Fisheries Research 161 (2015) 102–108

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Post-release survivorship studies on common thresher sharks (*Alopias vulpinus*) captured in the southern California recreational fishery

C.A. Sepulveda[a,*], C. Heberer[b], S.A. Aalbers[a], N. Spear[c], M. Kinney[c], D. Bernal[d], S. Kohin[c]

[a] Pfleger Institute of Environmental Research (PIER), Oceanside, CA 92054, United States
[b] National Marine Fisheries Service (NMFS), Southwest Region, Carlsbad, CA 92011, United States
[c] NMFS, Southwest Fisheries Science Center, La Jolla, CA 92037, United States
[d] Department of Biology, University of Massachusetts Dartmouth, Dartmouth, MA 02747, United States

ARTICLE INFO

Article history:
Received 20 March 2014
Received in revised form 27 June 2014
Accepted 28 June 2014
Handling Editor A.E. Punt

Keywords:
Trailing gear
Circle hook
Survival
Catch-and-release mortality
Fishery

ABSTRACT

The common thresher shark (*Alopias vulpinus*) is the focus of a popular southern California recreational fishery that targets individuals using multiple fishing gears and techniques. Despite increasing trends in the use of catch and release techniques in the recreational fishery for thresher sharks, a comprehensive estimate of post-release survival is not available for all modes of capture. This study focused on assessing post-release survival in two modes of capture routinely observed in the southern California recreational fishery: (1) sharks that are caught using caudal-based angling techniques and unintentionally released with trailing gear left embedded and (2) sharks that are caught and released using mouth-based angling techniques. Post-release survivorship was assessed using pop-up satellite archival tags programed for 10- and 90-day deployments, with the former used for mouth-caught sharks and the latter for individuals with trailing gear. Post-release survivorship estimates for the trailing gear studies were based on data from nine common thresher sharks (111-175 cm FL) while the mouth-based experiments utilized data from an additional seven sharks (125-187 cm fork length, FL). For the trailing gear studies, six sharks died within 5 days after release, one died after 81 days, and two sharks survived the deployment period for an overall survivorship rate of 22%. All seven mouth-hooked common thresher sharks survived the acute (~10 days) effects of capture (100% survivorship). These results suggest that in the southern California recreational thresher shark fishery, caudal-based angling techniques, which often result in trailing gear left embedded in the shark, can negatively affect post-release survivorship. This work also reveals that mouth-based angling techniques can, when performed properly, result in high survivorship of released sharks.

1. Introduction

The common thresher shark (*Alopias vulpinus* Bonnaterre) is a highly migratory species that is targeted extensively by both commercial and recreational fishers off the west coast of the United States (Cailliet and Bedford, 1983; Heberer et al., 2010). It is one of eleven federally managed species under the Fishery Management Plan for West Coast Fisheries for Highly Migratory Species (PFMC, 2005). Similar to other pelagic shark species, the common thresher shark is relatively long-lived, bears few pups each year and is considered to be highly vulnerable to over-exploitation (Cailliet and Bedford, 1983). Existing west coast management regimes include time and area closures placed on commercial operations (Hanan et al., 1993) as well as bag limits for recreational fishers. Currently, there are no restrictions on the use of catch and release techniques for this species.

Thresher sharks are morphologically distinct from most shark species in that the upper caudal lobe is as long as the trunk of the body and used to stun or immobilize prey (Hanan et al., 1993; Aalbers et al., 2010). Given this unique feeding strategy, the common thresher is routinely targeted by recreational fishers using a variety of techniques that result in different degrees of capture-related stress imparted on the animal. The most common strategy used by southern California recreational fishers entails the use of trolling lures rigged with baited J-hooks, which typically results in the shark being hooked in the caudal fin and pulled backwards during the fight (Heberer et al., 2010). This approach often results in the parting of the line, as mature thresher sharks (>200 kg) are

* Corresponding author at: Pfleger Institute of Environmental Research, 2110 South Coast highway, Suite F Oceanside, CA 92054, United States.
Tel.: +1 760 721 1404; fax: +1 760 721 1475.
E-mail addresses: chugey@pier.org, chugey@hotmail.com (C.A. Sepulveda).

