



Insights into catch-and-release survivorship and stress-induced blood biochemistry of common thresher sharks (*Alopias vulpinus*) captured in the southern California recreational fishery

C. Heberer^a, S.A. Aalbers^b, D. Bernal^c, S. Kohin^d, B. DiFiore^e, C.A. Sepulveda^{b,*}

^a National Marine Fisheries Service (NMFS), Southwest Region, Carlsbad, CA 92011, USA

^b Pflieger Institute of Environmental Research (PIER), Oceanside, CA 92054, USA

^c Department of Biology, University of Massachusetts Dartmouth, Dartmouth, MA 02747, USA

^d NMFS, Southwest Fisheries Science Center, La Jolla, CA 92037, USA

^e Department of Biology, Middlebury College, Middlebury, VT 05753, USA

ARTICLE INFO

Article history:

Received 29 June 2010

Received in revised form

24 September 2010

Accepted 27 September 2010

Key words:

Thresher shark

Survivorship

Mortality

Fishery

ABSTRACT

The common thresher shark (*Alopias vulpinus*) is the focus of a popular southern California recreational fishery that typically captures individuals by hooking them in the caudal fin. This technique reduces the ability for forward locomotion and the capacity for ram ventilation. This study assessed the post-capture survivorship of tail-hooked adult and sub-adult common thresher sharks using pop-up satellite archival tags (PSATs) and quantified physiological indicators of capture stress in the blood. Survival of the acute effects of capture was determined from the depth and temperature records of 10-day PSAT deployments. Survivorship estimates were based on 19 common thresher sharks [160–221 cm fork length (FL); ~67–151 kg] captured in southern California from 2007 to 2009 using recreational stand-up tackle (36 kg). Five mortalities were observed over the course of the study resulting in an overall post-release mortality estimate of 26%. All mortalities occurred in large individuals (≥ 180 cm FL) with fight times ≥ 85 min. The archived depth and temperature data from surviving sharks resembled those of previous common thresher movement studies with a diel depth distribution predominantly within the uniformed temperature surface layer. Capture induced stress parameters measured from the blood of eight additional common thresher sharks that were not tagged revealed plasma lactate and hematocrit levels that were significantly elevated with increased fight time. Similarly, all thresher sharks showed heightened heat shock protein 70 (*hsp 70*) values relative to those obtained from blood that was allowed to recover *in vitro* for 24 h. Collectively, our findings indicate that large tail-hooked common thresher sharks with prolonged fight times (≥ 85 min) exhibit a heightened stress response which may contribute to an increased mortality rate. These results suggest that for larger individuals the current caudal-based capture methods used in the California recreational fishery may not be suitable for an effective catch-and-release based conservation strategy.

© 2010 Elsevier B.V. All rights reserved.

1. Introduction

The common thresher shark (*Alopias vulpinus* Bonnaterre) is a highly migratory species that supports economically important commercial and recreational fisheries off the west coast of the United States (Cailliet and Bedford, 1983; PFMC, 2007). Landings are monitored and subject to a harvest guideline due to the vulnerability of pelagic sharks to overexploitation (PFMC, 2003). After less than a decade of commercial exploitation during the late 1970s

and early 1980s, the common thresher shark population showed a marked reduction in size prompting the adoption of several regional conservation measures (Holts, 1988; Hanan et al., 1993; PFMC, 2003). The coupling of regulations on commercial fishing operations (e.g., time and area closures) to protect gravid females during the pupping season (March through August) as well as a switch in the primary target of the driftnet fishery from thresher sharks to swordfish (*Xiphias gladius* L.) has likely contributed to the recovery of the west coast resource over the past 25 years (PFMC, 2003). In recent years the increased availability of common thresher sharks in southern California has led to an increased targeting of this species by recreational fishers. Recent data suggest that the recreational fishing sector now significantly contributes to the annual harvest of this species in California (PFMC, 2008).

* Corresponding author at: Pflieger Institute of Environmental Research, 315 N. Clementine, Oceanside, CA 92054, USA. Tel.: +1 760 721 1404; fax: +1 760 721 1475.
E-mail addresses: chugey@pier.org, chugey@hotmail.com (C.A. Sepulveda).

Because the common thresher shark has a past history of over-exploitation, the recent expansion of the recreational fishery within the Southern California Bight (SCB) raises concern over the future sustainability of this valuable resource.

The primary techniques used in the southern California recreational fishery (SCRF) for common thresher sharks entails trolling weighted (~0.5 kg) lures outfitted with tandem baited J-type hooks (Bernal and Sepulveda, 2005; Aalbers et al., 2010). Since common thresher sharks utilize their elongate upper caudal lobe to immobilize prey before it is consumed the majority of thresher sharks captured in the recreational fishery are hooked in the caudal fin and hauled-in backwards (Aalbers et al., 2010). The common thresher is an obligate ram ventilator that requires forward motion to ventilate the gills (Roberts, 1978). The reduced ability to extract oxygen from the water during capture as well as the stress induced from these capture methods may influence recovery following release.

