example, higher temperatures to enhance high energy bursts to hunt, and low temperatures to save energy during digestion or recovery from exercise (Hight and Lowe 2007; Meese and Lowe 2019; Silva-Garay and Lowe 2021). This behavior is already observed in several benthic sharks and rays and may become even more widespread with ocean warming. Ocean acidification is likely to increase the energy costs during swimming, and to prolong recovery times after bursts, but is also likely to increase body size and favor underwater walking by increasing mineralization of pelvic fins which is observed in several benthic rays and sharks already (Bilecenoglu and Ekstrom 2013; Jung et al. 2018; Di Santo 2019; Wheeler et al. 2020, 2021).

## Conclusions and future directions

Locomotor efficiency is a major trait determining the capacity of elasmobranchs to fare well in climate change, however very few studies have examined how it will be affected by ocean warming, acidification and other related stressors like hypoxia. Ocean warming and acidification exert

both single, synergistic and antagonistic effects on elasmobranch locomotion efficiency by affecting skeletal mineralization, increasing metabolic rates during swimming, and prolonging the time it takes to recover from exercise, and to locate food (Rosa et al. 2014, 2017b; Pistevos et al. 2015; Di Santo 2016; Gervais et al. 2021). These morphological and physiological impairments, in combination with hypoxia, pollution, fishing and habitat destruction, may act to reduce elasmobranch survival (Parsons and Carlson 1998; Carlson and Parsons 2001; Field et al. 2009; Dulvy et al. 2014; Crear et al. 2019; Bouyoucos et al. 2019). However, there is dearth of empirical studies on the capacity of elasmobranchs to swim efficiently under simulated future ocean conditions. We suggest that future studies quantify the single and combined effect of ocean acidification, warming and other stressors such as hypoxia on multiple locomotor behaviors within the same species of sharks and rays to identify potential trade-offs (Fig. 2). In particular, more studies are needed on the effect of these stressors on burst and steady swimming energetics and biomechanics (including metabolic rates, maximum and optimal swimming speeds, endurance, tail beat frequency, head and tail amplitude, waves speed and length, body angle and curvature) and ontogenetic studies to understand long term consequences on morphology (body size, skeletal mineralization, fin flexibility and shape) and swimming mechanics. Moreover, it is just as important to quantify intraspecific variation in responses to stressors (Feder et al. 1987; Pough 1988). Intraspecific variation in performance can clarify which traits make individuals more or less efficient during swimming under different environmental conditions. Finally, more studies should be conducted to understand the effect of climate change on swimming in larger elasmobranchs. These species are typically more difficult to study in laboratory settings but technological advances in field equipment paired with laboratory testing (Whitney et al. 2007; Lawson et al. 2019; Papastamatiou et al. 2021) can allow us to understand how sharks and rays may exploit the variation in their environment to save energy during locomotion.

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**Fig. 2** Major knowledge gaps on the effect of climate changes stressors on elasmobranch locomotion. Here, we outline the major climate-related stressors that may affect locomotor performance in elasmobranchs and the intrinsic characteristics of

physiotypes that can modulate individual responses to changes in the environment, such as local adaptation, acclimation capacity, intersex variation in responses, parental and transgenerational effects

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