http://dx.doi.org/10.1016/j.fishres.2014.06.014
0165-7836/

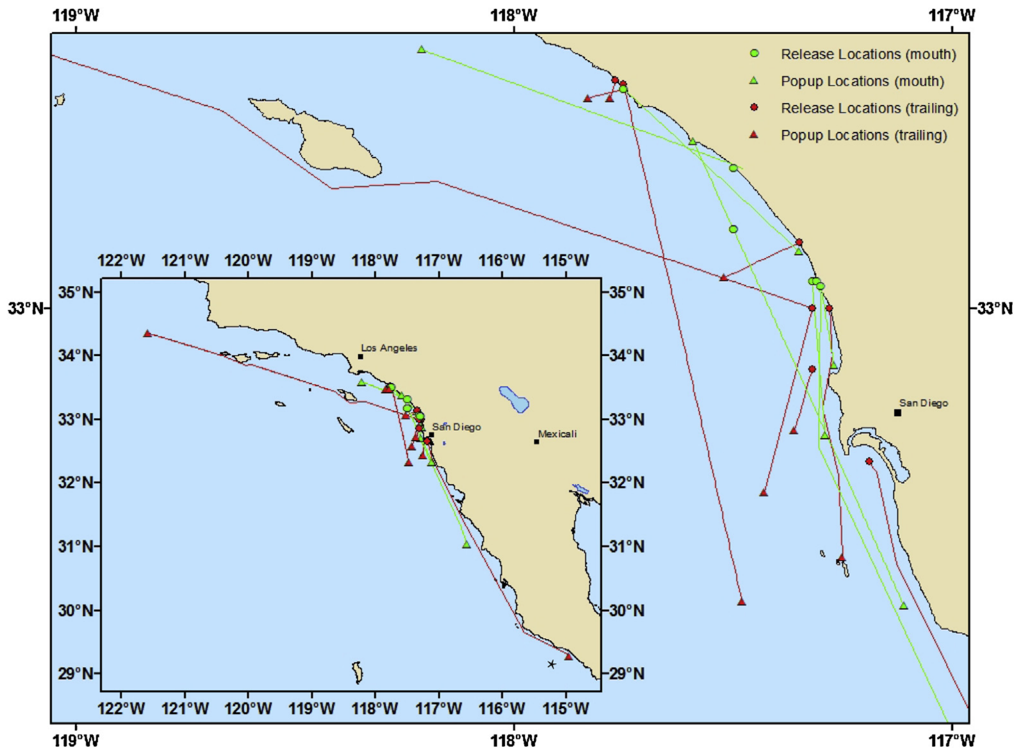

Fig. 1. Map of tagging and pop-off locations. *Shark #11A0555 with the longest point-to-point movements (446 km).

common during the spring pupping season (March through July), and can exert immense force when hooked in the caudal fin (i.e., foul-hooked). As a result, sharks are often unintentionally set free with terminal tackle, such as hooks and weights, left embedded in the caudal fin (i.e., trailing gear). The fate of sharks burdened with trailing gear is unknown and this has been suggested to be an important parameter in assessing the impacts that recreational fisheries have on the common thresher fishery (PFMC, 2010).

Common thresher sharks are also hooked by the mouth in the southern California recreational fishery. Mouth-based techniques typically require the use of circle hooks or alternative rigging methods to prevent the caudal fin from becoming foul-hooked upon the initial strike (Aalbers et al., 2010). Mouth-based techniques have been suggested to be less invasive, as they allow the sharks to swim and ventilate during the fight because common thresher sharks are obligate ram ventilators and must swim forward in order to ventilate their gills (Heberer et al., 2010). Despite management recommendations on the use of circle hooks and mouth-hooking techniques, there are no data on the post-release survival of common thresher sharks caught and released using these methods.

Because the majority of thresher sharks captured in the recreational fishery are hooked in the caudal fin, an initial study was performed to estimate post-release survival of tail-hooked individuals caught using standard fishery techniques (Heberer et al., 2010). The Heberer et al. (2010) study revealed high post-release survivorship in smaller sharks that were captured quickly (<85 min), which was contrasted by high mortality rates in large individuals that endured prolonged fight times. Because catch and release fishing for thresher sharks continues to gain popularity in California, the present study focused on the assessment of post-release survival for individuals captured using alternative methods. The objectives of this work were to use pop-off satellite archival tags (PSATs) to quantify post-release survivorship in: (1) common thresher sharks captured with caudal-based angling techniques and released with trailing gear (simulating the parting of line during the fight), and (2) sharks captured and released using mouth-based angling techniques.

2. Methods

Tagging operations were performed from May, 2009 through December, 2012 in the southern California Bight (SCB) from Laguna Beach, California (~33°28 N, 117°45 W) to the US–Mexico border (~32°33 N, 117°10 W) (Fig. 1). Fishing techniques and equipment were standardized to follow current recreational methods employed in the southern California recreational fishery for common thresher sharks. For all sharks, mass was estimated from fork length (FL) using a length–weight conversion for common thresher sharks (Kohler et al., 1995). Fight duration was defined as the time from initial hook-up to the time of release; mean (±SD) values are reported.

2.1. Tag specifications

Wildlife Computers (Redmond, Washington, USA) MK10 PSATs were programed to record depth, ambient temperature, and light level every 30 s for the duration of the deployments. Deployment schedules for the two experimental treatments (mouth-based and trailing gear) are discussed in Section 2.4. The PSATs were programed to release prematurely if depth values remained constant (±5 m) over a 48-h period, consistent with a mortality or shed tag. Tag rigging and attachment methods followed the protocol outlined in Heberer et al. (2010) and included the use of a Wildlife Computers (Richmond, Washington, USA) depth guillotine that severed the tag leader at 1500 m in the event of a mortality. Tag anchors used in this study consisted of a double-barbed nylon dart head [BFIM-96 (Floy Tag) Seattle, WA, USA]. Directed efforts were made to recover and re-use PSATs that released from sharks near

Table 1
Catch information and post-release fate of common thresher sharks in this study.

