Global change biology

Biological responses of sharks to ocean acidification

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Sharks play a key role in the structure of marine food webs, but are facing major threats due to overfishing and habitat degradation. Although sharks are also assumed to be at relatively high risk from climate change due to a low intrinsic rate of population growth and slow rates of evolution, ocean acidification (OA) has not, until recently, been considered a direct threat. New studies have been evaluating the potential effects of end-of-century elevated CO₂ levels on sharks and their relatives’ early development, physiology and behaviour. Here, we review those findings and use a meta-analysis approach to quantify the overall direction and magnitude of biological responses to OA in the species of sharks that have been investigated to date. While embryo survival and development time are mostly unaffected by elevated CO₂, there are clear effects on body condition, growth, aerobic potential and behaviour (e.g. lateralization, hunting and prey detection). Furthermore, studies to date suggest that the effects of OA could be as substantial as those due to warming in some species. A major limitation is that all past studies have involved relatively sedentary, benthic sharks that are capable of buccal ventilation—no studies have investigated pelagic sharks that depend on ram ventilation. Future research should focus on species with different life strategies (e.g. pelagic, ram ventilators), climate zones (e.g. polar regions), habitats (e.g. open ocean), and distinct phases of ontogeny in order to fully predict how OA and climate change will impact higher-order predators and therefore marine ecosystem dynamics.

1. Introduction

Chondrichthyan fishes (sharks, skates, rays and chimaeras) are one of the most successful marine groups, having been able to survive all five mass extinctions over the last 400 million years [1]. The first reports of their most reliable diagnostic feature—the tessellate mode of cartilage mineralization—are from late Devonian deposits (approx. 380 Mya) [2], though the first scales and spines of Chondrichthyans appeared already in the Lower Silurian [3,4]. Presently, the cartilaginous fishes (comprising approximately 1200 species) are found throughout all of the world’s oceans, and many occupy high trophic levels in marine habitats [5,6] where they can exert a fundamental influence (top-down control) on the structure and function of communities [7,8]. Although chondrichthyans have evolved to fill many aquatic habitats and niches, their ability to adapt quickly to human-induced environmental changes is assumed to be limited [9–11]. In contrast to most marine fishes, they generally have a K-selected life-history strategy: slow growth, late age at maturity, low fecundity, and few offspring, long gestation periods and long lifespans [6]. These life-history traits have important implications for fisheries’ sustainability, management and conservation [12–14]. For sharks in particular, it is widely accepted that the major threats to their populations are overfishing and habitat degradation, but this group is also at relatively high risk from climate change [15,16].
2. Ocean acidification

The anthropogenic emissions of greenhouse gases to the atmosphere are driving rapid changes in the Earth’s climate system, which are expected to accelerate in the current century. Atmospheric carbon dioxide (CO\(_2\)) levels have risen to 400 \(\mu\)atm [17] for the first time in at least 800,000 years and are expected to exceed 900 \(\mu\)atm by 2100 if the current emissions trajectory is maintained [18]. The pCO\(_2\) of the ocean is rising as the same rate as the atmosphere [19], and the uptake of additional CO\(_2\) from the atmosphere is causing ocean pH to decline. Ocean surface pH is projected to decrease by 0.13–0.42 units by the end of the 21st century, depending on CO\(_2\) emission scenarios [18]. These changes in seawater chemistry and the subsequent shift in the relative proportion of species of dissolved inorganic carbon (DIC), together known as ocean acidification (OA), will have cascading effects on marine ecosystems [20,21].

Higher ambient CO\(_2\) levels act to acidify the blood and tissues of water-breathing marine organisms [22]. Teleost fishes, however, are assumed to be quite resilient to elevated CO\(_2\) because of their ability to regulate acid-base balance by bicarbonate accumulation and ion exchange across (primarily) the gills [23–25]. Sharks and their relatives use a similar mechanism to that of teleost fishes [26]. Yet, it is worth noting that they are osmoconformers, whereas teleost fishes are osmoregulators. Being an osmoconformer in seawater means that the blood plasma has roughly the same osmolality as the seawater, which largely comes from high concentrations of urea and trimethylamine N-oxide (TMAO) [27–29].

