At-vessel and post-release mortality of the dusky (*Carcharhinus obscurus)* and sandbar (*C. plumbeus*) sharks after longline capture

Heather Marshall[a,b,*], Gregory Skomal[c], Paige G. Ross[d] and Diego Bernal[a]

SEDAR101-RD-19

April 2026

Fisheries Research 172 (2015) 373–384

Contents lists available at ScienceDirect

Fisheries Research

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

At-vessel and post-release mortality of the dusky (*Carcharhinus obscurus*) and sandbar (*C. plumbeus*) sharks after longline capture

Heather Marshall[a,b,*], Gregory Skomal[c], Paige G. Ross[d], Diego Bernal[a]

[a] *University of Massachusetts Dartmouth, 285 Old Westport Road, North Dartmouth, MA 02747, USA*
[b] *Mote Marine Laboratory, 1600 Ken Thompson Parkway, Sarasota, FL 34236, USA*
[c] *Massachusetts Division of Marine Fisheries, 1213 Purchase St., New Bedford, MA 02740, USA*
[d] *Eastern Shore Laboratory, Virginia Institute of Marine Science, College of William & Mary, P.O. Box 1346, Gloucester Point, VA 23062, USA*

ARTICLE INFO

Article history:
Received 3 December 2014
Received in revised form 30 June 2015
Accepted 10 July 2015
Available online 24 August 2015

Keywords:
Sandbar
Dusky
Shark
Longline
Mortality

ABSTRACT

Since the mid 1990's, stock assessments of shark populations in the northwest Atlantic by the National Marine Fisheries Service (NMFS) have indicated that sandbar (*Carcharhinus plumbeus*) and dusky (*C. obscurus*) populations are overfished. In response to these assessments, the dusky shark bottom longline fishery was closed in 2000, followed by the sandbar fishery in 2005. A common management strategy is to mandate the release of prohibited species if caught as bycatch. However, a major assumption is that most released sharks survive, which may not be the case. Longline operations were conducted during 2011 and 2012 to capture and tag sandbar and dusky sharks, in order to assess (1) at-vessel mortality, (2) post-release mortality, and (3) investigate the effects of soak-time on each of these variables for each species. Our findings show that dusky sharks experience high at-vessel and post-release mortality, with mortality occurring more frequently after 3–5 h on the line. While time-on-the-line (TOL) increased dusky shark at-vessel (16% when less than 3 h TOL; 27.5% when more than 3 h TOL) and post-release mortality (11% when less than 3 h TOL; 42% when more than 3 h TOL), sandbar shark at-vessel mortality was low (0% when less than 3 h TOL). Nonetheless, the apparently hardier sandbar sharks did exhibit 29% post-release mortality after 3 h TOL. The total mortality (at-vessel + post-release, including moribund individuals) for dusky sharks was 97% after being captured on a demersal longline when TOL surpassed 3 h. These data clearly elucidate an interspecific difference in vulnerability to longline gear between these species.

1. Introduction

The overfishing of many shark species has prompted the development of federal and complementary regional fisheries management plans (FMPs) to rebuild shark populations (NMFS, 2008). Specifically, on the east coast of the US, the National Marine Fisheries Service (NMFS) has implemented measures to reduce fishing mortality by mandating the release of several shark species, including the prohibited sandbar (*Carcharhinus plumbeus*) and dusky (*Carcharhinus obscurus*) sharks (Family Carcharhinidae) (NMFS, 2008). These two species are found in warm-temperate to tropical waters worldwide, primarily with a coastal distribution (near shelves and bays; Carwardine and Watterson, 2002; Hueter et al., 2004; Hussey et al., 2009; Rechisky and Wetherbee, 2003; Skomal, 2007). During the late 1970s and the 1980s, commercial fisheries for sharks expanded rapidly along the east coast of the US, within which sharks were caught as both targeted and incidental catch (NMFS, 2006). As catches increased, several shark stocks, including sandbar and dusky sharks, started to show signs of decline. The dusky shark was designated a Species of Concern (NMFS, 2014) in 1997 and prohibited from retention (i.e., subjected to mandatory release) in 2000 (NMFS, 2008). In 2008, new stock assessments indicated that both species were overfished and overfishing was still occurring (NMFS, 2008). As a result, NMFS established a shark research fishery, commercial quotas, retention limits (e.g., no recreational retention), and time/area closures to further reduce sandbar and dusky shark landings (NMFS, 2008). Despite these measures, the most recent stock assessments have determined that both species remain overfished (NMFS, 2011), and additional measures may be required to further reduce fishing mortality (NMFS, 2013a).