	Shark #ID	Date deployed	Sex	FL (cm)[b]	Mass (kg)[c]	Net movement (km)[d]	Days at liberty	Fight time (min)	Mortality
Tail-hooked, trailing gear	11A0552	09/25/12	F	111	27	446	81	12	Y
	08A0247a	07/06/10	F	132	41	–	1	15	Y
	09A0298a	07/06/10	F	134	43	–	1	12	Y
	10A0118	09/27/11	F	138	46	–	2	10	Y
	09A0297a	05/29/10	F	140	48	–	2	20	Y
	09A0296	05/29/10	?	142	49	–	–	25	N/A[e]
	11A0553	09/27/11	F	149	56	–	5	20	Y
	09A0297b	06/01/12	F	152	59	–	2	12	Y
	11A0556	09/27/11	F	157	64	425	90	20	N
	09A0299	09/27/10	M	175	84	135	62[a]	25	N
Mouth-hooked	09A0301	05/22/11	F	125	36	5	24[a]	9	N
	10A0119	06/24/11	M	130	40	90	88[a]	25	N
	09A0298b	10/10/11	F	135	44	43	10	12	N
	10A0120	06/22/11	M	137	45	69	90	15	N
	08A0787	11/15/12	M	168	76	44	10	22	N
	08A0247b	11/19/12	F	168	76	13	10	20	N
	11A0555	11/15/12	F	187	99	241	10	25	N

[a] Tags that malfunctioned and detached from animals earlier than scheduled.
[b] Fork length.
[c] Body mass estimated from Kohler et al. (1995).
[d] Horizontal distance determined from site of tag deployment and pop-off location.
[e] Tag failed to report.

(<50 km) the deployment location following established methods (Sepulveda et al., 2010; Heberer et al., 2010).

2.2. Trailing gear experiments

The trailing gear component of this study was designed to simulate the events that occur when the line is parted during the fight. Gear design was based on industry standard tackle currently employed in the southern California troll fishery for thresher sharks (Heberer et al., 2010). Briefly, 0.5 kg lead-headed trolling lures prerigged with wire leaders (length ∼2 m) and tandem 8/0 J hooks (Leadmasters, Hesperia, CA, USA) were baited with chub mackerel (*Scomber japonicus* Houttuyn) and slow trolled behind the tagging vessel. All common thresher sharks were fought and brought to the boat using 36-kg tackle with a drag pressure of 9 kg with a commercially available stand-up fighting harness (Table 1).

Once boatside, the sharks were restrained, quickly measured (<2 min), and sex was determined. Prior to release, a PSAT was implanted into the dorsal musculature proximal to the base of the dorsal fin. To simulate the events that occur during fishing operations that result in sharks released with trailing gear (i.e., parting the line during the fight), this study did not employ any post-capture revival or resuscitation exercises. Upon release, the monofilament mainline was severed above the swivel and the tagged shark was set free with the trolling lure and ∼2 m of leader material embedded in the caudal fin.

2.3. Mouth-based experiments

Fishing tackle and techniques for the mouth-hooking trials were based on methods currently used by fishers that practice catch and release fishing for common thresher sharks, and similar to techniques used for other highly migratory species (Prince et al., 2007). Terminal tackle consisted of 8/0–10/0 non-offset circle hooks (Eagle Claw L2004, USA) with 2 m of 50 kg monofilament leader material. Chub mackerel were either slow trolled or drifted in areas of high bait concentration or locations in which thresher sharks had been observed. To be consistent with the methods currently employed in the recreational fishery, a drag pressure setting of 5–8 kg was used without the aid of a fighting harness. Once boatside, the hook was removed from the mouth and the shark was measured, a PSAT affixed, and released.

2.4. Survivorship estimates

Post-release survivorship was assessed from depth and temperature profiles following protocols previously used to infer mortality from PSAT data records (Graves et al., 2002; Horodysky and Graves, 2005; Heberer et al., 2010). A 90-day pop-off schedule was used to account for delayed mortality that may have ensued as a result of the burden (i.e., physical and/or physiological) associated with the trailing gear. For the mouth-hooking component of this research, a 10-day pop-off schedule was chosen for the majority of animals, following the protocol used in the previous common thresher survivorship study (Heberer et al., 2010). For three mouth-hooked individuals, 90-day tags were deployed because of the lack of 10-day tags available during the mouth-based trials. For statistical comparisons of mouth-hooked versus trailing gear sharks, a Cox regression-based test for equality of survival curves was used with all tracks truncated to an equivalent deployment period (10 days). For all statistical analyses, an α of 0.05 was used to infer significance.

To determine how time on the line may predict post-release mortality a binomial generalized linear model (GLM) was run with a binomial logit link function (i.e., the continuous framework, based on a transformation of the categorical dependent variable, upon which linear regression is conducted). Unlike a logistic regression, the binomial GLM can assume a normal distribution of categorical data (e.g., live versus dead). The binomial response variables were set as live (=0) versus dead (=1) for the sharks of this study. The resultant logistic regression function was used to determine explanatory probabilities based on the generated model of mortality events increasing with time on the line. Prior to running the GLM, a Levene's Test for homogeneity was used to ensure homoscedasticity between live and dead groups.

