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The physiological and physical response to capture stress in sharks

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Abstract

Exhaustive exercise leads to severe metabolic, acid-base, ionic and hematological changes in sharks. It has been shown that these changes are species-specific and are affected by the magnitude of the cumulative effects of physiological and physical trauma associated with capture. Blood lactate, glucose and pH levels are reliable indicators of the shark stress response and have been extensively studied. Several shark species have been reported to be able to survive physiological stress unless severe physical trauma occurs. As comprehensive information about post release mortality is missing, future investigations should focus on the relationship between physiological disruption and survival rates of tagged and released sharks.

Keywords: Exhaustive exercise; Physiological response; Physical trauma; Survival rates

Introduction

Sharks are extensively exploited by recreational and commercial fisheries throughout the world (Stevens et al. 2000). Most species are actually caught as by-catch of fisheries targeting other species, and discarded back to the sea (Harrington et al. 2005). The catch status (the condition of the animal when brought alongside the boat) varies widely depending on the species. Beerkircher et al. (2002) reported that tiger (*Galeocerdo cuvier*) and blue sharks (*Prionace glauca*) have the highest rate of survival (97% and 81.8% respectively), but the three most commonly caught species - silky (*Carcharhinus falciformis*), dusky (*Carcharhinus obscurus*) and night sharks (*Carcharhinus signatus*) - had much higher mortality rates (66.3%, 48.7% and 80.8%, respectively). The percentage distribution of catch disposition (i.e. whether the elasmobranchs were released alive or dead) was also highly variable, ranging from 12.1% released alive for the night shark to 93.9% for the tiger shark (Table 1). At-vessel mortality rates have been reported to vary among sharks of different species: Morgan et al. (2007) reported that mortality rate of the blacktip shark (*Carcharhinus limbatus*, 88%) was much higher than that of the sandbar shark (*Carcharhinus plumbeus*). Little is known about the immediate and post-release mortality associated with catch and release. Regardless of the fishing gear, captured fish are exposed to varying degrees of stress, which includes the cumulative impacts of physical trauma and physiological stress, the magnitude of which depends on capture and handling methods (Skomal 2007).

Table 1. Catch status and disposition of elasmobranchs in the pelagic longline fishery off the southeastern U.S., 1992-2000 (Adapted from Beerkircher et al. 2002)

Species	% Dead at capture	% Discarded dead	% Released alive	% Retained
Silky	63.3	44.1	25.9	30.0
Dusky	48.7	38.7	36.7	24.6
Night	80.8	61.9	12.1	26.0
Blue	12.2	12.4	87.3	0.2
Tiger	3.0	4.6	93.9	1.5
Scalloped hammerhead	61.0	51.8	34.2	14.1
Oceanic whitetip	27.5	14.5	61.1	24.4
Sandbar	26.8	19.6	57.1	23.2
Bigeye thresher	53.7	43.9	40.2	15.9
Shortfin mako	35.0	0.0	27.6	72.4

As fish body mass is made of more than 30% white muscle and only 3-6% circulating blood, changes in muscle biochemistry are strongly reflected in the blood and can provide quantitative information about the magnitude of the stress (Wells et al. 1986; Skomal 2007). Sharks exhibit a broad range of aerobic and anaerobic swimming capacities (Bernal et al. 2003). Recovery from anaerobic exercise is thought to be prolonged in elasmobranchs as they lack several mechanisms for maintaining or increasing oxygen delivery that are present in teleosts (Brill et al. 2008). Wood (1991) and Kieffer (2000) presented comprehensive reviews of stress physiology in fish. During sustained exercise, muscle metabolism is largely aerobic and is supported by the red muscle. When exhaustive exercise occurs, such as in capture events, the capacity for aerobic swimming is exceeded and exercise is largely supported by anaerobic glycolysis within the white muscle. The anaerobic glycolysis causes a significant depletion of glycogen and an associated accumulation of lactic acid, which quickly dissociates into lactate and metabolic protons. Some of the protons leak into the blood and their accumulation causes a rapid

reduction in both muscle and blood pH. The metabolic acidosis is often accompanied by a respiratory acidosis (P_{CO_2} elevation), which further increases the pH depression.