Until recently, there were no experimental data with which to assess the possible effects of OA on sharks and their relatives. Only through ‘Ecological Risk Assessments’ (ERAs) for climate change was it argued that OA would not directly affect sharks, although it may indirectly affect them via changes in habitat, marine community structure and prey availability [11]. The underlying reasoning behind these conclusions was the fact that the modern sharks evolved in the Devonian, when atmospheric CO\(_2\) levels were many times greater than the current day [29], and therefore it was expected that they should be highly tolerant of high CO\(_2\) due to their evolutionary history. However, teleost fishes also evolved in a period of high CO\(_2\) and this has not conferred an overarching tolerance to high CO\(_2\) in all extant species [30]. Furthermore, new studies have revealed empirical evidence that sharks and their relatives may be more sensitive to OA than previously predicted, especially during their early life stages (embryos, newborns and juveniles). Here, we present the first review on the subject and apply a meta-analysis approach to assess the direction and magnitude of biological responses of sharks to OA (i.e. simulated end-of-century elevated CO\(_2\) conditions). More specifically, we use the meta-analysis to test whether OA will have a negative effect on survival, growth, physiology and behaviour in the species investigated to date and how these effects will interact with environmental warming (methodological details in electronic supplementary material).

Also, depending on how long the embryos are retained by the mothers, shark species can be divided by oviparous (egg-laying) or viviparous (live-bearing) reproduction. Oviparous species retain the fertilized eggs for short periods, after which the eggs are attached to benthic structures until hatching. To our knowledge, no studies have yet examined the possible effects of OA on embryonic development in viviparous species, and only three studies to date have evaluated the possible effects of OA on the embryonic development of oviparous species—the tropical bamboo (Chiloscyllium punctatum) and epaulette (Hemiscyllium ocellatum) sharks and the temperate Port Jackson shark (Heterodontus portusjacksoni) (table 1). Overall, these studies found no significant effects of OA on embryo survival and development time (figure 1). Moreover, specific growth rates, yolk consumption, tail oscillations and gill movements were not significantly different in embryos exposed to control conditions when compared with those reared under elevated CO\(_2\) conditions [32,37,39]. As expected, elevated temperature significantly increased the rate of embryonic development, but there was no interaction with elevated CO\(_2\) [32,39] (figure 2). It is possible that oviparous shark species may display adaptive mechanisms that confer tolerance to elevated CO\(_2\) conditions inside the egg capsules. Nonetheless, it is worth noting that in another chondrichthyan group (skates), Di Santo [42] found that CO\(_2\)-induced acidification exacerbated the effects of high temperature stress on the embryogenesis in the little skate (Leucoraja erinacea). Although early development was not significantly affected by elevated CO\(_2\) in the shark-related studies conducted to date, more studies are necessary to increase replication, to focus on critical developmental periods (e.g. the pre-gill formation period is normally linked to higher mortalities [37]) and to consider oviparous species that thrive at higher latitudes.

4. Physiology

The physiological effects of simulated end-of-century elevated CO\(_2\) conditions have only been evaluated in four relatively sedentary, benthic species: the temperate lesser-spotted (Scyliorhinus canicula) catshark [38] and Port Jackson (H. portusjacksoni) sharks [39,40] and the tropical bamboo (C. punctatum) [32–34] and epaulette (H. ocellatum) sharks [35,36] (table 1). Previous studies investigating physiological processes under elevated CO\(_2\) in sharks have been conducted at very high CO\(_2\) levels (>8–10 mm Hg, approximately 10 000–13 000 \(\mu\)atm) (e.g. [29]) that are not ecologically relevant to the impacts of near-future ocean acidification. Consequently, they are not included in this review and meta-analysis. Although there was no overall effect of OA-relevant CO\(_2\) levels on the survival of recently hatched and juvenile sharks, some physiological impairments have been detected (figure 1). For instance, while there were no modifications to growth in S. canicula, significant changes in resting metabolic rate, aerobic scope and blood chemistry (increased HCO\(_3\) and Na\(^+\) levels) were detected. Similar acid-base compensation, blood haematology variables (e.g. haematocrit, haemoglobin concentration, and mean cell haemoglobin concentration) and respiratory (resting oxygen consumption rates, citrate synthase activity and hypoxia tolerance via Pcrit) responses to elevated CO\(_2\) were observed in H. ocellatum [35]. The latter authors suggested that these physiological responses
Table 1. Summary of the available experimentally based studies on the impacts of ocean acidification (OA) in sharks. Abbreviations: C, control; T, treatment; dph, days post-hatching; Hct, haematocrit; Hb, haemoglobin; MCHC, mean cell haemoglobin concentration; R-h, recently hatched; NA, not applicable.

