Physiological response to capture stress in endemic Southern African catsharks (family Scyliorhinidae)

Valentina Scarponi | Enrico Gennari | William Hughes

1School of Life Science, University of Sussex, Brighton, UK
2Oceans Research Institute, Mossel Bay, South Africa

Correspondence
Valentina Scarponi, School of Life Sciences, Sussex University, Brighton BN1 9RH, UK.
Email: v.scarponi@sussex.ac.uk

Abstract
Fishing is the major threat to marine fish populations, particularly to higher trophic-level predators such as sharks. Many sharks, and other fish, are caught as commercial by-catch or for recreational purposes and then released; therefore, it is important to understand the effects of capture stress on their physiology and subsequent survival. Nonetheless, although important data have been collected for some sharks, there can be substantial interspecific differences, and the consequences of capture stress are still poorly understood for most species. In this study, the authors quantified the physiological effect of capture on four catshark species endemic to Southern Africa, which are regularly discarded as by-catch and targeted by recreational fisheries. Fifteen pyjama sharks, nine leopard sharks and nine shysharks were captured, and a blood sample was collected to measure their physiological response to capture stress. Stressed blood biochemistry was compared to samples obtained after the sharks recovered for 24 h in an underwater pen. Levels of pH and K+ were significantly lower, and lactate levels were significantly higher, in sharks immediately after capture stress compared to after the 24 h recovery period. Although the species showed a similar response to capture stress, they differed significantly in pH, K+ and lactate levels, and there was some evidence of size affecting the strength of the response to capture stress. The substantial physiological response elicited by even the relatively quick capture event in this study suggests that common fishing practices will have a stronger impact on catshark homeostasis because of longer hooking times and more disruptive fishing gear. Although the relationship between survival and physiological changes elicited by capture needs further investigation, the results provide further evidence that minimizing stress would be beneficial to maximize the survival of sharks and other fish following capture-and-release fishing practices.

KEYWORDS
capture-and-release, elasmobranchs, Haploblepharus, Poroderma, secondary stress response

INTRODUCTION

Fishing is arguably one of the major threats facing most fish populations today, particularly for higher trophic-level fish such as sharks that are often preferentially targeted and slower to recover (Musyl & Gilman, 2018; Vázquez-Rowe, 2020). Overfishing has been the leading cause of the steep declines in shark population numbers globally (Danylchuk et al., 2014; Frick et al., 2010a; Worm et al., 2013).
Recent estimates of total landings are in excess of 750 thousand tons of sharks and rays, or c. 100 million individuals, caught annually because of the increasing demand for shark products and fisheries by-catch (Davidson et al., 2015; Myers et al., 2007; Worm et al., 2013). A key problem in shark and ray fisheries management remains the incomplete reporting of catches, with individuals caught-and-released by either commercial or recreational fisheries not usually being reported to national and international management agencies (Cooke et al., 2013; Cooke & Schramm, 2007; Worm et al., 2013). Sharks and rays are particularly vulnerable to overexploitation because of their K-selected life-history strategy (Afonso & Hazin, 2014; Danylchuk et al., 2014; Musyl & Gilman, 2018). Concerns have been raised over the impact that fishing has on the populations of sharks and rays worldwide and on the overall health of marine ecosystems affected by the dramatic decrease of apex and mesopredators (Afonso & Hazin, 2014; Danylchuk et al., 2014; Myers et al., 2007).

In general, commercial fisheries of sharks and other fish are managed either by input controls in terms of gear restrictions and spatio-temporal limitations, or by output controls that limit the legal sizes and quotas of animals and species that can be retained, with others generally being discarded as by-catch (Afonso & Hazin, 2014; Butcher et al., 2015). Recreational fishing is generally managed by either forbidding capture or requiring release after capture of designated species (Cooke et al., 2013; Cooke & Schramm, 2007; Gallagher et al., 2017). Such management practices are based fundamentally on the assumption that the effects of the capture event on discarded individuals have no impact on their survival (Butcher et al., 2015; Cooke et al., 2013; Cooke & Schramm, 2007; Gallagher et al., 2017; Musyl & Gilman, 2018). It is therefore important to assess the physiological effects that capture-and-release has on sharks and their subsequent survival (Bouyoucos et al., 2018a; Bouyoucos et al., 2019; Cooke et al., 2013; Cooke & Schramm, 2007; Frick et al., 2010a; Frick et al., 2010b; Musyl & Gilman, 2018). More reliable estimates of mortality rates could then be incorporated into yearly landing quotas to provide a more realistic picture on shark global declines.

