THE EFFECT OF CLIMATE CHANGE ON THE PREDATORY SUCCESS OF SHARKS

A Paper
Submitted to the Graduate Faculty
of the
North Dakota State University
of Agriculture and Applied Science

Ву

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In Partial Fulfillment of the Requirements for the Degree of MASTER OF SCIENCE

Major Program: Natural Resource Management

April 2021

Fargo, North Dakota

North Dakota State University Graduate School

Title

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MASTER OF SCIENCE	
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ABSTRACT

This literature overview focuses on how shark species, are faring with the anthropogenically induced climatic changes. The ocean is drastically affected by this, which has major implications on the aquatic life. Some effects include increasing temperature, carbon dioxide and acidity levels. This has led to shifts in the predatory success in sharks, which will only increase in severity as climate change intensifies, because changes in climate induce other changes in most aspects of the shark's life. These can be grouped into three categories: shifts in body functions, behaviors and habitat. Some changes in body function include difficulty integrating sensory cues through reduced neuron receptor function, decreased brain/muscle aerobic potential and changes in growth/development. Behavioral changes include shifted swimming patterns, interacting with different species assemblages and prey behaviors. Lastly, habitat changes affect the shark's ability to capture prey through increases in salinity, degradation of critical habitat and reduction in dissolved oxygen.

ACKNOWLEDGMENTS

I'd like to extend a thank you out to my advisor Dr. Jason Harmon for leading me through the process of writing this paper and helping me with everything. I would also like to thank Dr. Timothy Grieves and Dr. Gary Clambey for being on the advisory committee and taking the time to read and evaluate this thesis.

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INTRODUCTION

In the past century, climate change has become an increasing global issue that brings with it farreaching effects. Many areas are threatened by a whole host of threats including but not limited to
warming temperatures and natural disasters that are increasing in frequency. These changes are felt
directly and indirectly by the organisms inhabiting this planet, and overwhelmingly carry with them
negative effects. Sharks are no exception to feeling these negative and far-reaching effects of climate
change. They are feeling the pressures of climate change in numerous ways such as changes in their
body functions, behavior and habitat. This review will explore the changes in predatory behavior that have
ensued due to the anthropogenically induced change in climate.

Since the ocean covers a vast majority of the planet, it is also influenced by this warming. The temperature of tropical surface waters has increased approximately 0.5-0.6°C since the 1850's, due to the decrease in atmospheric circulation and the increase of surface air temperature (1). As the atmosphere heats up, a portion of that kinetic energy is absorbed by the oceans which negatively impacts many species in their ability to thrive or even just survive. This is especially pronounced in tropical regions where species may already be near their thermal tolerance limits (2). Tropical species also tend to be less tolerant to fluctuations, as they evolved under conditions that were quite stable, as opposed to subtropical or temperate species (3). Another issue that will pose problems for aquatic life is that the pH of the oceans has been decreasing. Carbon dioxide is at the highest level (>395 ppm) it has been at in the past 800 000 years, and it is steadily increasing (5,6). The level would be much higher if the oceans would not pose as sinks, absorbing about 25% of the excess carbon dioxide (7). This leads to a reaction with the seawater, which gives rise to an excess of hydronium ions. It has been hypothesized that the oceans pH may drop by 0.14 and 0.5 pH units by the end of the twenty-first century (4).

Sharks are very important players in the marine ecosystems, as they are apex predators and thus exert top-down controls over the ecosystem. Their cascading effects influence many aspects such as the structure, function and the overall health of these ecosystems (8). Unfortunately, sharks have a very slow rate of evolution and low phenotypic plasticity, which puts them at an innate risk to the rapid changes caused by human influences on the environment such as climate change. This can be attributed to their K selected life histories which include slow growth, late age at maturity, low fecundity, few offspring, long

gestation periods and long lifespans (9). According to IUCN, approximately a third of all pelagic shark species are at some risk of extinction, and 64 of those are on the Red List (10). This means that many ecosystems are experiencing negative effects due to the decrease in shark populations.

The predatory behaviors of sharks are imperative to their survival as they are carnivorous and thus it is their only way of acquiring nourishment. There are many factors that play into their success as a predator. As previously mentioned, this paper will focus on three overarching factors that play a role in the success of sharks as predators and are affected by climate change. These factors are body functions, behaviors and habitat. Sharks have isophisticated sensory organs that relay on chemical and electrical signals. With the changes in water chemistry, these messages are affected in multiple ways. Their metabolism, ventilatory capabilities, growth and development are other body functions that have felt the burden of climate change (11, 12, 13). Behavioral changes that have been documented are lethargy, changes in competition, and co-occurrence and prey responses (11, 14, 15). The last factor, changes in habitat that effect shark predation encompasses shifts in habitat, and the speed of these shifts, water quality, and primary production (16, 17). Climate change has affected sharks in numerous ways and this paper is in no account a complete analysis of every way they are affected. The scientific community has not explored every aspect of this dilemma to begin with and probably never will, as this is virtually impossible. From the data that are available, there are certain themes that kept reoccurring and made it possible to group them into broad topics. Three topics tended to be the most prevalent and, thus, the objective of this paper became to analyze those three topics. These themes are how climate change induces shifts in body functions, habitat and behavior, which create cascading effects that end in the alteration of the shark's feeding ecology.