Because of the common thresher shark's life history characteristics (i.e., slow growth and low fecundity; Cailliet and Bedford, 1983), the practice of catch-and-release is commonly advocated by both managers and conservative recreational groups. However, to be an effective conservation tool, post-release survivorship must be high. Currently, the fate of released common thresher sharks is unknown and this complicates efforts to both estimate fisheries mortality and design an effective management strategy for common thresher sharks off the California coast. Therefore, the objectives of this work were to: (1) use pop-off satellite archival tags (PSATs) to assess post-release survivorship of common thresher sharks captured using the caudal-based techniques, and (2) quantify the changes in blood stress indicators that manifest from the use of current angling methods.

2. Methods

2.1. PSAT tagging

Tagging operations were performed from May, 2007 through May, 2009 in the SCB from Newport Beach, CA (~33°35'N 117°53'W) to the U.S.–Mexico border (~32°33'N, 117°10'W). Techniques and equipment were standardized to follow current recreational trolling methods used to capture common thresher sharks in southern California. Lead-headed lures [(0.5 kg); Leadmasters, Hesperia, CA, USA] were rigged with tandem 8/0 Mustad 7691 J-hooks (Mustad, Gjøvik, Norway), baited with chub mackerel (*Scomber japonicus* Houttuyn) and slow trolled behind the tagging vessel. All common thresher sharks were landed using conventional stand-up tackle (36 kg) set to 9 kg of drag pressure. Tail-hooked sharks were fought with a commercially available stand-up fighting harness and the vessel was not used to assist the angler during the fight. Once boat-side, the sharks were stabilized by gripping the tip of the caudal fin at which time the embedded hooks were removed. The shark was brought alongside the boat for tagging and fork length (FL) and gender were recorded. Animal masses were estimated from FL using the length–weight conversion for common thresher sharks (Kohler et al., 1995). Boatside handling was minimized and kept to <2 min for all tagged individuals. Fight duration was defined as the time from initial hook-up to the time of release. Average values (\pm standard deviation) are reported.

Wildlife Computers (Redmond, WA, USA) MK10 PSATs were programmed to record depth, ambient temperature, and light level every 30 s for a 10 day deployment. PSATs were programmed to release prematurely if depth values remained constant (\pm 5 m) over a 48-h period, consistent with a dead shark on the ocean floor or a shed tag that was floating at the surface. Tag tethers were rigged with an 11 cm section of 100 kg monofilament, stainless-steel crimps and a Wildlife Computers (Richmond, WA, USA) depth

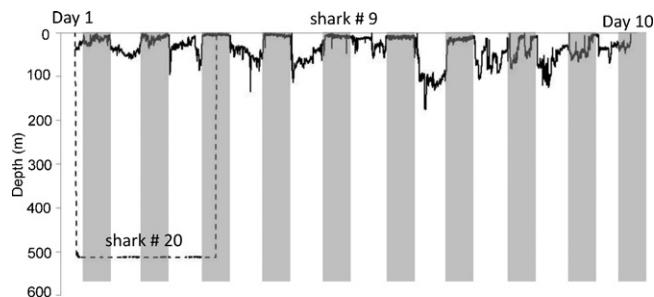


Fig. 1. Post release vertical movements of two common thresher sharks. The solid line shows data from shark # 9 (F, 180 cm FL) which survived and the dashed line shows the depth record for shark # 20 (F, 221 cm FL) which died and sank immediately. The PSAT remained at ~500 m for >48 h at which time it released from the shark, floated to the surface, and began to transmit. Shaded areas indicate night time.

guillotine that functioned to sever the leader at 1500 m. Tag anchors used in this study consisted of a double-barbed nylon dart head [BFIM-96 (Floy Tag) Seattle, WA, USA].

Directed efforts to recover PSATs that released from sharks near (<50 km) the deployment location were initiated within 24 h of receiving a signal from the Argos server. A signal direction finder (DDF 6000, Doppler Systems Inc., Carefree, AZ, USA) was used to triangulate the position of the floating tag as described by Sepulveda et al. (2010). After recovery, the archived depth and temperature data were downloaded, and the PSAT was sent to the manufacturer for refurbishment and subsequently re-deployed.

Survivorship was assessed using the depth and temperature profiles following the protocols previously used to infer mortality from PSAT data records [(Graves et al., 2002; Horodysky and Graves, 2005) Fig. 1].

Because this study observed marked variability in the vertical movements immediately following release, which ranged from prolonged surface swimming (shark 12) to repeated diving below the thermocline (shark 15), the initial 6-h period of each track was excluded from the depth statistics and distribution analyses (Table 1; Fig. 2). The exclusion of the initial movement data was performed to reduce potential biases associated with immediate post-release stress and followed the protocol established from previous thresher shark tagging studies which found tail-hooked threshers to have an increased rate of movement during the initial six hours of tracking. (Cartamil, 2009; Cartamil et al., 2010). A single contour plot of the joint distribution of depth and time was generated from the archived datasets using MATLAB (R12; Natick, MA, USA) to illustrate trends in vertical behavior over a 24-h period. Due to the limited duration of the tag deployments geolocation estimates were not performed. Overall net horizontal movement was calculated as the great circle distance between deployment and pop-off locations.