<table>
<thead>
<tr>
<th>Shark species</th>
<th>Region and life strategy</th>
<th>Life stage</th>
<th>pCO₂ (µ-atm)</th>
<th>pH</th>
<th>Temperature (°C)</th>
<th>Acclimation period (days)</th>
<th>OA effects</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chiloscyllium punctatum</td>
<td>tropical and benthic</td>
<td>embryos and r-h juveniles (30 dph)</td>
<td>371–382</td>
<td>1383–1481</td>
<td>8.0</td>
<td>7.5</td>
<td>25.9–26.2</td>
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<td>juveniles</td>
<td>397–384</td>
<td>608–876</td>
<td>8.2</td>
<td>8.0–7.9</td>
<td>28.5</td>
</tr>
<tr>
<td>Hemiscyllium ocellatum</td>
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<td>juveniles</td>
<td>400</td>
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<td>8.0</td>
<td>7.9–7.8</td>
<td>28.8</td>
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<td>945</td>
<td>8.1</td>
<td>7.9</td>
<td>28.3</td>
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<tr>
<td>Scyliorhinus canicula</td>
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<td>juveniles</td>
<td>401</td>
<td>993</td>
<td>8.1</td>
<td>7.7</td>
<td>12.7</td>
</tr>
</tbody>
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(Continued.)
were associated with *H. ocellatum* living in shallow reef and lagoon habitats that naturally experience variable CO2 levels, which could confer them a certain degree of tolerance to projected future CO2 concentrations. Contrary to these two studies that encompass acclimation periods varying between 30 and 60 days (table 1), other studies performed in recently hatched juveniles exposed to elevated CO2 during the entire embryogenesis (more than 200 days of acclimation; table 1) observed significant changes in Fulton’s condition index [32], aerobic potential (citrate synthase activity), peroxidative damage in the brain, cholinergic neurotransmission [33] and digestive enzyme activities [34], among other physiological variables. Most of these effects also exhibited significant interactions with elevated temperatures (figure 1). Thus, in addition to the limited number of studies, the different duration of the experiments also challenges our ability to make strong inferences on effect size, since studies with shorter acclimation periods (less than three months; see table 1) have contrasting effects to studies with much longer acclimation times.

Another key aspect of shark physiology that could alter blood pCO2 and thus make some species more or less sensitive to elevated water CO2 is the ability to pump water over their gills. While some sharks use buccal pumping (usually less active and benthos-associated species), others oxygenate...
the gills by opening their mouth while swimming – ram ventilators (more active and pelagic species). All species studied to date fall within the first category and, therefore, there is a complete lack of knowledge necessary to predict the effects of OA on the behavioural and physiological ecology of the larger and more active sharks, such as those belonging to the Carcharhinidae (requiem) and Sphyrnidae (hammerhead) families. In other fast-swimming (non-obligate) ram ventilators (e.g. mackerels) it has been shown that as swimming speed increases blood pCO2 declines in a linear way [43]. Thus, ram-ventilating sharks may be more susceptible to OA because they have lower internal pCO2 values than their benthic counterparts. The smaller differential between ambient and internal pCO2 in ram ventilators could make them more sensitive to OA because of the larger relative increase in internal pCO2 when exposed to increasing ambient CO2 levels [44].