METHODS

The first step I took in the process of constructing this literature review was compiling scientific papers that pertain to my topic of interest. I did this by using the North Dakota State University online data base and Google scholar throughout the 2020 and 2021 school year. I only included articles that were published in English and in peer-reviewed journals. I first focused on how climate change could be influencing sharks but decided to narrow it down to how it is affecting their feeding ecology because the prior topic produced an overwhelming amount of data in a vast number of different topics. After collecting some data, I refined my question even further to focus purely on their predatory success in the sense of their ability to successfully capture prey. I also looked at species that were closely related to sharks, as there are certain situations that pertain to sharks.

The search terms that I used were multiple combinations of words associated with climate change, sharks, ocean acidification, feeding ecology, ocean warming, predation and behavior. For articles that were exceptionally relevant to my study, I scanned the references for more papers that were of interest to me. In a Word document I listed all the papers that I had collected and for each one I recorded the significant information that it presented. This allowed me to get a good overview of what I had and what I might have missed. This strategy helped me organize the papers into topic groups of body functions, behavior and habitat. It also aided me in determining the overall results. Utilizing this information, I was able to write a review on what the scientific community has ascertained about sharks, their predatory success and how this has been affected by climate change.

This literature review was not meant to be an exhaustive search of all articles that relate to how climate change is affecting the predatory success of sharks, as there is such a wide range of articles that investigate some aspect of this topic in sharks and other species closely related to them. I ended up with 46 articles published between 1978 and 2020.

RESULTS AND DISCUSSION

Throughout the scientific literature, there is a significant number of studies that focus on some aspect of climate change and shark predation. Three topics that seemed to stand out in the fact that they were commonly addressed themes, were papers that investigated some aspect of their body functions, behavior or habitat. These three topics are very interconnected, so many of the papers touched on more than one of these topics if not all three. Picking these apart was quite a difficult task and in some cases impossible and therefore certain discussion points will be addressed in multiple sections, with only one going into depth as this repetition would be unnecessary. In each section I will discuss the findings of the relevant papers, how this is currently affecting the ability for sharks to acquire prey and speculate what this will mean for future populations.

Over all three topics, a predominant catalyst of change was ocean acidification. Throughout the literature, there are many studies published that show that increasing dissolved CO2 levels have the ability to impact many aspects of ocean life. This includes but is not limited to habitat qualities such as water pH, which possibly affects internal biological processes. Some of these processes are receiving and integrating sensory cues, which are then closely tied to formulating appropriate behavioral responses in aquatic organisms (12, 18, 19). In experiments where marine organisms, including sharks, are exposed to CO2 levels (and consequently acidity levels) that are predicted to occur in the ocean by 2100, their ability to differentiate and make decisions as a result of auditory (20) and olfactory cues (12,18,19) was greatly impaired. This led to a reduced homing ability, habitat selection and a higher risk of predation if they were in a juvenile state or meso predators that feed at a middle trophic level (12). This is where the separation between body functions and behavioral effects becomes murky as one leads right into the next.

Body functions

As a start for this section, it seems appropriate to continue with the example from the previous paragraph on how an increase in carbon dioxide affects the internal mechanisms of shark. One of these effects is an impairment in its ability to receive and integrate sensory cues. Scientists have proposed that the reason for this impairment is because of a change in ion concentrations (12). When species that are exposed to high levels of CO2 and thus acidity, they will try to regulate this by accumulating HCO3-. This

is always accompanied by an equimolar decrease in CI- (39). These changes of CI- and HCO3- gradients in the neuron membranes interfere with the GABA receptor's function, as these chemicals are heavily involved in the deactivation and activation of this receptor. This leads to abnormal behaviors such as olfactory abnormalities. Additional research is still needed to provide stronger evidence for this, but as this receptor is heavily conserved in its function it is likely the case.

The increases in CO2 which alter the ability to pick up and integrate olfactory cues have an especially pronounced effects in sharks, as they rely heavily on their superior olfactory senses for locating food, mating, predator detection, homing and navigation. This is in part because many shark species are nocturnal (21, 22, 23) which makes visual cues less useful. To demonstrate these sensory changes and their importance, a study on dog fish sharks revealed that when kept under normal circumstances, they preferred squid odor, but when subjected to ~1000 µatmCO2, the sharks strongly avoided it (12). This obviously impacts their ability to locate and thus catch prey. Another reason why olfaction is so important in sharks, is that these signals can move a lot farther than visual, mechanical, or electrical signals, as water currents can transport them much further. That being said, when their normal or preferred sensory cues are not available, sharks are able to switch to alternative senses in order to still detect, track and capture their prey successfully (24). In most species of sharks, olfaction is the first sense activated, followed by vision, hydrodynamic imaging and then electroreception as the individual got closer to its prey, with touch being the last but nonetheless still very important for orienting, striking at, and capturing the prey. Sharks can use multiple sensory cues at once or switch between different ones in a hierarchical order as they advance on their prey. This ability to be flexible with their sensory cues gives some hope to their ability to deal with the sensory issues posed by climate change as they can switch to different sensory pathways if one is being disproportionately impacted, allowing them to still succeed in a changing environment.