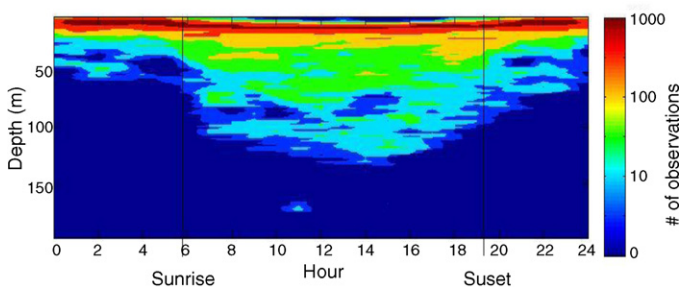


Fig. 2. Joint distribution of depth and time plotted over a 24-h period for all datasets obtained from recovered tags ($n=6$; 60 days and 155,047 observations).

Table 1
Catch information for 20 common thresher sharks used for the catch-and-release mortality estimate.

| Shark #ID | Date | Sex | FL ^a (cm) | Mass ^b (kg) | Net movement ^c (km) | Fight time (min) | Mortality |
|-----------------|------------|-----|----------------------|------------------------|--------------------------------|------------------|------------------|
| 1 | 09/29/2008 | F | 160 | 67 | 22 | 45 | N |
| 2 | 10/06/2008 | F | 163 | 70 | 95 | 40 | N |
| 3 | 10/01/2008 | M | 165 | 73 | 43 | 55 | N |
| 4 | 10/01/2008 | F | 165 | 73 | 53 | 65 | N |
| 5 | 05/10/2007 | M | 168 | 76 | 15 | 49 | N |
| 6 | 05/11/2007 | F | 170 | 78 | 46 | 32 | N |
| 7 | 10/01/2008 | F | 175 | 84 | 51 | 65 | N |
| 8 | 05/01/2009 | F | 178 | 87 | 64 | 50 | N |
| 9 | 09/29/2008 | F | 180 | 90 | 21 | 75 | N |
| 10 | 05/15/2009 | F | 180 | 90 | – | 90 | Y |
| 11 ^d | 05/12/2008 | M | 181 | 91 | – | 140 | Y |
| 12 | 05/11/2007 | F | 191 | 104 | 41 | 49 | N |
| 13 ^e | 05/02/2009 | F | 193 | 107 | – | 100 | N/A ^e |
| 14 | 05/14/2009 | M | 193 | 107 | 34 | 45 | N |
| 15 | 04/29/2008 | M | 193 | 107 | 9 | 74 | N |
| 16 | 05/02/2009 | F | 198 | 114 | – | 85 | Y |
| 17 | 05/15/2009 | F | 203 | 122 | 211 | 75 | N |
| 18 ^d | 05/01/2009 | M | 206 | 127 | – | 135 | Y |
| 19 | 05/16/2009 | F | 220 | 149 | 358 | 65 | N |
| 20 | 05/10/2007 | F | 221 | 151 | – | 105 | Y |

^a Fork length.

^b Body mass estimated from length (Kohler et al., 1995).

^c Horizontal distance determined from site of tag deployment and pop-off location.

^d Dead on arrival at boat, tag not deployed.

^e Tag failed to report.

2.2. Blood stress indicators

To avoid confounding the survival study, all stress analyses were performed on individuals that were not used in the survival experiments. Immediately after the sharks were restrained, a 2 ml blood sample was taken from the caudal vein with an 18 ga needle and placed into a pre-chilled, heparinized 10 cc syringe. A 1.5 ml subsample was centrifuged at 2200 × g for 5 min to separate blood plasma from the red blood cells prior to storage in liquid nitrogen. Hematocrit (packed erythrocyte volume percentage) was measured after centrifugation (IEC Model MB Microhematocrit) at 12,000 × g for 5 min. Plasma samples were subsequently thawed and diluted three fold. Electrolytes (i.e., Na⁺, Cl⁻, K⁺, Ca⁺⁺, Mg⁺⁺) and metabolites (glucose and lactate) were quantified using an automated blood chemistry analyzer [NOVA CCX Statprofiler (Waltham, MA, USA)]. The presence of heat shock protein 70 (*hsp70*) in the red blood cells was determined by lysing the red blood cell pellet in the presence of a protease inhibitor (ROCHE Complete-mini), separating the proteins by size using SDS-PAGE, and transferring the proteins to a polyvinylidene difluoride (PVDF) membrane using a western blot method. The presence of *hsp70* on the PVDF membrane was detected through primary antibodies specific against *hsp70* (Agriseria AS05-083) and secondary antibodies marked with a fluorescent dye at 680 nm (Licor IRDye680) that could be visualized using a fluorescent scanner (Odyssey Infrared Imager) and subjected to densitometry analysis (Odyssey ver. 3.0.16). Positive controls were run using *hsp70* standards (Sigma Aldrich, St. Louis, MO, USA). One blood sample, drawn from the 178 cm FL individual, was subdivided and half was incubated *in vitro* for 24 h post-capture at 4–6 °C under constant aeration with humidified air and gentle rotation. This incubated sample was assumed to represent blood from an unstressed individual. An additional blood sample drawn from the 155 cm FL shark was also subdivided and allowed to recover *in vitro* for 4 h.