2.5. Movement data

Depth and temperature data were not analyzed for ecological significance due to the limited duration of the majority of mouth-based deployments and the unknown effects of trailing gear. However, vertical movement data were compared with previous tagging data (Cartamil et al., 2010, 2011; Heberer et al., 2010) to assess whether surviving sharks exhibited vertical movement patterns that were consistent with diving profiles from previous studies. Horizontal movement was calculated as the net displacement between tag deployment and pop-off locations.

3. Results

3.1. Survival with trailing gear

A total of 10 common thresher sharks (111-175 cm FL) were tagged and released with trailing gear left embedded in the caudal fin (Table 1, Fig. 1). Fight times ranged from 10 to 25 min (average of 17 ± 6 min) and were lower than those reported by Heberer et al. (2010) for tail hooked threshers. One of the ten tags failed to report information and therefore was not considered in the survival estimate. Of the nine reporting tags, three sharks (33%) survived the acute effects of capture (10 days), and two survived the duration of the tag's deployment (22%) (Table 1). All but one mortality occurred within 5 days of release (1.5 h–100 h, mean 34.1 ± 39.3 h), with shark 11A0552 suffering a delayed mortality 81-day post-release. While at liberty, the three common thresher sharks that survived for at least 60 days of the deployment moved on average 335 ± 174 km at a mean rate of 4.1 km day^{-1} (range 2.3-5.3 km day^{-1}) from the initial tagging site (Fig. 1). The shark with the greatest horizontal displacement was 11A0552, which moved 446 km (5.5 km day^{-1}) over its 81-day deployment period before suffering a delayed mortality under unknown circumstances.

The predicted at-vessel values for lactate in the blood of tail-hooked sharks released with trailing gear ranged from 7 to 12 mM based on the equation: lactate (mM) = [fight time (min) × 0.34(±0.25)] + 4.4, $n = 7$, $r^2 = 0.71$, $p < 0.001$ [error = 95% CI] (Fig. 2). Based on the physiological and post-release survival data collected by Heberer et al. (2010) these lactate values are lower than those published for sharks that experienced post-release mortality. Thus, the low fight times (up to 25 min) for the tail-hooked thresher sharks of this study would result in a near zero probability of post-release morality (Fig. 2a and b).

3.2. Survival using mouth-based techniques

A total of seven common thresher sharks (125-187 cm FL) were captured, tagged and released to assess survivorship of mouth-hooked individuals (Table 1). Fight times ranged from 9 to 25 min with an average of 18 ± 6 min. All individuals survived the acute (10 days) effects of capture with three 90-day PSATs indicating survival at 24-, 88- and 90-day post-release (tag #s 09A0301 and 10A0119 prematurely released from live individuals) (Table 1). A comparison of mouth-based and trailing gear sharks revealed a significant difference in survival rates. The average horizontal movement (derived from the tagging and pop-off locations) was 107 ± 87 km and the greatest net displacement was displayed by shark 11A0555 (187 cm FL), which moved 241 km into northern Baja California, Mexico during the 10-day deployment (Fig. 1; 24.1 km day^{-1}).

The predicted at-vessel values for lactate in the blood of released mouth-hooked sharks ranged from 7 to 13 mM. Based on the regression analyses, these values do not suggest a high probability of post-release morality (Fig. 2a and b; Heberer et al., 2010).

3.3. Vertical movement

Of the 16 functioning tags, 9 were recovered, offering detailed archival records of vertical movements, while the remaining 7 tags provided binned transmitted data of lower resolution. The deepest documented dive was 224 m, recorded by shark 11A0555, the lowest registered temperature was 9 °C, recorded by shark