Continuing with the increasing temperatures combined with acidity effects on body functions, it has been experimentally shown that when juvenile sharks were exposed to these conditions, they expressed a significant decrease in brain and muscle aerobic potential (citrate synthase activity).

Interestingly the brain and muscle anaerobic potential (lactate dehydrogenase) increased in these conditions (41). Furthermore, the shark fitness and survival were very closely correlated with the brain's

aerobic potential, and the brain's anaerobic potential was inversely correlated with its overall survival. As the shark adjusted to these conditions, they experienced shifts in metabolic activity which then led to an increase in the individual's metabolic demand. This was then followed by an increase in reactive oxygen species (ROS). To counteract the ROS the body will produce an increased amount of antioxidant enzymes but unfortunately, this increased production of antioxidants was not enough to completely counteract the effects of the ROS. This led to an increase in brain's peroxidative damage and cholinergic neurotransmission. A potential implication of this could be that in future conditions we could be seeing deleterious deficiencies being elicited in the sharks' critical body functions such as reduced neurotransmitter excess in the synaptic clefts. This could then lead to similar behavioral changes as above, such as avoiding food odors or reduced attack behavior.

Another effect that the environmental changes have on sharks' body functions involves their growth and development (25). Starting at the embryonic stage, certain species showed a decrease in survival and an increase in developmental rate due to the increased temperature. These increased temperatures combined with elevated CO2 concentrations also lead to increased energetic demands through a reduced metabolic efficiency. When this is combined with the before mentioned degradation of the olfactory senses (meaning reduced predatory success) the results led to stunted growth due to malnourishment. This would affect their ability to prey on larger organisms and thus limit the spectrum of their diet. This problem is also magnified by the fact that most sharks receive no parental care and thus must rely on themselves right from birth. If there are born in poor condition, they are at a disadvantage and survival becomes increasingly difficult. There are however certain sharks that can handle very high concentrations of CO2 without any metabolic impairments, such as the epaulette shark (13). These types of sharks will most likely be the ones that will have the upper hand in the future and could increase their proportion of the shark community. Other sharks occupy a middle ground of being able to cope with these conditions by not having stunted growth but exhibit other impairments (11). This shows that there is a continuum of ability to cope, and those with the lowest ability should be of greatest concern.

Not only is juvenile growth affected by these temperature rises but also the natural weight fluctuations that happen in correlation with the changing seasons (40). In areas such as Australia, where there is a distinct dry season, many species tend to lose body mass due to the harder conditions. The

current ocean conditions have led some sharks to lose up to 0.17% of their body mass per day. Under future climate change conditions, it has been predicted through bioenergetic models, that species could potentially reach lethal levels of weight loss during the dry season as soon as before the end of the century. This means that species with slower metabolic rates would be better equipped to survive in these conditions. Overall, this would impact the sharks in that they would need to increase their intake in order to combat the increased weight loss. The problem with this is that more activity (in the sense of hunting more prey) would lead to an even greater energy expenditure meaning that there is a delicate balance. Also, prey would probably be limited in the dry season making it harder to find, meaning an even bigger expenditure.

Ocean acidification is a big factor that can affect the internal mechanisms of sharks and other marine organisms. In a study focusing on the blood chemistry of small-spotted catsharks in relation to ocean acidification, these sharks were able to cope with certain aspects of this change in environment but there were also aspects that they did not fare well with. They exhibited no significant effects on growth, resting metabolic rate, aerobic scope, skin denticle ultrastructure or skin denticle morphology in the four-week exposure (13). But just like the results in one of the previous paragraphs, the elevated CO2 levels caused the sharks to buffer the internal acidosis by accumulating HCO3- which led to changes in Na+ and CI- concentrations. The scientists hypothesized that the changes in these concentrations could lead to a decrease in the hyperpolarization of neurons, which in turn could reduce the inhibition of CNS motor regions. If motor neurons of the central nervous system (CNS) region in the spinal cord were affected, a whole host of problems could potentially ensue. These neurons connect and transmit impulses to muscles, glands and organs throughout the body. Thus, it could affect anything from intestinal peristalsis to secretion of hormones or not being able to properly control their movements while striking prey. Being that this study was relatively short, it was not possible to determine if all these effects would take place, as longer exposure time would be needed.