3. Results

3.1. Survival assessment

A total of 20 common thresher sharks (160–221 cm FL, ~67–151 kg, 6 males and 14 females) were captured using the

caudal-based techniques, tagged and released to assess post-release survival (Table 1). Fight times ranged from 32 to 140 min with an average of 72 ± 30 min and generally increased with body size. One PSAT failed to report any information and this individual was not considered in the survival estimate. Fourteen of the sharks survived 10 days at liberty (Table 1). Five (26%) sharks (one male and four female) did not survive the acute effects of capture. The two sharks with the longest fight times (135 and 140 min) were already dead when brought to the side of the boat. All mortalities occurred within 4 h of release. All five common thresher sharks with fight times ≥85 min did not survive the capture event and were 180 cm FL or larger.

3.2. Movement patterns

Depth statistics were compiled from the six recovered PSATs. The average day depth was 24 ± 16 m and the average night depth was 10 ± 5 m. Although depths of up to 405 m were recorded (shark # 6, 170 FL), the sharks predominantly remained within the uniformed temperature surface layer during both day and night [average thermocline depth was 32 ± 12 m; determined from the strongest temperature gradient (*dT/dz*) for each track]. A plot of the joint distribution of time and depth over a 24 h period constructed from 60 days of vertical movement data illustrates the diel distribution within the uniformed temperature surface layer (Fig. 2). The average horizontal movement (derived from the tagging and pop-off locations) for the 10 day deployment period was 76 ± 95 km and the greatest displacement observed was by shark # 19 (220 cm FL), which moved 358 km into northern Baja California, Mexico.

3.3. Blood biochemistry

Of eight blood and plasma parameters examined (Na⁺, Cl⁻, K⁺, Ca⁺⁺, Mg⁺⁺, glucose, lactate, and hematocrit) only lactate and hematocrit increased significantly (*P* < 0.05) with fight time (Table 2, Fig. 3A). Plasma lactate values ranged from a low of 5.1 mM (20-min fight time) to 27 mM (75-min fight time). The corresponding hematocrit values were 34–47%, respectively. All thresher blood samples showed *hsp70* levels that were elevated above those from blood that was allowed to recover *in vitro* for 24 h (Fig. 3B) but there

Table 2
Electrolytes and metabolites in the blood of recreationally caught common thresher sharks.

| Hook position | FL (cm), mass ^a (kg) | Sex | Fight time (min) | Na ⁺ (mM) | Cl ⁻ (mM) | K ⁺ (mM) | Ca ⁺⁺ (mM) | Mg ⁺⁺ (mM) | Glucose (mM) | Lactate (mM) | Hct (%) |
|------------------------|---------------------------------|-----|------------------|----------------------|----------------------|---------------------|-----------------------|-----------------------|--------------|--------------|----------|
| Mouth | 157, 64 | M | 8 | 263 | 260 | 3.66 | 1.89 | 0.78 | 72 | - | 19 |
| Pectoral fin | 102, 21 | M | 12 | 279 | 270 | 4.71 | 2.88 | 1.26 | 129 | 0.9 | - |
| Tail-hooked | 194, 103 | F | 20 | 258 | 255 | 3.36 | 1.56 | 0.66 | 66 | 5.1 | 34 |
| | 190, 102 | F | 30 | 288 | 269 | 3.39 | 2.76 | 1.23 | 147 | 18.0 | - |
| | 155, 62 | M | 37 | 293 | 280 | 5.07 | 2.43 | 0.93 | 93 | 15.0 | 42 |
| | 178, 86 | F | 40 | 271 | 258 | 4.50 | 2.13 | 1.41 | 153 | 24.0 | 33 |
| | 134, 43 | M | 40 | 294 | 279 | 6.87 | 2.70 | 1.47 | 93 | 19.5 | 34 |
| | 188, 99 | F | 60 | 296 | 277 | 4.65 | 2.79 | 1.41 | 102 | 25.2 | 44 |
| | 188, 99 | M | 75 | 279 | 256 | 4.50 | 2.55 | 1.32 | 123 | 27.0 | 47 |
| Mean ± SD ^b | | | | 283 ± 14 | 268 ± 11 | 4.62 ± 1.2 | 2.41 ± 0.44 | 1.20 ± 0.30 | 111 ± 32 | 19.1 ± 7.5 | 38 ± 5.9 |

^a Body mass estimated from length (Kohler et al., 1995).

^b Mean values presented for tail-hooked individuals only.