5. Behaviour
Sharks are generally considered to possess superior olfactory sensitivities when compared to teleost fishes due to sharks’ particularly large olfactory structures, which play a key role in their capabilities for predator avoidance, prey detection and navigation [45]. Sharks and their relatives also possess unique and elaborate (ampullary) electroreceptor systems that facilitate geomagnetic navigation and detection of preys’ bioelectric fields [46]. Contrary to the other phenotypic responses, elevated CO2 has been found to significantly affect shark behaviour (figure 1). For instance, Pistevos and colleagues showed that Port Jackson sharks reared under simulated end-of-century elevated CO2 conditions (approx. 67 days in mesocosms) took nearly four times longer to detect their prey than those reared in control conditions [39]. However, in combination with elevated temperatures, the amount of time to detect prey was reduced by one third. This temperature effect was recurrent in other studies and is highlighted in figure 2. In a subsequent study [40], the same team revealed that although warming increased prey location rate in H. portusjacksoni, future CO2 conditions inhibited the chemical and visual behavioural responses that allow effective hunting in the test arenas. Similarly, Dixson et al. [41] found that high CO2-treated smooth dogfish (Mustelus canis) were less attracted to a water stream containing a food stimulus and reduced attack behaviour when compared to their control counterparts. Lesser-spotted (Scylorhinus canicula) catsharks exposed to elevated CO2 levels exhibit increased absolute lateralization and significantly fewer swimming events [38]. Together, these studies
demonstrate that exposure to elevated CO2 can significantly impair critical feeding behaviours and activities in sharks. On the contrary, however, the behaviour of the benthic reef-dwelling H. ocellatum was unaffected by the projections for ocean CO2 by 2100 [36]. Again, the absence of phenotypic effects in this species was explained by adaptations to the die fluctuations in oxygen and CO2 that are found in their shallow, reef habitat, illustrating that sensitivity to higher CO2 levels may be habitat specific.

The broadly similar behavioural changes to OA observed in marine teleosts have been attributed to interference between acid-base regulation in a high CO2 environment and the function of the GABA-A receptor, the primary inhibitory neurotransmitter receptor in the vertebrate brain [47]. The GABA-A receptor is an ion-channel with conductance for Cl- and HCO3- and under normal (control) conditions, ion inflow leads to membrane hyperpolarization and inhibited neural activity. Under elevated CO2, marine teleosts make regulatory adjustments in blood and tissues that affect such transmembrane gradients in some neurons [22]. Consequently, GABA-A receptors can become depolarizing and excitatory, resulting in behavioural impairments [22,47–49]. The same explanatory mechanism could apply to sharks, since they possess the same GABA-A neurotransmitter receptor [50] and accumulate HCO3- from the environment in exchange for Cl- from the body to buffer eventual pH disturbance. A pharmacological approach (e.g. the use a GABA-A receptor antagonist such as gabazine) to test this hypothesis in sharks has not yet been undertaken but warrants investigation.

6. Conclusion and future directions

The structure of marine food webs has already been altered due to dramatic declines in shark populations from overfishing and habitat deterioration [7,9,10,14]. Until recently, ocean acidification was not considered a direct threat to sharks. Recently available empirical evidence suggests that they may be more susceptible than previously assumed. Physiological impairments due to elevated CO2 exposure were less evident than behavioural impairments, and revealed greater interspecific variability. Future studies should choose species with different lifestyles, from different climate zones and habitats, and/or species with different niche preferences. Aware that short-term studies do not consider the potential for adaptation over the time frame that CO2 levels will rise by the end of the century [51], future research should also attempt to conduct transgenerational (multiple generations; namely in oviparous species) approaches. More empirical data are thus required to directly assess the risk and vulnerability of sharks to climate change and ocean acidification, which will assist managers and policy makers to make informed decisions targeting the most endangered species.

Data accessibility. The meta-analysis methodology is provided in the electronic supplementary material.

Competing interests. We declare we have no competing interests.

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