The last effect on body function that I will discuss is how ocean acidification and warming impacts digestive enzyme levels. When juvenile tropical bamboo sharks were exposed to future ocean conditions, it was revealed that they experienced significant drops in digestive enzyme activity such as trypsin and alkaline phosphatase (42). It was suggested that the exposure to these future conditions could potentially

alter the sharks processing of ingested prey which could then lead to decreased available energy needed to fuel crucial body functions and thus result in a slower metabolism and reduced general fitness. When a shark's energy and physical fitness are reduced, they are obviously at a disadvantage for finding and capturing prey. This is because they may not have the strength to capture larger prey items or have the speed to catch fast ones. This narrows their range of possible prey. They will also have more bouts of unsuccessful hunts which uses up even more energy that they do not have to spare. This could potentially produce a vicious cycle of decreasing energy. The type of shark used in this study generally has a lower metabolic rate than certain other species, as they are benthic and have buccal ventilation, which is the done by forcing of water over the gills by opening and closing the mouth. Studies focusing on pelagic ones with ram ventilation, which is the act of forcing of water over the gills through swimming and thus meaning that they have higher energetic demands, would be invaluable to the scientific community and shark conservation programs.

Behavior

Continuing onto behavioral changes that affect the success of sharks as predators, there are many changes that have been documented already. As environmental conditions change, many species may shift their activity periods or habitat in general due to the deterioration of essential habitats. This changes the assemblage of other species they interact with, as not all species experience these shifts or shift to a different degree. This in turn causes changes in the populations, community structure and interactions, such as competition and niche overlap. This has been documented with black-tipped and bull sharks, whose co-occurrence and interspecific competition increased, causing bull shark populations to decrease in order to reduce this competition (14).

In the afore mentioned study on small spotted cat sharks (13), the changes in the internal functions of the individual were hypothesized to be the reason for the recorded shifts in behavior. The nocturnal swimming patterns shifted from many starts and stops to a non-stop pattern. They also exhibited increased lateralization of the brain. These types of non-stop movements use a lot more energy leading to the shark tiring out faster. With less energy available, the chance of successfully catching prey decreases, which sets the shark up for a downwards spiral of decreasing energy availability. Also, due to before mentioned changes in olfaction and brain chemistry, sharks consume their food slower and do not

respond as fast or at all to the olfactory cues of their potential prey (25). This again would ultimately result in increased energy expenditure as the shark must forage longer until a prey is found and eating slower would expose them to a greater risk of being attacked by higher order predators.

If a nocturnal shark is experiencing a reduced olfactory capacity and is forced to switch to alternative senses such as vision to hunt, there may be the distinct possibility that they would alter their hunting bouts to the daytime (25). This would allow them to take in better visual cues and increase their change of having a successful hunt. That being said, when comparing this to the shark hunting with a completely functional olfactory sense, they still would be at a disadvantage, as olfaction is their preferred and primary sense. This would also mean that their niche would shift in multiple ways. They might start preying on and competing with a different array of species. This could produce many cascading effects in their immediate and surrounding environments, especially if they are key stone species.

Overall, most organisms have some sort of ability to acclimate to environmental stressors by altering different characteristics to cope with changes. When sharks are burdened with the reduced olfactory capacity, they tend to leave some potential prey undetected (25). Thus, to combat this reduction in prey, the shark would spend more of its time searching for a prey item before it successfully catches one. If the shark is a meso-predator or juvenile, this change in hunting duration would also increase their vulnerability to higher-order predators.

Not only the sharks, but also their prey can fall victim to altered behavior due to the implications of anthropogenic climate change. Under normal acidity levels in freshwater systems, when fish are exposed to alarm cues, they have an innate response of predator avoidance behavior, which includes decreasing their activity levels, hiding or engaging in tighter group cohesion (26). When the pH of the environment was decreased, their predator avoidance behavior was reduced or ceased completely when the alarm cues were released into the environment (27, 29). In conjunction with that, when they were exposed to basic chemical food stimuli, they also exhibited a reduced response to it, if at all (28). In marine ecosystems, the changes observed were a little different due to the differences in how acidification affects the species. This however is not to say that both may be observed in either habitat. In certain marine species, under mildly acidified conditions a reduced ability to discriminate between the olfactory cues of suitable versus unsuitable habitats, kin and non kin and predator and non-predators was

observed (18). When the waters were acidified even further, they either lost the ability to discriminate completely or became attracted to the cues that they usually avoided. Juveniles also exhibited more active and riskier behavior by venturing out further from their shelters. At first these behavioral changes would make them easier targets for sharks and other predators but if predators were to take advantage of this, there is the potential that these fish stocks would eventually be depleted, radically reducing the replenishment of fish populations (34). In the long run, this would make finding prey, especially adult individuals, increasingly difficult for predators. However, when a predator does encounter a suitable prey, it would have an easier time catching it, as the fish would be weaker from the lack of food, be out in the open, and would not respond as readily or even be attracted to the presence of the shark.