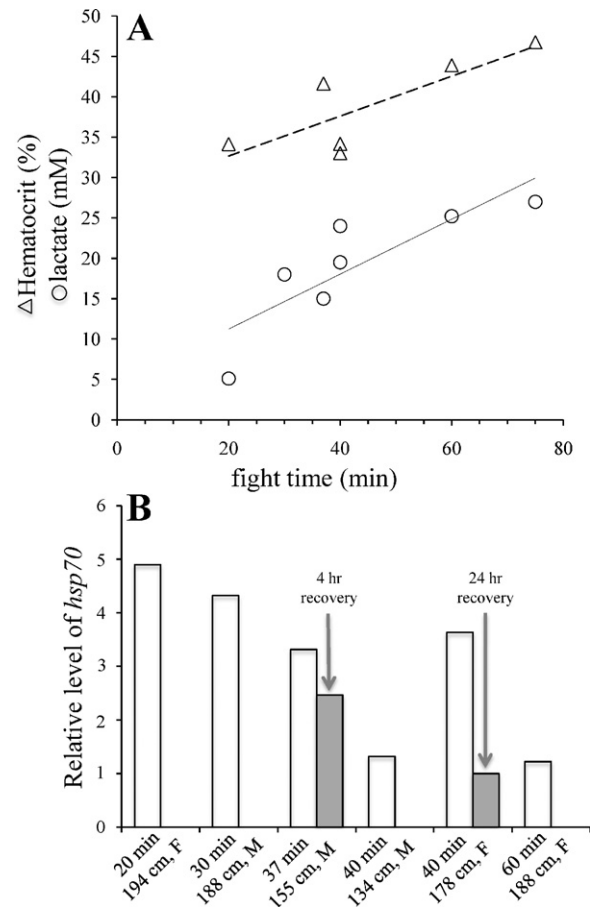


Fig. 3. Changes in stress indicators in the blood of tail-hooked thresher sharks. (A) hematocrit (triangles) and plasma lactate (circles), lines represent significant ($P < 0.05$) relationships between measured parameters and fight time (min): dashed line, Hct (%) = $27.7 + 0.247 \times (\text{fight time})$ [$r^2 = 0.65$, $n = 6$]; solid line, lactate (mM) = $2.65 + 0.367 \times (\text{fight time})$ [$r^2 = 0.71$, $n = 7$]. (B) Relative change in heat shock protein 70 (*hsp70*) levels in the red blood cells in relation to fight time. Shaded bars show values for two individuals in which the blood was allowed to recover *in vitro*. Values were normalized to 1 using the band density of the 24 h recovery sample.

was no significant relationship between *hsp70* levels and fight time. Relative *hsp70* values at the time of capture decreased by 26% and 72% for the two individuals for which the blood was allowed to recover for 4 and 24 h, respectively (Fig. 3B).

4. Discussion

This study provides the first estimate of post-release survival for common thresher sharks caught using the caudal-based techniques developed in the SCRF. This work was designed to replicate the fishing methods and equipment predominantly used in the SCRF for common thresher sharks. Parameters shown to influence post-release survival (i.e., hook location, handling time, bait type, and angler experience) were standardized to the extent possible across all individuals despite differences in body size (reviewed by Muoneke and Childress, 1994; Skomal, 2007). Similar caudal-based capture methods have been used in telemetry studies to track common threshers in the SCB; however, no immediate mortalities were reported in the movement studies (Cartamil et al., 2010). This discrepancy is likely due to the reduced fight times of the sharks of the Cartamil et al. (2010) work (20 min vs. 72 ± 29 min, Table 1) and possibly the smaller mean size of the sharks studied (~130 cm FL vs. 185 ± 18 cm FL, Table 1). In this study, heightened mortality rates and an elevated stress response were observed for large individuals with extended fight times. When captured by the caudal

fin, fight duration appears to correlate with post-release survival, as all tagged individuals with prolonged fight times (≥ 85 min) did not survive.

Direct comparison with other hooking mortality studies is problematic, as the caudal-based techniques of the SCRf are unique to this fishery and likely induce different stressors than more traditional capture techniques. Hook location influences post-release survival in many species (Muoneke and Childress, 1994); however, mortality is typically associated with damage to the gills or visceral tissue caused by deeply embedded hooks rather than from impaired locomotion or hypoxia (Prince et al., 2007; Lyle et al., 2007). Skomal (2007) discussed the importance of “fishery-specific” estimates of post-release survival, as different gear types likely induce varying degrees of physiological disruption. Nonetheless, the observed mortality rate (26%) for tail-hooked sharks does fall within the range of hooking mortality estimates published for other pelagic species (reviewed by Muoneke and Childress, 1994; Skomal, 2007). It does however exceed the 20% threshold which Muoneke and Childress (1994) considered to be unacceptably high for an effective catch-and-release management strategy. Further, when our results are segregated by size, it is evident that there were no mortalities in the smaller individuals (< 180 cm FL) whereas over 41% of the larger sharks ≥ 180 cm FL did not survive.

4.1. Factors potentially contributing to mortality

The common thresher shark is a pelagic, ram-ventilating species that must have forward motion to ventilate the gills. The orientation of the gill slits and the strapped-gill morphology of elasmobranchs preclude water flow over the gills when the individuals are pulled backwards (Wegner et al., 2010). Therefore, the caudal-based capture methods lead to reduced water flow over the gills as the sharks can only ventilate during brief periods of forward swimming. The finding that all sharks with fight times ≥ 85 min died suggests that there may be a temporal threshold for post-release survival. Other works have also identified angling time as a critical factor in post-release survivorship (Cooke and Suski, 2005), but it may be that fight time is particularly critical when using caudal-based capture techniques. For all fishing operations, a standard drag pressure of 9 kg was used regardless of the size of the sharks on the line. This drag pressure resulted in the smaller sharks having reduced fight times, which may contribute to the high survivorship recorded for the smaller individuals (< 180 cm FL) in our study as well as in the Cartamil et al. (2010) work.