The necessity for a comprehensive and global assessment of the effects of fishing on shark survival and fitness has motivated many recent studies (e.g., Adams et al., 2018; Bouyoucos et al., 2017; Bouyoucos et al., 2018a; Bouyoucos et al., 2018b; Brooks et al., 2012; Butcher et al., 2015; Cooke et al., 2013; Skomal, 2007). The evidence strongly suggests that, depending on the capture method and duration (the “fight” time the animal spends resisting capture), the physiological consequences of fishing capture can negatively affect growth, feeding and swimming behaviours (Bouyoucos et al., 2018a; Frick et al., 2010b), resistance to disease (Brooks et al., 2012; Skomal, 2007), reproductive output of females and fitness of their young (Guida et al., 2017), can cause reflex impairment (Gallagher et al., 2014), capture-induced parturition and abortion in viviparous species (Adams et al., 2018), and can eventually lead to death (Bouyoucos et al., 2018b; Skomal, 2007). Moreover, shark physiology, response to capture stress and consequent survival rate differ substantially between families (Dapp et al., 2016; Ellis et al., 2017; Mandelman & Skomal, 2009; Morrison et al., 2016). Physiology and capture stress within the same species can also vary depending on biotic factors such as sex and size (Cooke et al., 2013; Dapp et al., 2016; Ellis et al., 2017; Hyatt et al., 2018; Morrison et al., 2016). Sex-related differences in shark mortality and physiological response to capture have been reported in scalloped and bonnethead hammerhead sharks (Lotti et al., 2011; Manire et al., 2007), blue sharks (Coelho et al., 2013) and Carcharhinus species (Butcher et al., 2015). The relationship between size, capture stress and consequent survival remains ambiguous with size having been found to influence the physiological response to capture in some species (e.g., Gallagher et al., 2014; Keebone et al., 2013; Lotti et al., 2011) but not in others (e.g., Hoffmayer & Parsons, 2001; Mandelman & Farrington, 2007), and remains unknown for many species (e.g., Gallagher et al., 2017; Morgan & Carlson, 2014; Musyl & Gilman, 2018). A better understanding of the physiological effects of capture stress as a function of species, sex and size is therefore important for the conservation of shark populations and their cascading trophic effects as predators in many marine ecosystems, especially considering that most fishing regulations are based on size and location restrictions (Butcher et al., 2015; Dapp et al., 2016; Mandelman & Farrington, 2007; Morgan & Carlson, 2014; Musyl & Gilman, 2018; Myers et al., 2007).

There is strong evidence of interspecific differences in the physiological effects of capture and subsequent survival (Bouyoucos et al., 2018b; Brooks et al., 2012; Butcher et al., 2015; Ellis et al., 2017; Mandelman & Skomal, 2009; Morrison et al., 2016; Skomal, 2007; Worm et al., 2013). This emphasizes the need for the assessment of a broad range of shark species affected by commercial and recreational fisheries to determine the relationship between the physiological changes experienced by the animals and their condition and resilience post capture-and-release (Bouyoucos et al., 2018b; Bouyoucos et al., 2019; Brooks et al., 2012; Mandelman & Skomal, 2009; Skomal, 2007). Despite these growing concerns about the consequences of capture-and-release stress on shark survival, and the recent increase in research efforts aimed to characterize the physiological response to capture in some shark and rays species (reviewed in Skomal & Mandelman, 2012; Dapp et al., 2016; Ellis et al., 2017), there remains an enormous gap in knowledge for the vast majority of species, including the effects of gear types, hooking times and biotic factors like sex and size. This is due to the difficulties in obtaining species-specific physiological profiles of post-recovery animals (controls) that are based on empirical data rather than on mathematical or theoretical predictions and that can be used for comparison with the physiological profiles of stressed sharks (Barragán-Méndez et al., 2019; Cooke et al., 2013; Skomal, 2007). Given the diversity of shark life history, metabolic rate, respiratory mode and swimming behaviours, it would be inaccurate to apply a stress response model from one species to another based on the limited knowledge available, strongly reinforcing the need to study a much broader range of species (Dapp et al., 2016; Jerome et al., 2018; Skomal & Mandelman, 2012).