Lastly, a note on the before mentioned shark species that have a higher capacity to handle increases in carbon dioxide such as the previously mentioned epaulette shark. Since they experienced no known shifts in metabolic, neurological or other activities their behavior was also unaffected (13).

Habitat

The last broad topic that will be discussed in this paper is the habitat alterations and its effects on shark predation. As covered in the introduction, climate change has rapidly changed many factors in the environment such as water pH, temperature and chemistry. Certain areas of the ocean are more affected than others which gives migratory species an advantage as they can move to more favorable/less altered environments. However, not all shark species are migratory, and these species may therefore be restricted to small areas. This is especially true for juvenile sharks, which concurrently is also their most vulnerable stage (25). Species that are bound to fresh water, estuarine or reef environments are also at great risk as these environments tend to be hit the hardest with fluctuations and extremes in temperature, salinity and ocean currents. Yet migratory species are not free of risk either, as they tend to be the larger species which is usually coupled with a slower growth rate and tend to bear smaller numbers of off springs. This means that they would have a harder time adapting to the rapidly changing conditions.

The species that are migratory would most likely extend their habitat more pole wards to escape the increasing temperatures, as their fundamental thermal range as defined by physiological tolerances will have shifted that way (30, 31). This would change the food webs and therefore the ecology of both the habitats that were left behind and those they moved to, as the shark species i.e., apex and/or meso

predator have left/been added. This could also impact the shark community, as species might change their diet depending on what is available. This could increase inter- and intraspecies competition, leading to a decreased food availability in the new habitats if there are a lot of sharks moving in. Shark species that are very aggressive hunters would have the upper hand potentially forcing the less aggressive species to lower quality habitats in search of food.

Increasing water temperatures not only could force a change in migratory behavior but also decrease overall fitness and success with the most substantial drop happening after 32 degrees Celsius (45). To top it off, temperature has also been shown to be a potential predictor of daily and monthly variability in predation rates of sharks (16). Whether this is due to direct impacts or indirect ones like changes in prey availability is unknown. Either way, water temperature was not the main cause of the change, as other signals such as the temperature variability over the season was a stronger predictor.

Also, water temperature did not seem to affect the inter-annual variability in predation rate at all. Instead, wind, water visibility, and the occurrence of El Niño and La Niña events tended to predict this. Other experiments that dealt with water temperature observed different noteworthy patterns. When sharks and other aquatic predators were experimentally exposed to increased water temperatures in a laboratory setting, their hunting efforts as well as feeding rate showed a significant increase (32, 33). When extrapolating the results to the long-term, this could change ecological processes, such as predation intensity.

When considering the effects of pH and carbon dioxide on the ecosystem, it is important to also consider the natural fluctuations that occur. If sharks live in an environment that naturally quite variable or just constantly high in these parameters, they may already be adequately adapted to these changes making them more tolerant to the effects (26). Especially in freshwater ecosystems, there may be wide range of conditions that a species must deal with. Even rainfall events of 30 mm have the capacity to decrease the acidity by 0.2-0.6 pH units. Some freshwater systems also have a poor buffering capacity and can fluctuate almost 1 pH unit in a single day. Similarly, in marine systems such as shallow coral reefs where water exchange is restricted, there can also be steep fluctuations. This is caused by the changing dissolved carbon dioxide concentrations through the fluctuating balance between respiration and photosynthesis from night and day.

For many species of sharks, coastal and estuarine waters are considered critical habitats for the juveniles, as they have high productivity, in part through their shallow, protected waters (35). Coral reefs are often found in these areas and they have experienced detrimental effects from climate change such as coral bleaching. As the reefs degrade, this essential habitat is lost for not only the sharks but also many species that they prey on. This results in the reduction of food quality and quantity which ultimately leads to an increase in competition. The competition is most pronounced for juveniles that are not as adept as the mature sharks and would lead to a reduced recruitment in the population. Unfortunately, for many species, these essential habitats haven't been identified yet, as it is quite intensive work. This is because a large majority of sharks use a large range of habitats that span over vast distances, meaning they tend to have low densities (36). This makes preserving their critical habitats difficult as it is largely unknown and thus sharks continue to lose these habitats through climate change.

Increased salinity is another factor that anthropogenic climate change has imposed on aquatic environments (37). This influences the distribution and migration patterns of shark species, (35) as salinity and the cost of osmoregulation are strongly correlated. If the salinity is high enough, proper osmoregulation can become impossible ultimately killing the animal. This is then no surprise that the hypersaline environments are strongly avoided by sharks, as they function best in moderate to low salinities (based on the species). In certain areas such as Texas, the shifts in the climate have also had the effect of reducing the inflows of freshwater into the coast (38) which then only increases the salinity issue as there is less of a dilution effect. To make matters worse, this area in Texas has been deemed a critical habitat for sharks. This provides yet another handicap for sharks looking for prey as their body is either becoming increasingly salty, leading to internal complications or they are spending an increasing amount of energy on osmoregulation that could have been put towards hunting.