4.2. Blood biochemistry

Acute stress resulting from a capture event can elicit a host of potentially lethal physiological changes that can be quantified though changes in the blood biochemical parameters (Hoffmayer and Parsons, 2001; Mandelman and Skomal, 2009; Wood et al., 1983; Skomal and Bernal, 2010). In addition, the recovery from stress is energetically costly as evidenced by temporal increases in metabolic rate and increases in plasma glucose levels (Hoffmayer and Parsons, 2001; Skomal, 2007). Although we did not observe changes in plasma electrolytes (Na^+ , Cl^- , K^+ , Ca^{++} , Mg^{++}) and glucose, there were significant increases in both plasma lactate and hematocrit with fight time. Because capture-related burst swimming (i.e., struggling) is primarily powered by the white myotomal muscle (comprising $\sim 50\%$ of body mass; Sepulveda et al., 2005), the continuous recruitment of this anaerobic tissue leads to the intramuscular accumulation of lactate and protons. When not processed, these metabolic byproducts may result in muscle acidosis and potentially cause long-lasting and irreversible damage to myotomal tissue and function (Arthur et al., 1992; Milligan, 1996). A recent study by Moyes et al. (2006) classified longline-captured

blue sharks (*Prionace glauca* L.) as either “moribund” or “survivors” according to plasma lactate concentration, with moribund blue sharks having lactate levels that were 5-times higher than surviving specimens (28 ± 4 mM). The elevated lactate levels in moribund blue sharks were similar to those obtained from the sharks of this study subjected to the longest fight times further suggesting the compromised physiological state of the individuals that spent the longest time on the line. The lactate values we measured are also comparable to those documented for longline-captured common threshers (Hight et al., 2007); however, the post-release survivorship and physical state of the sharks in the Hight et al. (2007) study were not quantified.

The mean hematocrit for all thresher sharks observed in this study was at the high end of the range for active sharks (Emery, 1986; Bernal et al., 2001; Carlson and Parsons, 2003). Further, the caudal-based techniques used in this study confound comparisons with most works to date, as severe hypoxia from being hauled in backwards could have triggered the release of additional erythrocytes from the spleen.

Heat shock proteins (*hsps*) are expressed in cells to maintain appropriate protein interactions and can be induced in response to thermal and oxidative stressors (Iwama et al., 2006). Shark nucleated red blood cells (RBCs) are capable of producing *hsps* within minutes of exposure to a stressor (Currie et al., 1999). Moyes et al. (2006) found that *hsp70* was significantly elevated in moribund blue sharks when compared to survivors, thus providing a framework for using *hsp70* along with other variables (e.g., plasma lactate) to predict survivability. Our findings show that the relative levels of *hsp70* for all tail-hooked thresher sharks were elevated up to five times when compared to *hsp70* values from blood that was allowed to recover from the capture event (Fig. 3B). Evidence of recovery was determined by a decrease in lactate relative to at-capture levels and the lack of any red blood cell lysis, suggesting that the *in vitro* blood samples were still viable and that irreparable damage to the cells had not occurred. We also opportunistically sampled two thresher sharks that were not hooked by the tail (i.e., one was mouth-hooked, the other hooked in the pectoral fin). These sharks had lower fight times and relative *hsp70* levels when compared to the tail-hooked threshers (Table 2).

4.3. Vertical and horizontal movements

The depth distribution of this study was similar to that previously documented for acoustically tracked and archivally tagged sub-adult and adult common thresher sharks in the SCB (Cartamil et al., 2010). For all individuals, the predominant depth distribution was within the uniformed temperature surface layer, with a slightly greater depth distribution during the day than at night (Figs. 1 and 2). Archived depth records were markedly similar throughout the duration of all tracks, suggesting that the sharks were not lethally injured by the capture and tagging event.

The net horizontal movements ranged from 9 to 358 km, with the two largest surviving individuals traveling the greatest distance (sharks 17 and 19; Table 1). Although previous works suggest a northward migration along the CA coast in spring months (Smith and Aseltine-Neilson, 2001) the movements we observed were predominantly southward ($n = 12$ sharks moved south) with only two animals moving to the north. Despite the short duration of the deployments, several of the tagged sharks moved across the U.S.–Mexico international border corroborating previous reports on the importance of international conservation and management for this trans-boundary resource.

4.4. Additional management concerns

Recreational thresher shark landings peak during the spring months when large numbers of pregnant females enter the SCB

to pup (Smith and Aseltine-Neilson, 2001). The high mortality rates recorded for larger individuals in this study suggests that the mature thresher sharks present in the SCB during the spring (≥ 180 cm FL; Hanan et al., 1993) are vulnerable to heightened post-release mortality. Although regulations have been implemented to reduce commercial landings in the spring months, the recent expansion of the recreational fishery may require complementary regulations as well. We suggest that future management recommendations consider excluding catch-and-release as a viable conservation recommendation for larger individuals captured using the caudal-based techniques. Further, survival estimates from sharks captured by alternative gear types and fishing techniques should also be assessed to fully understand their impact on released individuals.