---

* Corresponding author at: Mote Marine Laboratory, 1600 Ken Thompson Parkway, Sarasota, FL 34236, USA. Fax: +1 941 388 4312.
E-mail addresses: hmarshall@mote.org (H. Marshall), gregory.skomal@state.ma.us (G. Skomal), pg@vims.edu (P.G. Ross), dbernal@umassd.edu (D. Bernal).

http://dx.doi.org/10.1016/j.fishres.2015.07.011
0165-7836/© 2015 Elsevier B.V. All rights reserved.

Despite attempts to reduce and/or prohibit the capture of dusky and sandbar sharks, both species are still taken as bycatch in demersal longline fisheries. In a recent report, NMFS (2013b) estimated that 3,872 dusky and 22,855 sandbar sharks were incidentally captured in fisheries off the southeastern US in 2010. Current regulations mandate the release of these sharks, however, the post-release condition and mortality rates remain unknown (Hale et al., 2011; NMFS, 2008; Romine et al., 2009). Recent work has shown that the extent to which sharks are impacted by the physiological stress associated with interactions with fishing gear (e.g., commercial longline) is highly species-specific (e.g., Mandelman and Skomal, 2009; Marshall et al., 2012). Indeed, reported at-vessel mortality (i.e., percentage of individuals brought to the vessel dead upon gear retrieval) rates for sharks range from 7% (blue shark, *Prionace glauca*) to 91% (Atlantic sharpnose, *Rhizoprionodon terraenova*), with sandbar and dusky sharks having at-vessel mortality rates of 36% and 81%, respectively (Morgan and Burgess, 2007; Morgan and Carlson, 2009; Yokota et al., 2006).

Recent studies on post-release mortality (i.e., sharks that experience delayed mortality after release) have taken advantage of new tagging technologies (i.e., pop-up satellite archival tags, PSATs) that allow for monitoring of post-release behavior of sharks in the wild (e.g., Campana et al., 2009; Graves et al., 2009; Heberer et al., 2010; Moyes et al., 2006; Musyl et al., 2009). Results show that released fishes (a scenario that would be reported as a live fish by fishermen or observers) can experience delayed (hours-days or days-weeks) post-release mortality (e.g., Heberer et al., 2010; Horodysky and Graves, 2005; Mandelman and Farrington, 2007; Moyes et al., 2006; Musyl et al., 2011).

Given the most recent stock assessment for dusky sharks, which indicates that after more than a decade of protection this species is still overfished and fishing mortality remains high (NMFS, 2011), post-release mortality may be impacting population recovery. Moreover, the sandbar shark population remains overfished, and population rebuilding hinges on effective and continued management measures such as mandated release (which is already in place). For these reasons, there is a critical need to investigate the effects of capture and assess the rates of post-release mortality in these species. The objective of this study was to determine both at-vessel mortality and post-release survival rates of sandbar and dusky sharks as a function of time hooked on commercial fishing gear.

2. Methods

All work conducted for this project was approved by the Institutional Animal Care and Use Committee (#10-01, University of Massachusetts Dartmouth; IACUC-2010-06-14-6761-rwbril, Virginia Institute of Marine Science).