Other changes that were discovered in the Texas estuaries were that there was a reduction in dissolved oxygen and increase in temperatures (44), which together vastly decreased the habitat quality and, if not dealt with, might lead to the loss of essential habitats. This would be a massive hit to the shark community as it would exponentially impair their recruitment and hunting abilities. Increased occurrences of hypoxic conditions have been observed in many other places as well. Especially larger obligate ramventilating species will suffer under these conditions as they need higher oxygen levels. This is because

in order to breath, they must be in constant motion to keep a continuous flow of water passing through their open mouths and over the gills. Therefore, this constant motion uses more energy. If these levels are not met, their fitness and predatory success will decrease very fast as they will not be able to create as much ATP meaning they will have limited energy. This has been shown in juvenile sandbar sharks when they were subjected to lower dissolved oxygen concentration (44). They experienced the steepest drop in overall performance when the levels fell below 3.5 mg/L. The increasing occurrence of hypoxic environments has the potential to reduce the available shark habitat and negatively impact their overall population numbers, not to mention the overall health of the ecosystem. This would then lead to greater difficulties in finding healthy prey and catching it would also become increasingly difficult as the reduction of oxygen limits metabolic energy.

CONCLUSIONS

Over the last couple decades, climate change has rapidly changed vast tracts of habitat in multiple ways which ultimately has led to many species being forced to adapt, find new habitat or die off. Many species are having difficulties coping with this and are feeling the effects with increasing intensity. Sharks are among these species. One aspect that climate change has already and will continue to influence in sharks, is their predation. Three overarching areas that were discussed in this paper that climate change has affected and greatly play into these changes are shifts in their internal chemistry, behaviors and habitat.

All these effects that have been discussed in this paper are more than likely just scratching the surface of what these species are actually experiencing. Much is still not known, and scientists have hypothesized that the reality is far more complex (25). This is especially in light of the fact that many sharks are predators and key stone species, which are experiencing a reduced ability to hunt effectively, are thus not able to exert as strong of top-down controls over various food webs.

With all these potential and far-reaching effects that climate change imposes on sharks and the rest of the ecosystems of the world, it is becoming increasingly more important to take action. While there is already a good amount of knowledge on how climate change affects sharks and other marine species in general, we still and probably never will know the full extent of the damage that is being caused. That does not mean that it is not important to continue to research this topic because the greater of an understanding we have, the better we will be able to manage the problems that we are faced with. With all the knowledge we have at the moment, we can already effectively employ management strategies for combating these adverse situations and this must be done on a greater scale and strongly enforced if we do not want to lose species or even entire ecosystems.

As stated, there are still many gaps in the knowledge concerning this topic, as sharks are quite elusive and thus not the easiest species to study. Also, logistical and technological short comings often play a role of why certain studies have not been undertaken yet. But with ever-increasing technological advancements, the ability to conduct new experiments is always increasing. Throughout my research, I noticed certain trends of gaps in the knowledge. In my opinion, the ones that are the most pressing to be filled, are ones that look at long term effects (years to decades), as almost all the studies were only short

term. To be more specific, one that stood out to me was that water temperature increased the hunting effort and feeding rate in the short term in a laboratory setting (32, 33). This would be of great value to recreate in a natural setting for an extended period of time. Also, in my mind the most important thing to do is more in-depth identification of critical shark habitat, as this is an essential component for sustainable resource and species management. Often marine organisms are closely associated with specific physical or biological habitats and preserving these would massively help shark populations. Both these topics become closely related here, as long-term studies as well as conservation require the critical habitats to be identified and protected. Overall, as sharks are keystone species in many aquatic habitats, it is imperative for us to improve our ability to manage shark populations and habitats, especially as we are already seeing declines in shark populations (44).