Acknowledgements

This material is based upon work supported by the Bycatch Reduction and Engineering Program of the National Oceanic and Atmospheric Administration and the National Science Foundation (NSF Grants IOS-0617384 & IOS-0617403). Any opinions, findings, or conclusions expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation. Additional support was provided by the George T. Pfleger Foundation and the William H. and Mattie Wattis Harris Foundation. Special thanks are offered to Natalie Spear, Heidi Dewar, Nick Wegner, Thomas Fullam, Jeanine Sepulveda, Victoria Wintrode, Lorraine Bohnet, Doug Syme, Jake Ness, Trevor Young, and Jock and Charlie Albright. We appreciate the logistical support from J. Valdez, S. Adams and T. Tazo. We sincerely thank Thomas Pfleger and Family for their continued dedication towards marine research.

References

- Aalbers, S.A., Bernal, D., Sepulveda, C.A., 2010. The use of the caudal fin in the feeding ecology of the common thresher shark, *Alopias vulpinus*. *J. Fish Biol.* 76, 1863–1868.
- Arthur, P.G., West, T.G., Brill, R.W., Schulte, P.M., Hochachka, P.W., 1992. Recovery metabolism of skipjack tuna (*Katsuwonus pelamis*) white muscle: rapid and parallel changes in lactate and phosphocreatine after exercise. *Can. J. Zool.* 70, 1230–1239.
- Bernal, D., Dickson, K.A., Shadwick, R.E., Graham, J.B., 2001. Analysis of the evolutionary convergence for high performance swimming in lamnid sharks and tunas. *Comp. Biochem. Physiol.* 129A, 695–726.
- Bernal, D., Sepulveda, C.A., 2005. Evidence for temperature elevation in the aerobic swimming musculature of the common thresher shark, *Alopias vulpinus*. *Copeia* 2005, 163–168.
- Cailliet, G.M., Bedford, D.W., 1983. The biology of three pelagic sharks from California waters, and their emerging fisheries: a review. *Cal. Coop. Ocean. Fish. Inv. Rep.* 24, 57–69.
- Carlson, J.K., Parsons, G.R., 2003. Respiratory and hematological responses of the bonnethead shark, *Sphyrna tiburo*, to acute changes in dissolved oxygen. *J. Exp. Mar. Biol. Ecol.* 294, 15–26.
- Cartamil, D.P., 2009. Movement patterns, habitat preferences, and fisheries biology of the common thresher shark (*Alopias vulpinus*) in the Southern California Bight. Doctoral Dissertation, UC San Diego: California Sea Grant College Program. Available from: <http://www.escholarship.org/uc/item/3908d6cv>.
- Cartamil, D., Wegner, N.C., Aalbers, S.A., Sepulveda, C.A., Baquero, A., Graham, J.B., 2010. Diel movement patterns and habitat preferences of the common thresher shark (*Alopias vulpinus*) in the Southern California Bight. *Mar. Freshw. Res.* 61, 596–604.
- Cooke, S.J., Suski, C.D., 2005. Do we need species-specific guidelines for catch-and-release recreational angling to effectively conserve diverse fisheries resources? *Biodiv. Conserv.* 14, 1195–1209.
- Currie, S., Tufts, B.L., Moyes, C.D., 1999. Influence of bioenergetic stress on heat shock protein gene expression in nucleated red blood cells of fish. *Am. J. Physiol.* 276, R990–R996.
- Emery, S.H., 1986. Hematological comparisons of endothermic vs. ectothermic elasmobranch fishes. *Copeia* 1986, 700–705.
- Graves, J.E., Luckhurst, B.E., Prince, E.D., 2002. An evaluation of pop-up satellite tags for estimating postrelease survival of blue marlin (*Makaira nigricans*) from a recreational fishery. *Fish. Bull.* 100, 134–142.
- Hanan, D.A., Holts, D.B., Coan Jr., A.L., 1993. The California drift gill net fishery for sharks and swordfish, 1981–82 through 1990–91. *Fish. Bull.* 175, 89–95.
- Hight, B.V., Holts, D., Graham, J.B., Kennedy, B.P., Taylor, V., Sepulveda, C.A., Bernal, D., Ramon, D., Rasmussen, R., Lai, N.C., 2007. Plasma catecholamine levels as indicators of the post-release survivorship of juvenile pelagic sharks caught on experimental drift longlines in the Southern California Bight. *Mar. Freshw. Res.* 58, 145–151.
- Hoffmayer, E.R., Parsons, G.R., 2001. The physiological response to capture and handling stress in the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*. *Fish. Physiol. Biochem.* 25, 277–285.
- Holts, D.B., 1988. Review of U.S. west coast commercial shark fisheries. *Mar. Fish. Rev.* 50, 1–8.