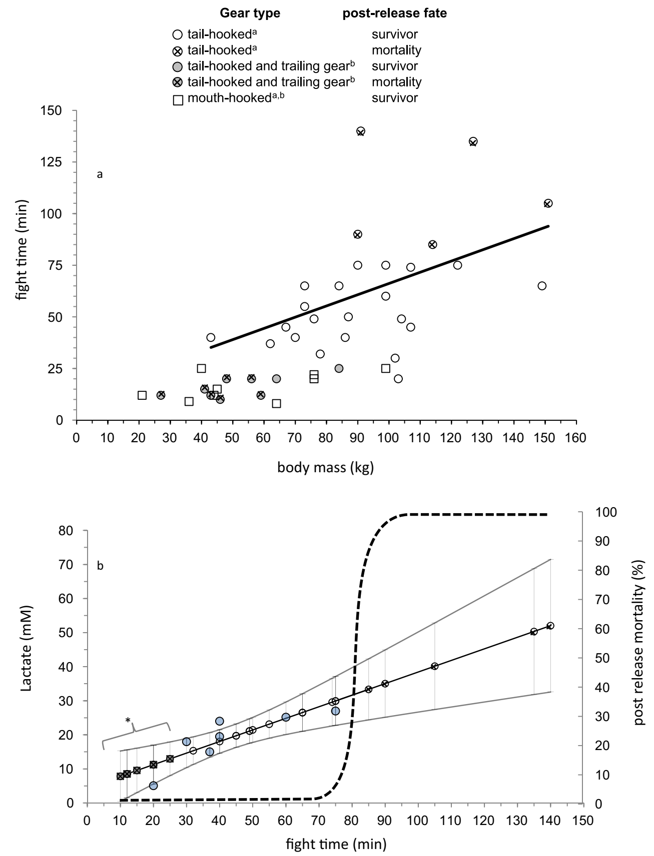

Fig. 2. (a) The effect of thresher shark body size on fight times using different capture techniques. Black lines represent the relationship between body mass and fight time for tail-hooked common thresher sharks: fight time (min) = [body mass (kg) × 0.54(±0.44)] + 11.7, $n = 26$, $r^2 = 0.21$, $p < 0.001$ [error = 95% CI]. (b) Plasma lactate concentrations as a function fight time in all tail-hooked captured sharks. Predicted lactate values were estimated using the relationship: lactate (mM) = [fight time (min) × 0.34(±0.25)] + 4.4, $n = 7$, $r^2 = 0.71$, $p < 0.001$ [error = 95% CI] derived from Heberer et al., 2010 (blue circles). Secondary axis shows the probability of post-release mortality as a function of fight time. *Sources*: [a]Heberer et al. (2010), [b]this study, *tail-hooked sharks released with trailing gear. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

10A0120, both individuals were caught using mouth-hooking techniques.

All sharks spent the majority of their time in the upper 50 m of the water column. Two distinct diving modes, 'Shallow' and 'Deep', as previously described by Cartamil et al. (2011), were evident in most records of sharks that survived the acute effects of capture (Fig. 3a and b). Vertical movement data for sharks released with trailing gear were limited due to only 3 individuals surviving more than 5 days, and only one tag being recovered. The vertical rate of movement, calculated from the initial 10 day of fine-scale depth records, was similar for the one individual that survived the 90-day deployment with trailing gear (1.69 ± 2.53 m min^{-1}) and the mouth-hooked individuals (range 1.01-1.70 m min^{-1}; mean 1.45 ± 1.76 m min^{-1}; $n = 5$). Despite the limited sample size it appears that sharks which managed to survive the acute effects of capture may be able to resume 'typical' diving behavior (Fig. 3b). However, more typically, threshers released with trailing gear died shortly after release (Fig. 3c).

4. Discussion

This study provides information on the post-release survival of common thresher sharks captured using two common fishing modes observed in the southern California recreational fishery.