Physiological stress is also responsible for a profound disruption of ionic, osmotic and fluid volume homeostasis. Concentrations of all major plasma electrolytes generally increases, as well as the circulating levels of plasma stress hormones, corticosteroids (e.g. cortisol) and catecholamines (e.g. noradrenaline and adrenaline). The acidosis and the physical trauma cause disturbances in haematological parameters such as haemoglobin and hematocrit levels.

The objectives of this paper are: (I) to provide a comprehensive review of the literature on the physiological and physical responses to stress associated with capture focusing on the major parameters involved; (II) to describe the inter-specific variation of the physiological stress; and (III) to provide future directions in the field of exhaustive exercise physiology in sharks.

Acid-base balance

Variations in pH have been used as a valid stress indicator in shark physiology studies. Cliff et al. (1984) reported a substantial decrease in both blood pH and bicarbonate ions (HCO_3^-) in dusky sharks caught on rod and reel. The decrease in pH confirmed Piiper et al. (1972) findings on spotted dogfish (*Scyliorhinus stellaris*) stimulated with electric shocks until fatigued, and was consistent with the use of anaerobic metabolism during exhaustive exercise: pH drops as lactic acid is produced and HCO_3^- decreases as it is used to buffer pH changes. For both shark species, pH drop was accompanied by an increase in $p\text{CO}_2$ in the muscles due to a disruption in ventilation and blood circulation which inhibits the offloading of CO_2 at the gills. In these species the acidosis was both metabolic ($[\text{H}^+]$ elevation and $[\text{HCO}_3^-]$ depression) and respiratory ($p\text{CO}_2$ elevation). Richardson et al. (2003) reported that arterial $p\text{CO}_2$ in the Pacific spiny dogfish (*Squalus acanthias*) was not affected by exhaustive exercise possibly due to the presence of extracellular carbonic anhydrase, facilitating CO_2 offloading at the gills. Interestingly, in a later study on the same species, $p\text{CO}_2$ was maximally disrupted by capture (Mandelman and Farrington 2007). These dissimilarities are likely due to differences in the duration and in the type of stress: Richardson et al. (2003) employed captive sharks chased in a tank prior to blood sampling. Mandelman et al. (2007) utilised wild sharks caught in otter trawls and brought on deck for blood sampling. Clearly, in the second case sharks were subjected to a higher and longer degree of stress, likely responsible for the respiratory disruption.

In the dusky shark, lactate levels continued to increase even after pH started rising (Cliff et al. 1984). Piiper et al. (1972) suggested that the discrepancy between blood pH and lactate may be due to some H^+ ions produced with lactate that are retained to improve the blood buffering capacity. HCO_3^- concentration in the dusky shark is in fact extremely low and quickly exhausted (Cliff et al. 1984). Holeton et al. (1978) found that the larger spotted dogfish extracted HCO_3^- through the gills from the external environment to regulate acid-base balance after capture. As more HCO_3^- is available in the blood, the buffering capacity increases, raising blood pH, as demonstrated by Mardaugh et al. (1967), who managed to increase arterial blood pH of the dogshark (*Squalus sp.*) by administering sodium bicarbonate.

Not all shark species showed immediately disturbed acid-base balances in response to stress. Blood pH of dogfish sharks (*Scyliorhinus canicula*), Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*) and blue sharks did not decline until 30, 15 and 20 min