In this study, the authors study the effect of capture stress on the physiology of four species of catsharks (family: Scyliorhinidae), one of the largest shark families (c. 160 spp.), with some 10% of species being of conservation concern and >55% still data-deficient (Jabado et al., 2017). Many catshark species are commonly caught as commercial by-catch or by recreational fisheries and then discarded because...
of their low commercial value (Barragán-Méndez et al., 2019; da Silva et al., 2018; DAFF, 2013; Fowler et al., 2005; Silva & Ellis, 2019). The authors investigated four species: pyjama catsharks (Poroderma africanum; Least Concern: IUCN 2020), leopard catsharks (Poroderma pantherinum; Least Concern: IUCN 2020), puffadder shysharks (Haploblepharus edwardsii, Endangered: IUCN 2020) and dark shysharks (Haploblepharus pictus, Least Concern: IUCN 2020). These understudied species of benthic catshark are endemic to South Africa, but despite concern for their population viability because of increasing fishing pressure (da Silva et al., 2015; da Silva et al., 2018; DAFF, 2013), the possible consequences that capture stress may have on them, as with most catsharks, are unknown. The primary objective of this study was therefore to quantify the physiological effects that capture stress has on these catsharks and whether these were similar between species. The authors secondarily investigated whether the physiological response to capture stress was affected by the sex or size of sharks. For the purpose of this study, the authors defined capture stress as the physiological alteration elicited in the shark by the complete capture process, including hooking, reeling in, handling, hook removal and temporary storage. The authors compared the physiological profile of sharks in response to this stress with the physiological profiles of the sharks after a 24 h recovery period. They could not of course remove stress entirely during this recovery period, but designed it based on the biology of the sharks to reduce the stress of the sharks as far as possible compared to the initial capture stress.

2 | MATERIALS AND METHODS

2.1 | Ethical statement

All experimental procedures were approved by the University of Sussex Ethical Review Committee (ARG/2/3), and all research was carried out under research permit RES2017-47 issued by the South African Department of Agriculture, Forestry and Fisheries.

2.2 | General methods

This study was conducted between 11 May and 30 October 2017, in Mossel Bay, South Africa (34.1747° S, 22.0834° E). Sharks were caught at one of the two local reefs in Mossel Bay (The Point Reef 34.189° S 22.1616° E or Hartenbos Reef 34.13° S, 22.13° E) depending on weather conditions. The fishing rod-and-line technique was used to catch all individuals for the study. Four to six 180 cm graphite fishing rods, equipped with 14 kg breaking strength line and 5/0 circle hooks, were baited and dropped to reach the ocean floor (depth: min = 5.6 m, max = 19.6 m, mean ± s.e. = 9.4 ± 0.8 m). A Tinytag Aquatic 2 temperature logger (Gemini Data Loggers manufacturers) was suspended from the research vessel to collect water temperature readings at the time that the sharks were hooked (mean ± s.e. = 15.1 ± 0.18°C).

Two individuals of any of the four study species were caught on any given day. Pyjama and leopard catsharks are easily recognized by their skin markings. Puffadder and dark shysharks can be hard to distinguish morphologically (van Staden et al., 2020), so were pooled as Haploblepharus shysharks. A total of 15 pyjama sharks (4 females TL = 67–94.5 cm, 11 males; TL = 57.5–95 cm), 9 leopard sharks (2 females TL = 67.5 cm, 7 males; TL = 52.5–69 cm) and 9 Haploblepharus shysharks (4 females TL = 58.5–62, 5 males TL = 55–71 cm) were captured and studied. An additional five pyjama sharks were used only as companion animals (see pairing information below), not for study, because of having been caught previously (two individuals) or having hook scars that indicated previous fishing capture (three individuals).