REFERENCES

- 1) Vecchi, G.A., Wittenberg, A.T., Held, I.M., Leetmaa, A., Harrison. M.J. (2006). Weakening of tropical Pacific atmospheric circulation due to anthropogenic forcing. *Nature*, *441*, 73-76.
- 2) Hoegh-Guldberg, O., et al. (2007). Coral reefs under rapid climate change and ocean acidification. *Science*, *318*, 1737-1742.
- 3) Tewksbury, J.J., Huey, R.B., Deutsch, C.A. (2008). Putting the heat on tropical animals. *Science*, 320, 1296-1297.
- Meehl, G.A., & Stocker, T.F. et al. (2007). In Climate change 2007: the physical science basis (eds S Solomon, D Qin, M Manning). 686 – 688. Cambridge University Press.
- Dlugokencky, E., Tans, P. (2013). Trends in atmospheric carbon dioxide. Global Monitoring Laboratory Earth System Research Laboratory, NOAA http://www.esrl.noaa.gov/gmd/ccgg/trends/global.html#global.
- 6) Lüthi, D., Le Floch, M., Bereiter, B., et al. (2008). High-resolution carbon dioxide concentration record 650 000–800 000 years before present. *Nature*, *453*, 379–382.
- 7) Ballantyne, A.P., Alden, C.B., Miller, J.B., Tans, P.P., White, J.W.C. (2012). Increase in observed net carbon dioxide uptake by land and oceans during the past 50 years. *Nature*, *488*, 70–72.
- 8) Roff, G., et al. (2016). The Ecological Role of Sharks on Coral Reefs. *Trends Ecol Evolution*, *31*(5), 395-407.
- 9) Compagno, L.J.V. (1990). Alternative life-history styles of cartilaginous fishes in time and space. *Environ. Biol. Fishes*, 28, 33–75. (10.1007/BF00751027)
- 10) Camhi, M.D., Valenti, S.V., Fordham, S.V., Fowler, S.L., Gibson, C. (2009). The Conservation Status of Pelagic Sharks and Rays: Report of the IUCN Shark Specialist Group Pelagic Shark Red List Workshop IUCN Species Survival Commission Shark Specialist Group, Newbury, UK
- 11) Rosa, R., et al. (2014). Early-life exposure to climate change impairs tropical shark survival. *Proceedings. Biological sciences*, 281(1793), 20141738. https://doi.org/10.1098/rspb.2014.1738
- 12) Dixson, D.L., Jennings, A.R., Atema, J. and Munday, P.L. (2015). Odor tracking in sharks is reduced under future ocean acidification conditions. *Glob Change Biol, 21,* 1454-1462. https://doi.org/10.1111/gcb.12678
- 13) Green, L., Jutfelt, F., (2014). Elevated carbon dioxide alters the plasma composition and behavior of a shark. *Biol. Lett.*, *10*, 20140538. (doi:10.1098/rsbl.2014.0538)
- 14) Matich, P., Mohan, J.A., Plumlee, J.D. et al. (2017). Factors shaping the co-occurrence of two juvenile shark species along the Texas Gulf Coast. *Marine Biology, 164*, 141 https://doi.org/10.1007/s00227-017-3173-2
- 15) Manríquez, P.H., Jara, M.E., Mardones, M.L., et al. (2013). Ocean acidification disrupts prey responses to predator cues but not net prey shell growth in Concholepas concholepas (loco). *PLoS ONE*, *8*(7). e68643.
- 16) Skubel, R.A., Kirtman, B.P., Fallows, C., Hammerschlag, N. (2018). Patterns of long-term climate variability and predation rates by a marine apex predator, the white shark Carcharodon carcharias. *Marine Ecology Progress Series*, *587*, 129-139.
- 17) Ortega, L.A., Heupel, M.R., Van Beynen, P., Motta, P.J. (2009). Movement patterns and water quality preferences of juvenile bull sharks (Carcharhinus leucas) in a Florida estuary. *Environmental Biology Fish*, *84*, 361–373.
- 18) Munday, P.L., Dixson, D.L., Donelson, J.M., et al. (2009). Ocean acidification impairs olfactory discrimination of homing ability of a marine fish. *Proceedings National Academy Science USA, 106*, 1848–1852.
- 19) Dixson, D.L., Munday, P.L., Jones, G.P. (2010). Ocean acidification disrupts the innate ability of fish to detect predator olfactory cues. *Ecology Letters*, *13*, 68–75.
- 20) Simpson, S.D., Munday, P.L., Wittenrich, M.L., Manassa, R., Dixson, D.L., Gagliano, M., Yan, H.Y. (2011). Ocean acidification erodes crucial auditory behavior in a marine fish. *Biology Letters*, 7, 917–920.
- 21) Schluessel, V., Bennett, M.B., Bleckmann, H., Blomberg, S., Collin, S.P. (2008). Morphometric and ultrastructural comparison of the olfactory system in elasmobranchs: the significance of structure-function relationships based on phylogeny and ecology. *Journal of Morphology*, 269, 1365–1386.