respectively from capture (Butler et al. 1979; Hoffmayer et al. 2001; Skomal et al. 2002). This may be the consequence of an increase in ventilation volume which resulted in respiratory alkalosis and counteracted the increased lactate concentration, causing a very small change in pH (Butler et al. 1979). These studies emphasize that the ability to cope with capture stress and the capacity to recover from it are species-specific. Mandelman and Skomal (2009) tested the stress response in five shark species and reported that the tiger shark and the sandbar shark were less impaired by capture than the dusky, the Atlantic sharpnose, and the blacktip shark, which showed lower pH and bicarbonate levels, and higher blood lactate. The tiger and the sandbar sharks have in fact been reported to have a lower at vessel mortality rates (Morgan et al. 2007), demonstrating they are better able to cope with stress. Manire et al. (2001) and Mandelman et al. (2009) suggested that the least impaired species may simply respond less vigorously on the longline, tempering ventilation and metabolic rates, thus avoiding potentially deadly physiological disturbances. Investigating the acid-base disruption caused by capture is effective only if post-release data are collected. Data from crittercam implemented on grey reef sharks (*Carcharinus amblyrhynchos*) after acid-base parameters were determined, demonstrated that if fight and handling times are short, the sharks exhibit natural behaviours after release, unless exposed to dramatic physical trauma (Skomal et al. 2007). The only grey reef shark that showed post-release aberrant behaviour did not have acid-base disturbances more severe than the other sharks but had experienced a critical blood loss when its eye was damaged at capture. The effects of capture on the acid base balance thus appear to be tightly linked to many different factors: the nature, severity and duration of the stress imposed, as well as the metabolic capacity of the species and its ability to recover from homeostatic disruption (Mandelman et al. 2009).

Serum osmolality

As a result of severe exercise, marine fish suffer an osmotic stress which has profound effects on electrolyte concentrations (Wells et al. 1986). Lactate increase during anaerobic metabolism causes a disturbance in cellular function which can compromise the integrity of cell membranes (Cliff et al. 1984). This can lead to leakage of the electrolytes from the muscle cells (Piiper et al. 1972). Cliff et al. (1984) reported increased concentrations of Mg^{2+} , K^+ , and Ca^{2+} and a 6% increase in osmolality in dusky sharks. Blue shark and mako shark (*Isurus oxyrinchus*) also had high levels of K^+ , Ca^{2+} , Cl^- , Na^+ and high osmolalities after capture (Wells et al. 1986). Mg^{2+} , K^+ , and Ca^{2+} were identified as the distinctive electrolytes which distinguished surviving from moribund blue sharks (Moyes et al. 2006). In the spiny dogfish, Ca^{2+} , Cl^- , Na^+ , K^+ and Mg^{2+} levels were profoundly impacted by capture, however, only Na^+ , K^+ and Mg^{2+} were further disturbed by transport (Mandelman et al. 2007).

Differently from the blue shark, K^+ levels of the two dogfish that died after capture did not differ from those of survivors, suggesting that the K^+ increase was not sufficient to induce mortality. Plasma K^+ in juvenile exercise-stressed sandbar sharks have been reported to be below normal levels, whereas plasma Ca^{2+} and Na^+ concentrations increased (Brill et al. 2008). Increasing K^+ levels could be caused by the K^+ movement associated with acidosis or with the exchange of glucose from the intracellular to the extracellular environment (Lai et al. 1990; Moyes et al. 2006). Hyperkalaemia has been suggested as the proximal cause of death in the mako and in the blue shark (Wells et al. 1986). Concentrations of K^+ above 7mM/l in fact compromise the electrochemical gradients necessary for the function of excitable tissues such as cardiac and skeletal muscle, inducing bradycardia, decreased cardiac output, and anaerobic metabolism in normally aerobic muscle cells (Lai et al. 1990). The variation in Mg^{2+} and Ca^{2+} may further impair

the muscle contraction and neuromuscular transmission (Cliff et al. 1984). Moyes et al. (2006) suggested that the increase in electrolytes may be reminiscent of a condition best studied in mammals and birds known as capture myopathy. The effects of this condition culminate in muscle damage and the subsequent release of myoglobin, muscle enzymes and disruption in electrolyte balance. Interpreting changes in electrolytes and osmolalities however is difficult because sharks are iso-osmotic to slightly hyper-osmotic to their environment (Hoffmayer et al. 2001) and their osmotic state changes with water salinity.