2.3 | Capture stress physiological profile

The capture stress stimulus included several components: hooking, reeling in, handling and temporary retention in a container. Sharks caught were reeled aboard the vessel in less than 1 min of being hooked, checked for hook scars or identification tags, and then placed individually in a plastic container of fresh sea water for 30 min before the blood sample was collected to measure the capture stress physiological profile. Each shark was kept for 3 min on the hook in the container to standardize the duration of the exposure to hooking stress. After 3 min, the hook was removed while the shark was held under water to prevent air exposure. The containers were covered by a dark towel to minimize external stressors and were 80 × 40 × 40 cm. All sharks rapidly adopted a resting state within the container. Although some of the sharks were longer than the length of the container, catsharks, including the species studied, naturally spend much of their time resting in small, confined crevices within rocky reefs (Dainty, 2002), so the limited size of the container was unlikely to cause stress to the sharks. The containers held c. 120 l of fresh sea water. This was not aerated, but contained ample oxygen to ensure that sharks were not exposed to hypoxic conditions during the 30 min period of retention [stressed catsharks (Scyliorhinus canicula) consume ~1–3 mg O2 min−1 kg−1 (Green & Jutfelt, 2014), so only 1–2% of the oxygen in the container would be required for respiration by the shark during 30 min]. The 30 min retention period was chosen because the secondary stress response has been found to peak 30 min after the stress stimulus in other catsharks (DeRoos & DeRoos, 1978). After 30 min, a blood sample from the shark was taken (see below) for measurement of capture stress physiology.

2.4 | Post-recovery physiological profiles

After the collection of the initial blood sample for measurement of the capture stress physiological profile, the sharks were transported to an underwater pen, in which they were kept for a 24 h recovery period after which a second blood sample was collected for the measurement of the post-recovery physiological profile. The water in the transport
within enclosures after capture is not stress inducing (Barragán et al., 2010a; Kneebone et al., 2013). As it was not always possible to catch two individuals of the same species, some individuals were paired with a conspecific and others with a heterospecific (see Supporting Information Table S1), and pair type was then controlled for in the analysis.

Keeping the sharks in the pen for a 24 h recovery period before collecting a second blood sample was to ensure that all sharks had been kept under standardized, controlled and relatively stress-free conditions before the collection of the post-recovery blood sample. Post-recovery physiological profiles have often been collected using sharks kept in captivity when assessing the response to capture stress, with the evidence from previous studies showing that being kept within enclosures after capture is not stress inducing (Barragán-Méndez et al., 2019; Frick et al., 2009; Frick et al., 2010a; Kneebone et al., 2013). The physiological profile of elasmobranchs returns to normal within 24 h after a stressor is perceived; therefore, a blood sample collected after a 24 h recovery period can be considered to give an accurate representation of the physiological profile of animals that have recovered from the stress elicited by capture (hooking, reeling in, handling, hook removal and temporary retention), transport from the capture site and the handling practices involved in placing the sharks in the underwater pen (Barragán-Méndez et al., 2019; Brooks et al., 2012; DeRoo & DeRoo, 1978; Kneebone et al., 2013). This was supported by the results of this study (see below). In addition, because all sharks were kept under the same conditions in captivity, the authors were able to avoid any differences in environmental conditions or experiences during the postcapture recovery period confounding the results of this study.

After the 24 h recovery period, one shark at a time was retrieved from the holding pen, and a blood sample was collected for the measurement of the post-recovery physiological profile (see below). This process took <5 min from the first contact with the shark. After blood collection, sharks were sexed and their total length measured from the tip of the snout to the tip of the caudal fin. Spaghetti tags provided by the Oceanographic Research Institute’s Cooperative Fish Tagging Project (ORI-CFTP) were inserted on the side of the first dorsal fins of the sharks to avoid recapture. The sharks were then transported back and released at the site of capture.