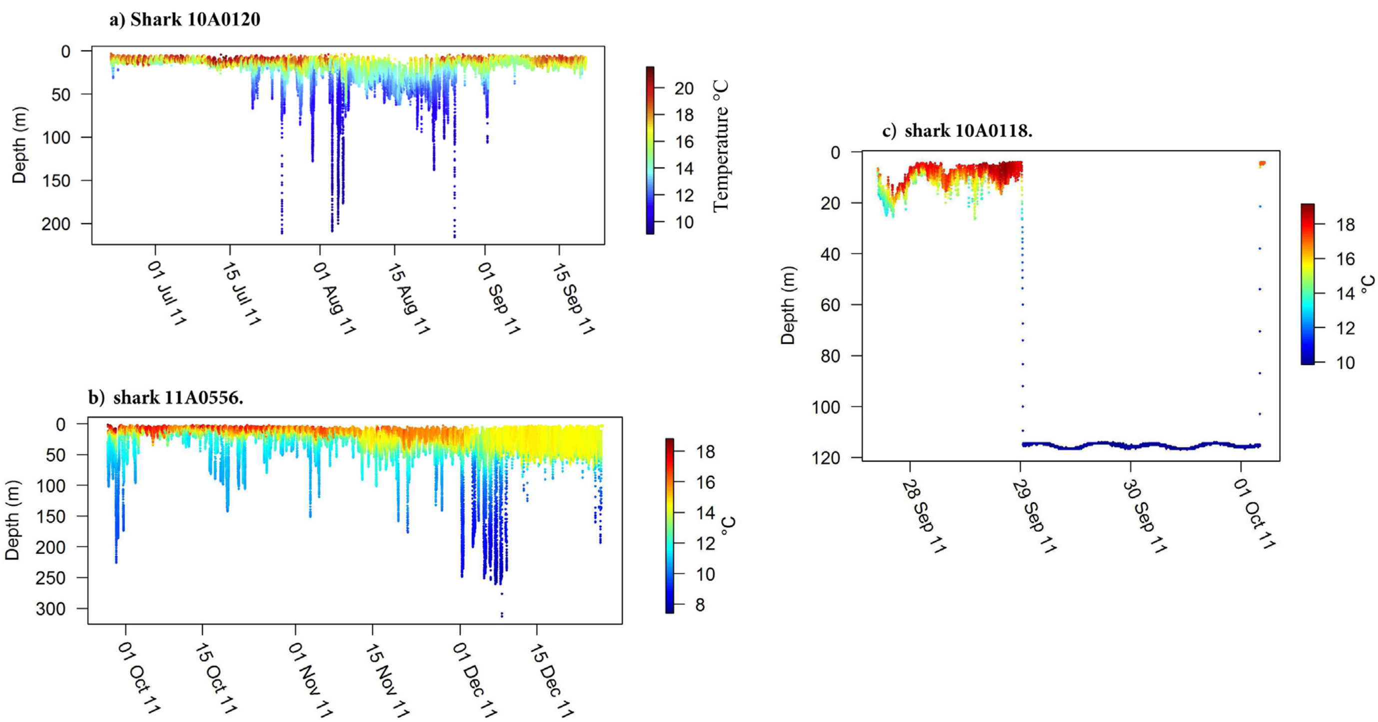

Fig. 3. Vertical use of the water column for three common thresher sharks in the study. (a) One mouth-hooked shark (10A0120; 90-day record), (b) one surviving tail-hooked shark released with trailing gear (11A0556; 90-day record, and (c) one tail-hooked shark with trailing-gear that did not survive (10A0118; 4-day record) showing less than 2 days of swimming behavior prior to sinking to the bottom. Each time series shows the depth color-coded by ambient water temperature.

Findings reveal that two thirds (67%) of the sharks burdened with trailing gear died shortly (<5 days) after release. These data suggest that trailing gear can negatively affect the survival of sharks unintentionally released during the fight (i.e., line parting during the fight). The ramifications of trailing gear in the southern California fishery are not consistent with conservation-based catch and release management strategies. In contrast, all of the sharks captured using mouth-based techniques survived the acute effects (10 days) of capture. Collectively, these findings support previous efforts to promote the use of mouth-based techniques as a management recommendation in the southern California recreational thresher shark fishery.

4.1. Trailing gear studies

Collectively, several factors may have accounted for the high post-release mortality rate observed in the trailing gear portion of this study. Capture-related burst swimming (i.e., struggling) is primarily powered white myotomal muscle (comprising ~50% of body mass; Sepulveda et al., 2005) and the continuous anaerobic recruitment of these tissues leads to the intramuscular accumulation of lactate and protons (Arthur et al., 1991; Skomal, 2007). In fish, the accumulation of these anaerobic metabolic byproducts has been shown to negatively affect muscle function and may negatively influence survival (Wood et al., 1983; Kieffer, 2000; Frick et al., 2012). Although elevated lactate levels resulting from capture are well documented in sharks, the slow leakage of this metabolite across the myofibrillar membrane may result in peak blood lactate values that are delayed for several hours after the capture event (Milligan and Wood, 1986; Frick et al., 2009; Marshall et al., 2012). Heberer et al. (2010) documented that post-capture lactate levels in tail-hooked common thresher sharks correlated with fight time reaching a peak of up to 27 mM. These lactate values are elevated when compared to other sharks sampled after a capture event (Frick et al., 2009, 2012; Marshall et al., 2012), and are likely due to the unusually long fight times that result from tail-based capture (Fig. 2a). In threshers, the repeated and potentially prolonged bouts of burst swimming during capture not only elevate lactate and protons in the muscle and blood, but also impair blood-oxygen binding at the gills and preclude adequate oxygen delivery to the working tissues, a critical step for recovery (Jensen et al., 1983). This cardio-respiratory distress may be exaggerated if the shark is not allowed to properly ram ventilate during the capture event, a scenario present when the shark is tailed-hooked and fight times are prolonged (>60 min, Heberer et al., 2010). By contrast, all of the tail-hooked sharks in this study ($n = 9$) were brought to the boat in less than 25 min (Fig. 2a) and the predicted mean lactate (9.9 ± 1.7 mM) is below that previously associated with post-release mortality (e.g., lactate: 19.1 ± 7.5, Heberer et al., 2010) (Fig. 2b). Based on Fig. 2b, the probability that tail-hooked sharks would have experienced post-release mortality after 25 min on the line is less than 5%. However, for most (6 of the 9) of the trailing gear sharks, it is possible that the individuals continued to elicit a post-release stress response due to the trailing gear, a scenario that may have prevented adequate recovery from the capture event.

Because 22% of the sharks released with trailing gear survived in this study, it is evident that the post-release effects of this stressor are not lethal in all cases. One possibility is that some individuals may have been able to shed the trailing gear from the caudal fin after release. Although the hooks used in this study have a relatively large barb to prevent shedding, it may be that the struggle while on the line was sufficient to tear the hook insertion site allowing the hook to be subsequently more easily shed. Alternatively, some sharks may be able to persist with the trailing gear affixed, as a comparison of the depth records from sharks that survived with and without trailing gear embedded, revealed similar movements patterns (Fig. 3a and b).