Metabolites and stress hormones

A significant rise in both blood lactate and glucose after exhaustive exercise has been reported for a large variety of shark species (spotted dogfish in Piiper et al. 1972; dusky shark in Cliff et al. 1984; mako and blue shark in Wells et al. 1986; smooth dogfish (*Mustelus canis*) in Barham et al. 1992; Atlantic sharpnose shark in Hoffmayer et al. 2001; bonnethead shark (*Sphyrna tiburo*) in Manire et al. 2001). Lactate is primarily produced as a result of muscle glycogen depletion during intense exercise and is indicative of the low aerobic capacities of sharks compared to higher vertebrates (Hoffmayer et al. 2001). Intracellular acidosis appear to be responsible for a lethal response, rather than the lactate *per se*: the greatest mortalities occur some hours after activity, when the acidosis is high, rather than earlier, when the lactate level reaches its peak (Wood et al. 1983). The fate of lactate once aerobic exercise is resumed is unknown, but the fact that it coincides with an increase in glucose, suggests that lactate may be retained intramuscularly and used for *in situ* glycogenesis (Gleeson 1996).

The increase in glucose levels in response to hyperactivity provides the muscle cells with large amounts of glycogen to sustain muscular exertion. The degree to which blood glucose rises depends on the initial level, which, in turn, depends on the food recently ingested. Hoffmayer et al. (2001) for example reported that Atlantic sharpnose sharks showed a large variation in initial blood glucose likely due to variation in feeding success. Both glucose and lactate for this species were higher than any other previously reported. The authors suggested that this could be explained by the higher metabolic rate of this species which lives in water temperatures 6 to 14° C higher than the majority of those reported by previous studies.

Rising circulating catecholamines appear to be the trigger for the release of glucose; further increase is usually due to corticosteroids facilitating gluconeogenesis (Hoffmayer et al. 2001). Adrenalin is also responsible for an overall increase of the anaerobic capacity through an increase in glycogen production, muscle response to nerve stimulation and a decrease in insulin levels (Hight et al. 2007).

Catecholamines have been used as indicators of the degree of stress in the shortfin mako, common thresher (*Alopias vulpinus*), and blue shark (Hight et al. 2007). Catecholamine levels after stress were as much as 1600 times above the pre-stress levels. Moribund mako sharks which had the highest mortality rates, had the highest value of adrenaline and noradrenaline, followed by blue sharks and common thresher sharks. Very high catecholamine levels can cause vasoconstriction, and in turn, irreversible organ and tissue damage; however, Hight et al. (2007) emphasized that it is not the catecholamine level *per se* that is fatal, but the high level of stress they are indicative of. Manire et al. (2007) explored the effect of stress on corticosterone (CS), in bonnethead shark after capture and reported that CS values increased following stress up to 24 h, and returned to pre-stress levels after 72 h. CS likely had some limited function in the stress response, but the

magnitude of concentration increase, which is inadequate for a primary stress response, suggests it could be rather involved in post-exercise recovery process (Kieffer 2000). Overall, data on catecholamines and corticosteroid variations after severe stress in sharks is scarce. They can be used as useful predictors of stress, but sex and seasonal variations in hormones concentrations must be taken into account.

Haematology

A range of stress effects on hematocrit has been reported, from no change to both haemodilution and haemoconcentration. This could in part reflect the fact that endothermal sharks have higher hematocrit levels than ectothermal ones (Emery 1986). Significant increases in these parameters have been reported for lemon sharks (*Negaprion brevirostris*), mako sharks and spiny dogfish (Bushnell et al., 1982; Wells and Davies, 1985; Wells, McIntyre et al., 1986; Mandelman and Farrington, 2007), likely as a result of erythrocytes' swelling which increases oxygen blood affinity (Wells et al. 1985; Wells et al. 1986). Mako sharks had particularly high levels suggesting that either pre-stress oxygen carrying capacity is very high, or that this species has an exceptionally high stress response (Wells et al. 1985).