### 2.5 Blood collection and analysis

For the collection of blood samples, the shark was gently removed from its container or pen, its eyes covered with a wet towel and placed with its ventral side upwards on a flat surface to induce tonic immobility (Brooks et al., 2011). Once in tonic immobility (<1 min), 0.5 ml of blood was harvested through caudal venipuncture using 22-gauge hypodermic needles (< 2 min). Although exposure to air involved in this procedure may cause physiological changes (Lawrence et al., 2017), and tonic immobility itself elicits physiological changes in sharks, the effects remain undetectable if blood is harvested within 2 min (Brooks et al., 2011). The quick bleeding procedure followed in this study is therefore considered to be the least invasive and physiologically taxing method of collecting blood from sharks, and has been used in many studies assessing the physiological profile of other shark species (Brooks et al., 2011; Cooper & Morris, 1998; Mandelman & Skomal, 2009; Skomal & Mandelman, 2012).

Each sample of fresh blood was loaded with a sterile syringe onto a clean disposable Test Card and analysed immediately with epoc® blood analyser (Woodley Equipment Company Ltd.) to obtain measures of glucose, pH, K+ and lactate as biomarkers of the stress response (Cooke et al., 2013; Mandelman & Skomal, 2009; Skomal & Mandelman, 2012). Similar blood readers set at 37°C have been used in other recent studies on teleost and elasmobranch fishes, as they provide reliable measures of pH (Bouyoucos et al., 2018b; Harter et al., 2015; Lennox et al., 2016; Toledo-Guedes et al., 2016). Following previous studies, all pH measurements obtained from blood analysis were corrected for temperature using the temperature of the water in the holding tank or pen in which the shark had been kept (Ashwood et al., 1983; Kneebone et al., 2013; Lennox et al., 2016; Mandelman & Skomal, 2009; Toledo-Guedes et al., 2016).

### 2.6 Statistical analysis

The authors used linear mixed effects models (lme4 package for mixed model analysis; Bates et al., 2015) to analyse the concentrations of blood biomarkers. They first carried out an overall analysis that included all three species to investigate whether there was a significant difference in the concentration of blood biomarkers between stressed and post-recovery blood samples, and if this differed between species. Treatment (stressed vs. post-recovery), species, sex and size were coded as fixed factors. Paring type (conspecific/congeneric or heterospecific/heterogeneric) was included as a fixed covariate solely to account for it in the analyses. Shark ID was included as a random factor. Tukey’s HSD post hoc tests were used to compare the three shark species for each of the three biomarkers (glht function of multcomp package;
**Figure 1** Effect of capture stress on shark blood bioindicators. Mean ± s.e. levels of (a) pH, (b) K⁺, (c) lactate and (d) glucose for pyjama catsharks (N = 15), leopard catsharks (N = 9) and shysharks (N = 9) immediately after capture (grey) and after a 24 h recovery period (white).

| Species          | Bioindicator | Statistic | Treatment | Size | Sex |
|------------------|--------------|-----------|-----------|------|-----|
| Pyjama shark     | pH           | F         | 49.4      | 1.97 | 0.19|
|                  |              | P         | <0.001    | 0.19 | 0.67|
|                  | K⁺           | F         | 6.24      | 0.06 | 0.2 |
|                  |              | P         | 0.03      | 0.81 | 0.66|
|                  | Lactate      | F         | 43.7      | 11.5 | 0.008|
|                  |              | P         | < 0.001   | 0.002| 0.93|
| Leopard shark    | pH           | F         | 24.2      | 0.04 | NA  |
|                  |              | P         | 0.001     | 0.83 | NA  |
|                  | K⁺           | F         | 9.0       | 18.9 | NA  |
|                  |              | P         | 0.01      | < 0.001| NA |
|                  | Lactate      | F         | 26.8      | 0.14 | NA  |
|                  |              | P         | <0.001    | 0.71 | NA  |
| Shyshark         | pH           | F         | 83.9      | 0.84 | 1.76|
|                  |              | P         | <0.001    | 0.39 | 0.24|
|                  | K⁺           | F         | 6.62      | 0.21 | 3.99|
|                  |              | P         | 0.03      | 0.67 | 0.1 |
|                  | Lactate      | F         | 33.6      | 0.97 | 0.24|
|                  |              | P         | <0.001    | 0.64 | 1.53|
|                  | Glucose      | F         | 2.48      | 0.68 | 0.84|
|                  |              | P         | 0.15      | 0.44 | 0.41|
Hothorn et al., 2008). Because of the complexity of the data, the authors then carried out separate analyses for each species to further investigate the effects of sex and size. In these species-specific models, sex was included as a fixed factor only for pyjama catsharks and shysharks, but not for leopard catsharks because of the small number of females captured. Pairing type was again included as a fixed covariate to account for it and shark ID as a random factor. Minimum adequate models were obtained by step-wise deletion of non-significant terms from the full factorial models (Table S2, Table S3). The significance of the fixed factors was derived using the package lmerTest based on Satterthwaite’s approximations (Kuznetsova et al., 2015). Likelihood ratios tests and AIC values were used to select the best model. All analyses were performed in R v3.5.1 (R Core Team, 2018).