4.2. Mouth-based studies

The finding that all mouth-hooked thresher sharks survived following capture supports previous hypotheses (Heberer et al.,

2010) and validates the utility of incorporating these techniques into future catch and release management strategies. The high survivorship reported in this study is likely a product of several factors, including the ability of the shark to swim forward during the fight. Forward momentum allows the shark to ram ventilate and initiate the processing of anaerobic metabolic end products that accumulate in the tissues as a result of the fight (Milligan, 1996; Arthur et al., 1991; Skomal and Bernal, 2010). Compared to the tail-hooked sharks studied by Heberer et al. (2010), the fight times for all sharks in this study were relatively low (<25 min), and the predicted levels of key stress response indicators should be less than those reported previously (Fig. 2a and b). Because the size of the mouth-hooked sharks did not influence fight time (Fig. 2a, Table 1), it may be that mouth-based capture methods provide a means to decrease the overall capture-related stress response by decreasing fight time alone.

Although long-term (+90 days) survivorship cannot be confirmed by the tagging techniques employed in this study, it has been shown that post-release mortality is highest in the immediate hours following release (e.g., Mason and Hunt, 1967; Jolley and Irby, 1979). Further, a comparison of the vertical movements of the sharks in this study (Fig. 3a and b) with those from previous works revealed similar movement patterns throughout the deployments (e.g., Cartamil et al., 2010, 2011; Heberer et al., 2010). Most records also revealed repeated vertical oscillations over the entire deployment period, behaviors that have been shown to be common among pelagic species (e.g., Sepulveda et al., 2004; Cartamil et al., 2011; Nakamura et al., 2011). These behaviors also contrast the depth records that have been associated with moribund sharks (Moyes et al., 2006; Heberer et al., 2010).

All sharks in this study caught on non-offset circle hooks were hooked in the outer region of the mouth and did not exhibit obvious gill or esophageal trauma. Circle hooks have been shown to reduce hook damage and subsequently lower post-release mortality rates for numerous species (e.g., Prince et al., 2002; Aalbers et al., 2004; Bartholomew and Bohnsack, 2005). In this study the use of circle hooks resulted in high rates of mouth-hooking and reduced incidence of foul-hooking in the caudal fin. This suggests that circle hooks may provide anglers with a way to enhance post-release survival rates, and should be considered in future catch-and-release management discussions.

4.3. Movements

The depth records from the surviving sharks of this study were similar to those presented in previous movement studies on this species (Cartamil et al., 2010, 2011; Heberer et al., 2010). For all individuals, the predominant depth distribution was within the uniformed temperature surface layer. A strong diel pattern was apparent with deep dives occurring principally during the day. Deep and shallow diving modes, as described by Cartamil et al. (2011), were evident in most individuals (Fig. 3a and b). The vertical data for the three sharks that survived >60-day post-release with trailing gear indicate that a return to “typical” diving behavior following release is possible, but the chance of survival is low, with two thirds of individuals released with trailing gear dying within 5 days.

Total horizontal displacement ranged from 5 to 446 km for all deployments, with the greatest rate of horizontal movement being from shark 11A0555 which moved on average 24 km day^{-1} during the 10-day deployment (Table 1, Fig. 1). The overall greatest displacement by shark 11A0552 (446 km) occurred over an 81-day period, during which time the shark moved from southern California to central Baja California before dying. The cause of death for this animal is unknown, but due to its survival for 81-day post-release it is possible that its death was unrelated to the trailing gear left attached upon release.

4.4. Management implications

This study provides post-release survivorship information for two recreational fishery modes that were previously not quantified in the southern California recreational fishery for thresher sharks. Accurately assessing the fishery impacts, whether they are in the form of direct removals or post-release mortality, is critical for understanding stock dynamics and promoting effective management (Muoneke and Childress, 1994; Skomal, 2007). When coupled with previous survivorship work on this species (Heberer et al., 2010), this study provides a more comprehensive estimate of the impacts recreational anglers have on the common thresher shark resource of southern California.

This work also supports the use of catch and release as a conservation strategy when common thresher sharks are hooked in the mouth and handled properly prior to release. The results from the trailing gear studies provide evidence for promoting the use of proper gear (i.e., tackle size, type) and fishing techniques that reduce the likelihood of line-parting, as sharks with trailing gear have low overall survivorship. The trailing gear findings may be most relevant for the southern California spring thresher run (March through June), a period when large gravid females enter the region to pup (Cailliet and Bedford, 1983). Although the primary commercial fishery off California is highly regulated during the pupping window, recreational angler harvest rates and the incidence of lost gear are highest during this period (PFMC, 2005; Heberer et al., 2010). Given the importance of this age class to the success of future generations, minimizing the release of sharks with trailing gear should support the health of the population at this critical developmental stage.

Acknowledgements

This material is based upon work supported by the Bycatch Reduction and Engineering Program of the National Oceanic and Atmospheric Administration (Req. # NFFR5200-11-05196). Additional support was provided by the George T. Pfleger Foundation, the William H. and Mattie Wattis Harris Foundation (Grant # 1.38) and the Flying Mako Tournament. Special thanks are offered to Paul Tutunjian, Corey Chan, Eddy Shook, Lyall Belquist, Thomas Fullam, Nick Wegner, James Wraith, James Hilger, Megan Winton, Jeanine Sepulveda, Victoria Wintrode, Jock and Charlie Albright. We would also like to thank the editor and reviewers of this manuscript for their valuable contributions.