Later studies confirmed that swimming performance of this species, as well as that of other lamnid species such as the salmon shark (*Lamna ditropis*), is enhanced by a unique anterior and centrally positioned red myotomal muscle, a higher capillary density, a greater capillary to fiber ratio and a higher myoglobin concentration (Bernal 2003; Sepulveda et al. 2007). These properties likely allow the mako shark to have a higher oxygen flux capacity than other sharks and could partially be responsible for the high survival rates reported for this species (Wood et al. 2007). In other species such as the blue shark, the Atlantic sharpnose, the blacktip, the bonnethead and the bull shark, hematocrit levels remained unchanged (Hoffmayer et al. 2001; Manire et al. 2001; Hight et al. 2007). Consequently these species were unable to maximise their blood affinity for oxygen in response to strenuous exercise as they lack typical teleostean responses. Such responses include red cell swelling, red cell injection from the spleen, decrease in red cell organic phosphate concentration, or catecholamine activation of red cell Na⁺-H exchangers, all of which allow the return of haemoglobin-oxygen affinity to pre-exercise levels in spite of significant acidosis (Brill et al. 2008).

However exceptions have been reported. Exercise-stressed sandbar sharks had high hematocrit and haemoglobin concentrations (Brill et al. 2008). The sandbar shark did seem to respond better than other elasmobranchs to anaerobic exercise due to mechanisms that minimized disruption of blood-oxygen transport associated with metabolic acidosis. Red cell ejection from the spleen, an increase in mean red cell volume, and a net movement of fluid from intravascular to extravascular compartments have all been suggested as possible mechanisms.

For other species such as the blue shark, data are conflicting. Different studies reported either an increase (Wells et al. 1986), a decrease (Moyes et al. 2006) or no significant variation (Hight et al. 2007) in their hematocrit levels following exhaustive exercise. It would be expected that blood loss has profound effects on the animal and that hematocrit and haemoglobin decrease has dire consequences for the shark. However, the blue shark with the lowest hematocrit survived for at least 244 days (Moyes et al. 2006). Other sharks which showed the greatest degree of muscle damage also survived long term. This clearly shows that even though many variables have a dramatic change after a stress event, the results are not necessarily lethal or irreversible.

Conclusion

Blood glucose, lactate and pH have been very useful indicators of physiological stress in shark species as their response to exhaustive exercise has been broadly investigated and it is now relatively clear. On the other side, the function and stress response of other parameters, such as hematocrit or plasma electrolytes, still need further investigation. These parameters in fact vary widely across elasmobranchs species and are affected by many physiological and physical factors, often difficult to identify. Overall, capture response has been reported to be species and fishery-specific. Even closely related species respond differently to the same type of stress; and variation in the magnitude and duration of a capture event have different impacts on individuals of the same species. Past studies focused on the physiological and physical trauma caused by capture. As a result, there is now a paucity of data on post-release mortalities. Blood chemistry information coupled with conventional, acoustic or PSAT tagging, have revealed that the magnitude of the physiological and physical disturbance is not always proportional to post-release mortality rates. Future studies should concentrate on the assessment of sub-lethal effects directly correlated to survival rates. Many shark species have been reported to be able to recover from the physiological stress associated with capture if handled properly; and post-release survival is mostly affected by physical trauma rather than physiological stress. One of the major limits to obtaining reliable stress physiology information for sharks is the lack of baseline data. Studying these elasmobranchs in their natural environment is complicated by several factors: their size and behaviour at capture; the fact that they live in a relatively inaccessible and concealing medium; the difficulty of maintaining these species in captivity; and complications in applying standard clinical procedures to such large and active fish (Sundstrom et al. 2002; Mandelman et al. 2009). This results in the inability to obtain unstressed animals as it is virtually impossible to take blood samples from wild sharks without causing a minimal stress response. Lastly, the role of many environmental factors that have been suggested to play a limiting role in exercise performance in fish, such as water temperature, oxygen levels and water salinity should be assessed in relation to shark stress response.

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