- 22) Johnson, R.H. & Nelson, D.R. (1978). Copulation and possible olfaction-mediated pair formation in 2 species of carcharhinid sharks. *Copeia*. 3, 539–542.
- 23) Heuter, R.E., Mann, D.A., Maruska, K.P., Sisneros, J.A., Demski, L.S. (2004). Sensory biology of elasmobranchs. Biology of Sharks and Their Relatives. 236–358. CRC Press.
- 24) Gardiner, J.M., Atema, J., Hueter, R.E., Motta, P.J. (2014). Multisensory integration and behavioral plasticity in sharks from different ecological niches. *PLoS ONE*, 9, e93036. doi: 10.1371/journal.pone.0093036
- 25) Pistevos, J., Nagelkerken, I., Rossi, T. et al. (2015). Ocean acidification and global warming impair shark hunting behavior and growth. *Sci Rep*, 5, 16293 https://doi.org/10.1038/srep16293
- 26) Leduc, A., Munday, P.L., Brown, G.E., Ferrari, M.C.O. (2013). Effects of acidification on olfactory mediated behavior in freshwater and marine ecosystems: a synthesis. *Philosophical Transactions: Biological Sciences*, 368(1627), 1-14.
- 27) Leduc, A., Kelly, J.M., Brown, G.E. (2004). Detection of conspecific alarm cues by juvenile salmonids under neutral and weakly acidic conditions: laboratory and field tests. *Oecologia*, 139, 318-324. (doi:10.1007/S00442-004-1 492-8)
- 28) Lemly, D.A., Smith, R.J.F. (1985). Effects of acute exposure to acidified water on the behavioral response of fathead minnows, Pimephales prometas, to chemical feeding stimuli. *Aquat. Toxicology*, 6, 25-36. (doi:10. 1 01 6/01 66-445x(85)9001 7-7)
- 29) Leduc, A., Roh, E., Brown, G.E. (2009) Effects of acid rainfall on juvenile Atlantic salmon (Salmo salar) antipredator behavior: loss of chemical alarm function and potential survival consequences during predation. *Mar. Freshwater Res.*, 60, 1223-1230. (doi:10.1071/mf08323)
- 30) Kearney, M. and Porter, W. (2009). Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters*, 12, 334-350. https://doi.org/10.1111/j.1461-0248.2008.01277.x
- 31) Allen-Ankins, S. & Stoffels, R.J. (2017). Contrasting fundamental and realized niches: two fishes with similar thermal performance curves occupy different thermal habitats. *Freshwater Science*, 36, 635–652.
- 32) Dowd, W.W., Brill, R.W., Bushnell, P.G., Musick, J.A. (2006). Estimating consumption rates of juvenile sandbar sharks (Carcharhinus plumbeus) in Chesapeake Bay, Virginia, using a bioenergetics model. *Fish Bull.* 104, 332–342.
- 33) Miller, L.P., Matassa, C.M., Trussell, G.C. (2014). Climate change enhances the negative effects of predation risk on an intermediate consumer. *Global Change Biology*, 20, 3834–3844.
- 34) Munday, P.L., Dixson, D.L., McCormick, M.I., Meekan, M., Ferrari, M.C.O., Chivers, D.P. (2010). Replenishment of fish populations is threatened by ocean acidification. *Proceedings of the National Academy of Science USA*, 107, 12930–12934.
- 35) Froeschke, J., Stunz, G.W., Wildhaber, M.L. (2010). Environmental influences on the occurrence of coastal sharks in estuarine waters. *Marine Ecological Progress Series*, 407, 279–292.
- 36) Musick, J.A., Burgess, G., Cailliet, G., Camhi, M., Fordham, S. (2000). Management of sharks and their relatives (Elasmobranchii). *Fisheries*, 25, 9–13.
- 37) Stott, P. A., Sutton, R. T. & Smith, D. M. (2008). Detection and attribution of Atlantic salinity changes. *Geophysical Research Letters*, 35, L21702, doi:10.1029/2008GL035874.
- 38) Ward, G. (2009). Water Resources. In: Schmandt, J., Clarkson, J., North, G.R. (eds) *The impact of global warming on Texas*. University of Texas Press, Austin
- 39) Nilsson, G.E., Dixson, D.L., Domenici, P., McCormick, M.I., Sorensen, C., Watson, S.A., Munday, P.L. (2012). Near-future carbon dioxide levels alter fish behavior by interfering with neurotransmitter function. *Nature Climate Change*, 2, 201–204.
- 40) Lear, K.O., Morgan, D.L., Whitty, J.M. et al. (2020). Divergent field metabolic rates highlight the challenges of increasing temperatures and energy limitation in aquatic ectotherms. *Oecologia* 193, 311–323. https://doi.org/10.1007/s00442-020-04669-x
- 41) Rosa, R., Ricardo Paula, J., Sampaio, E. et al. (2016). Neuro-oxidative damage and aerobic potential loss of sharks under elevated CO₂ and warming. *Marine Biology*, 163, 119. https://doi.org/10.1007/s00227-016-2898-7
- 42) Rosa, R., Pimentel, M., Galan, J.G. et al. (2016). Deficit in digestive capabilities of bamboo shark early stages under climate change. *Marine Biology*, 163, 60 https://doi.org/10.1007/s00227-016-2840-z

- 43) Applebaum, S., Montagna, P.A. & Ritter, C. (2005). Status and trends of dissolved oxygen in Corpus Christi Bay, Texas, U.S.A. *Environmental Monitoring and Assessment*, 107, 297-311.
- 44) Baum, J.K. and Myers, R.A. (2004), Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. *Ecology Letters*, 7, 135-145. https://doi.org/10.1111/j.1461-0248.2003.00564.x
- 45) Crear, D.P., Brill, R.W., Bushnell, P.G., et al. (2019). The impacts of warming and hypoxia on the performance of an obligate ram ventilator. *Conservation Physiology*, 7(1), coz026. doi:10.1093/conphys/coz026