- Horodysky, A.Z., Graves, J.E., 2005. Application of pop-up satellite archival tag technology to estimate postrelease survival of white marlin (*Tetrapturus albidus*) caught on circle and straight-shank (“J”) hooks in the western North Atlantic recreational fishery. *Fish. Bull.* 103, 84–96.
- Iwama, G.K., Afonso, L.O.B., Vijayan, M.M., 2006. Stress in fishes. In: Evans, D.H., Claiborne, J.B. (Eds.), *The Physiology of Fishes*. Taylor and Francis Group, Boca Raton, FL, pp. 319–342.
- Kohler, N.E., Casey, J.G., Turner, P.A., 1995. Length–weight relationships for 13 species of sharks from the western North Atlantic. *Fish. Bull.* 93, 412–418.
- Lyle, J.M., Moltschanivskiy, N.A., Morton, A.J., Brown, I.W., Mayer, D., 2007. Effects of hooking damage and hook type on post-release survival of sand flathead (*Platycephalus bassensis*). *Mar. Freshw. Res.* 58, 445–453.
- Mandelman, J.W., Skomal, G.B., 2009. Differential sensitivity to capture stress assessed by blood acid–base status in five carcharhinid sharks. *J. Comp. Physiol. B* 179, 267–277.
- Milligan, C.L., 1996. Metabolic recovery from exhaustive exercise in rainbow trout. *Comp. Biochem. Physiol.* 113A, 51–60.
- Moyes, C.D., Fragoso, N., Musyl, M.K., Brill, R.W., 2006. Predicting post release survival in large pelagic fish. *Trans. Am. Fish. Soc.* 135, 1389–1397.
- Muoneke, M.I., Childress, W.M., 1994. Hooking mortality: a review for recreational fisheries. *Rev. Fish. Sci.* 2, 123–156.
- PFMC, 2003. Fishery Management Plan and Environmental Impact Statement for U.S. West Coast Fisheries for Highly Migratory Species. NOAA award No. NA03NMF4410067. Pacific Fishery Management Council, Portland, OR. Available from: <http://www.pcouncil.org/wp-content/uploads/HMS.FMP.Aug09.pdf>.
- PFMC, 2007. Stock Assessment and Fishery Evaluation. Status of the U.S. West Coast Fisheries for Highly Migratory Species through 2006. Portland, OR, pp. 18–32. Available from: <http://www.pcouncil.org/wp-content/uploads/07.HMS.SAFE.pdf>.
- PFMC, 2008. Highly migratory species advisory subpanel report on changes to routine management measures for 2009–2010 season; Thresher Shark management measures. Pacific Fishery Management Council, Portland, OR. Available from: http://www.pcouncil.org/bb/2008/0908/SUP_H2b.HMSAS_0908.pdf.
- Prince, E.D., Snodgrass, D., Orbesen, E., Hoolihan, J.P., Serafy, J.E., Schratweiser, J.E., 2007. Circle hooks, ‘J’ hooks and drop-back time: a hook performance study of the south Florida recreational live-bait fishery for sailfin, *Istiophorus platypterus*. *Fish. Manage. Ecol.* 14, 173–182.
- Roberts, J.L., 1978. Ram gill ventilation in fish. In: Sharp, G.D., Dizon, A.E. (Eds.), *The Physiological Ecology of Tunas*. Academic Press, New York, pp. 83–87.
- Sepulveda, C.A., Wegner, N.C., Bernal, D., Graham, J.B., 2005. The red muscle morphology of the thresher sharks (family Alopiidae). *J. Exp. Biol.* 208, 4255–4261.
- Sepulveda, C.A., Knight, A., Nasby-Lucas, N., Domeier, M.L., 2010. Fine-scale movements of the swordfish in the Southern California Bight. *Fish. Oceanogr.* 19 (4), 279–289.
- Skomal, G.B., 2007. Evaluating the physiological and physical consequences of capture on post-release survivorship in large pelagic fishes. *Fish. Manage. Ecol.* 14, 81–89.
- Skomal, G., Bernal, D., 2010. Mechanisms and adaptations associated with physiological stress. In: Carrier, J.C., Musick, J.A., Heithaus, M.R. (Eds.), *Volume 2: The Biology of Sharks and Their Relatives. Physiological Adaptations, Behavior, Ecology, Conservation and Management of Sharks and Their Relatives*. CRC Press, pp. 459–490 (Chapter 11).
- Smith, S.E., Aseltine-Neilson, D., 2001. Thresher shark. In: Leet, W.S., Dewees, C.M., Klingbeil, R., Larson, E.J. (Eds.), *California Living Marine Resources: A Status Report*. University of California Agriculture and Natural Resource, Davis, CA, p. 592.
- Wegner, N.C., Sepulveda, C.A., Bull, K.B., Graham, J.B., 2010. Gill morphometrics in relation to gas transfer and ram ventilation in high-energy demand teleosts: scombrids and billfishes. *J. Morph.* 271, 36–49.
- Wood, C.M., Turner, J.D., Graham, M.S., 1983. Why do fish die after severe exercise? *J. Fish Biol.* 22, 189–201.