3 | RESULTS

There were no significant interactions between the fixed factors [treatment (stressed vs. post-recovery), species, sex and size] in any of the models. In the overall analysis, there were significant differences between the stressed and post-recovery levels of pH, K⁺ and lactate (respectively, $F_{1,32} = 130.7$, $P < 0.001$; $F_{1,32} = 20.2$, $P < 0.001$; $F_{1,32} = 76.9$, $P < 0.001$). Higher levels of lactate and lower pH and K⁺ were found in stressed compared to sharks post-recovery (Figure 1). Glucose concentrations for pyjama and leopard catsharks were too low for reliable quantification (the epoc® blood analyser was unable to give exact concentrations lower than 1.1 mmol l⁻¹). In shysharks, the level of glucose was somewhat lower in stressed compared to post-recovery samples (Figure 1), but the difference was

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**FIGURE 2** Effects of sex and size on the response to stress in pyjama sharks, *Poroderma africanum*. Mean ± S.E. percentage change in blood biomarkers (stressed – post-recovery) for pyjama sharks. (a), (c) and (e) show the response for females (white) and males (grey) for pH, K⁺ and for lactate respectively. (b), (d) and (f) show the change in the three blood biomarkers in relation to the size (cm) of the pyjama sharks. Line of best fit indicates a significant relationship. (— ) Line of best fit.
**DISCUSSION**

The levels of the pH, K⁺ and lactate bioindicators differed significantly between blood collected from sharks 30 min after capture stress and after the 24 h recovery period that was designed to reduce stress, showing that capture stress had physiological effects on the sharks. Although levels of the blood bioindicators differed between species, all species showed similar responses to capture stress. There was some evidence that the stress response was affected by the size of the sharks, but no clear evidence that it was affected by sex.

Anaerobic glycolysis following prolonged muscle contractions during capture likely drove Lactate⁻ ions from the muscle into blood circulation, causing the observed 55–63% increase in mean lactate concentration after capture (Barragán-Méndez et al., 2019; Brooks et al., 2011). Increases in lactate following capture stress have been reported for a variety of elasmobranch and teleost fish (Davis et al., 2001; Marshall et al., 2012; Toledo-Guedes et al., 2016; Lennox et al., 2016; Barkley et al., 2017; Jerome et al., 2018). Lactate is a highly informative predictor of shark stress and survival because it often correlates with behavioural impairment after release (Jerome et al., 2018). The lactate changes that the authors found were slightly lower than reported for another catshark using a similar comparison between capture stress and post-recovery blood samples (Barragán-Méndez et al., 2019), whereas lactate levels for larger sharks following capture can be much higher (Jerome et al., 2018; Marshall et al., 2012). This could reflect interspecific variation in physiology or differences in, e.g., duration of “fight” time on the hook.

The overall increase in lactate likely elicited the observed decrease in blood pH after capture (blood acidosis; Skomal & Mandelman, 2012; Bouyoucos et al., 2018b). Acidosis induced by acute stress is expected...
to cause hyperkalaemia, an increase in blood K⁺ following the efflux of potassium ions from the intra- to extracellular compartment (Cliff & Thurman, 1984; Skomal & Mandelman, 2012). Nonetheless, observed K⁺ levels were lower in stressed vs. post-recovery sharks. Because the efflux of K⁺ ions into the blood only occurs after acidosis, it is likely that changes in K⁺ took longer to occur compared to other blood bioindicators. In spiny dogfish, K⁺ concentrations were found to peak 2 h after capture, whereas other bioindicators reached high concentrations far more quickly (Mandelman & Farrington, 2007). The samples of this study taken 30 min after capture were likely very early to show hyperkalaemia.