References

Aalbers, S.A., Stutzer, G.M., Drawbridge, M.A., 2004. The effects of catch-and-release angling on the growth and survival of juvenile white seabass captured on offset circle and J-type hooks. N. Am. J. Fish. Manag. 24, 793–800.
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., 1991. 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.
Bartholomew, A., Bohnsack, J.A., 2005. A review of catch-and-release angling mortality with implications for no-take reserves. Rev. Fish. Biol. Fish. 15, 129–154.
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. Investig. Rep. 24, 57–69.
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.

Cartamil, D.P., Sepulveda, C.A., Wegner, N.C., Aalbers, S.A., Baquero, A., Graham, J.B., 2011. Archival tagging of subadult and adult common thresher sharks (*Alopias vulpinus*) off the coast of southern California. Mar. Biol. 158, 935–944.

Frick, L.H., Reina, R.D., Walker, T.I., 2009. The physiological response of Port Jackson sharks and Australian swellsharks to sedation, gill-net capture, and repeated sampling in captivity. N. Am. J. Fish. Manag. 29, 127–139.

Frick, L.H., Walker, T.I., Reina, R.D., 2012. Immediate and delayed effects of gill-net capture on acid–base balance and intramuscular lactate concentration of gummy sharks, *Mustelus antarcticus*. Comp. Biochem. Physiol. 162A, 88–93.

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 during the seasons 1981–1982 through 1990–1991. Calif. Fish Game Bull. 175, 1–95.

Heberer, C., Aalbers, S.A., Bernal, D., Kohin, S., DiFiore, B., Sepulveda, C.A., 2010. Insights into catch-and-release survivorship and stress induced blood biochemistry of common thresher sharks (*Alopias vulpinus*) captured in the southern California recreational fishery. Fish. Res. 106, 495–500.

Horodysky, A.Z., Graves, J.E., 2005. Application of popup 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.

Jensen, F.B., Nikinmaa, M., Weber, R.E., 1983. Effects of exercise stress on acid-base balance and respiratory function in blood of the teleost *Tinca tinca*. Resp. Physiol. 51, 291–301.

Jolley, J.W., Irby, E.W., 1979. Survival of tagged and released Atlantic sailfish (*Istiophorus platypterus*: Istiophoridae) determined with acoustical telemetry. Bull. Mar. Sci. 29, 155–169.

Kieffer, K.D., 2000. Review: limits to exhaustive exercise in fish. Comp. Biochem. Physiol. A 126, 161–179.

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.

Marshall, H., Field, L., Afiadata, A., Sepulveda, C., Skomal, G., Bernal, D., 2012. Hematological indicators of stress in longline-captured sharks. Comp. Biochem. Physiol. 162a, 121–129.

Mason, J.W., Hunt, R.L., 1967. Mortality rates of deeply hooked rainbow trout. Prog. Fish-Cult. 29, 87–91.

Milligan, C.L., Wood, C.M., 1986. Tissue intracellular acid-base status and the fate of lactate after exhaustive exercise in the rainbow trout. J. Exp. Biol. 123, 123–144.

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.

Nakamura, I., Watanabe, Y.Y., Papastamatiou, Y.P., Sato, K., Meyer, C.G., 2011. Yo-yo vertical movements suggest a foraging strategy for tiger sharks *Galeocerdo cuvier*. Mar. Ecol. Prog. Ser. 424, 237–246.

PFMC, 2005. Fishery Management Plan for U.S. West Coast Fisheries for Highly Migratory species. NOAA Award #: NA05NMF441008. Pacific Fishery Management Council, Portland, OR, Available from: http://www.pcouncil.org/wp-content/uploads/HMS-FMP-Jul11.pdf

PFMC, 2010. Stock Assessment and Fishery Evaluation Status of the U.S. West Coast Fisheries for Highly Migratory Species Through 2009. Portland, OR., pp. 159, Available from: http://www.pcouncil.org/wp-content/uploads/HMS_SAFE_2011_FINAL.pdf

Prince, E.D., Ortiz, M., Venizelos, A., 2002. A comparison of circle hook and J hook performance in recreational catch and release fisheries for billfish. Am. Fish. Soc. 30, 60–79.

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 sailfish, *Istiophorus platypterus*. Fish. Manag. Ecol. 14, 173–182.

Sepulveda, C.A., Kohin, S., Chan, C., Vetter, R., Graham, J.B., 2004. Movement patterns, depth preferences, and stomach temperatures of free-swimming juvenile mako sharks, (*Isurus oxyrinchus*), in the Southern California Bight. Mar. Biol. 145, 191–199.

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. Manag. 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.), The Biology of Sharks and Their Relatives. Physiological Adaptations, Behavior, Ecology, Conservation and Management of Sharks and their Relatives, vol. 2. CRC Press, Boca Raton FL, pp. 459–490.

Wood, C.M., Turner, J.D., Graham, M.S., 1983. Why do fish die after severe exercise? J. Fish Biol. 22, 189–201.