The non-significant decrease in glucose experienced by shysharks after capture suggests that they may be particularly slow at activating hepatic glycogen stores after perceiving a stressor, a response integral

**FIGURE 4**  Effects of sex and size on the response to stress in shysharks, *Haploblepharus* spp. Mean ± s.e. percentage change in blood biomarkers (stressed – post-recovery) for shysharks. (a), (c), (e) and (g) show the response for females (white) and males (grey) for pH, K⁺, glucose and lactate respectively. (b), (d), (f), and (h) show the change in the four blood biomarkers in relation to the size (cm) of the shysharks.
to survival in sharks as it provides the necessary energy for the flight or flight response (Jerome et al., 2018; Marshall et al., 2012). Because the highest concentration of glucose was found 30 min after capture in nursehound catsharks (family: Scyliorhinidae; DeRoos & DeRoos, 1978), it was reasonable to expect the change in glucose concentrations to peak 30 min after capture also in shysharks. The effect of stress on glycogen mobilization in captured pyjama and leopard catsharks deserves further investigation with more sensitive methods.

Interestingly, individuals of different size were not equally affected by the above metabolic and respiratory perturbations, depending upon shark species. The three smallest pyjama sharks and two of the smaller shysharks showed the expected hyperkalaemia at the 30 min sampling point, suggesting that the rate of K⁺ production and accumulation might decrease with size in pyjama catsharks and shysharks. Conversely, larger leopard sharks were affected by the highest change in K⁺, suggesting that they might need more time to reabsorb K⁺ ions from the peripheral circulations into the intraextracellular compartment. Similarly, the highest changes in concentration of lactate were experienced by larger pyjama catsharks. Large individuals might exhibit a longer or more acute struggle during capture compared to smaller sharks, or may take longer to recover from stress if their physiological homeostasis is disrupted by a greater accumulation of acute metabolic and respiratory perturbations.

Previous studies have found sex-related differences in the response to capture stress of sharks (Butcher et al., 2015; Ellis et al., 2017; Musyl & Gilman, 2018), as well as teleost fish (Teffer et al., 2017; Eliason et al., 2020), which may be because of differences in reproductive physiology or mating biology (Byrnes et al., 2016; Ellis et al., 2017; Musyl & Gilman, 2018; Pratt & Carrier, 2001). Nonetheless, there was no clear evidence of difference between sexes in the results of this study. Female pyjama catsharks and shysharks had a marginally larger response in most cases, whereas female shysharks had a smaller response than males for K⁺, but in all cases the difference between females and males was non-significant. Nevertheless, this aspect of the secondary response to capture stress in catsharks warrants further investigation.

Overall, all species showed significant responses to capture stress even after a 3 min capture event, considerably shorter than normal fishing practices, which will likely have a stronger impact on shark physiological homeostasis because of longer hooking times and use of disruptive fishing gear. While the study did not investigate the impact of capture on survival, finding such significant homeostatic disruptions in these catshark species after a short capture event strengthens the concerns about the resilience of sharks and other fish to capture stress, especially when captured with common fishing practices. It would, therefore, be prudent for fishing management plans to reflect that a significant proportion of sharks and other fish that are caught and released will be negatively affected by the stress of the event, with this impact depending on their species, sex and size. This will be particularly important for species that are of conservation concern or for which individuals are at risk of being caught on multiple occasions. Fishing quotas, areas, gear and handling practices may all potentially benefit from being adjusted to allow for or reduce capture stress and thereby achieve more realistic fishing management strategies.

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AUTHOR CONTRIBUTIONS
V. S. designed the experiments and carried out the experimental work, analysed the data and wrote the manuscript. W. H. supervised the work and the design of the experiments, and assisted with the data analysis and proofing the manuscript. E. G. supervised the experimental work and assisted with proofing the manuscript.

CONFLICTS OF INTEREST
The authors declare that there are no conflicts of interest.

ORCID
Valentina Scarponi https://orcid.org/0000-0002-4547-3560
Enrico Gennari https://orcid.org/0000-0002-4334-727X

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**SUPPORTING INFORMATION**
Additional supporting information may be found online in the Supporting Information section at the end of this article.

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