2.1. Fishing

Demersal longline fishing operations were conducted off the coast of Virginia's Eastern Shore during June and July of 2011 and 2012 (Fig. 1). Longlines were deployed from the *R*/V Scallop (Virginia Institute of Marine Science, Eastern Shore Lab, Wachapreague, VA) with gear specifications mirroring those of the NOAA/NMFS bottom longline research fishery (Personal Communication, Lori Hale, NOAA). In summary, 2 m gangions (318 kg monofilament, SNL Corporation, Sebastian, FL) were fitted with standard tuna-clips and spaced 15 m apart on a mainline (454 kg-test monofilament). Each gangion was equipped with a hook timer[1], and had a 18/0 circle hook (10° offset, Mustad ID#39960D) baited with ~0.2–0.5 kg of little tunny (*Euthynnus alletteratus*). When hooked, the sharks triggered the hook timer, which would subsequently allow for the calculation of time-on-the-line (TOL). The total number of hooks ranged between 50 and 100 per set with hook spacing remaining the same throughout all sets. Sash weights were added every 15 hooks (~3 per set) to keep the mainline on the bottom. A vertical water chemistry profile (depth, temperature, and salinity) of the water column was measured immediately after each set (CastAway-CTD, YSI Inc., Yellow Springs, OH).

2.2. Shark processing

Handling practices closely followed those of the commercial fisheries when fishermen bring the sharks on deck in order to remove the hook (Personal Communication, Edward Smith, VIMS, Wachapreague, VA). Although some fishermen do cut the hook and release unwanted species without bringing them onboard (Personal Communication, Captain Luke Hill, Key West, FL), handling of sharks for this project reflects the commercial practice of hauling sharks onto the gunnel for hook removal. When the longline was retrieved, the hooked shark was brought to the vessel, and TOL was immediately recorded from the hook timer. The gangion was unclipped from the mainline and the shark hauled by hand onto the boat gunnel for hook removal, the measurement of fork length (FL), blood sampling for a concurrent study, and to qualify condition as: (1) alive, (2) dead, or (3) moribund (eye and jaw response when stimulated, otherwise exhausted and unresponsive, as described by Moyes et al., 2006). Sharks exhibiting swimming muscle tetany (i.e., stiff body due to muscle rigor) were noted. Sharks gills were not irrigated during processing (as this is not a common commercial practice) and the time-out-of-water was recorded.

All sharks were tagged with a NMFS conventional roto-tag (Kohler and Turner, 2001) or Hallprint Pty Ltd., spaghetti tags (ref #T7191) and selected specimens were fitted with a pop-up satellite archival transmitting tag (Model MK10 or miniPAT, Wildlife Computers Inc., WA) tethered to a nylon intramuscular umbrella dart and inserted at the base of the dorsal fin and across the pterygiophores. The incision was closed with 3–4 interrupted sutures (2-0 PDS II, Ethicon Inc., NJ) to reduce the likelihood of tag loss due to interactions with bottom structure and/or vegetation in a coastal environment (Graves et al., 2009). PSATs were coated with clear anti-fouling paint (Trilux, Interlux) to avoid biofouling.

2.3. Post-release mortality

All PSAT tags were programmed for deployments of 30 days during which depth and temperature time-series data were collected and archived at 150 or 300-second intervals, respectively. The deployment of 30 days was chosen to capture both short- and long-term post-release mortality. All PSAT tags were also programmed to prematurely release if the tagged shark remained at a constant depth (± 1 m) for 48–168 h (indicative of post-release mortality). Data transmitted through the Argos satellite system were processed with the manufacturer's software (DAP Processor 3.0, Wildlife Computers, Inc., WA) and a visual inspection of the individual dive profiles was used to assess post-release mortality. Tag pop-up location was determined from the Argos data filtered by location quality.

2.4. Data analysis

The total number of sandbar and dusky sharks was tabulated based on condition (live, dead, or moribund) and analyzed relative to TOL and soak-time (defined as time interval from first hook in to first hook out). Binomial logistic regressions were run with a

---

[1] Hook timers designed by D. Somerton, S. Kaimmer, Applied Physics Laboratory, University of Washington, and assembled by Schippers & Crew, Inc. Seattle, WA.

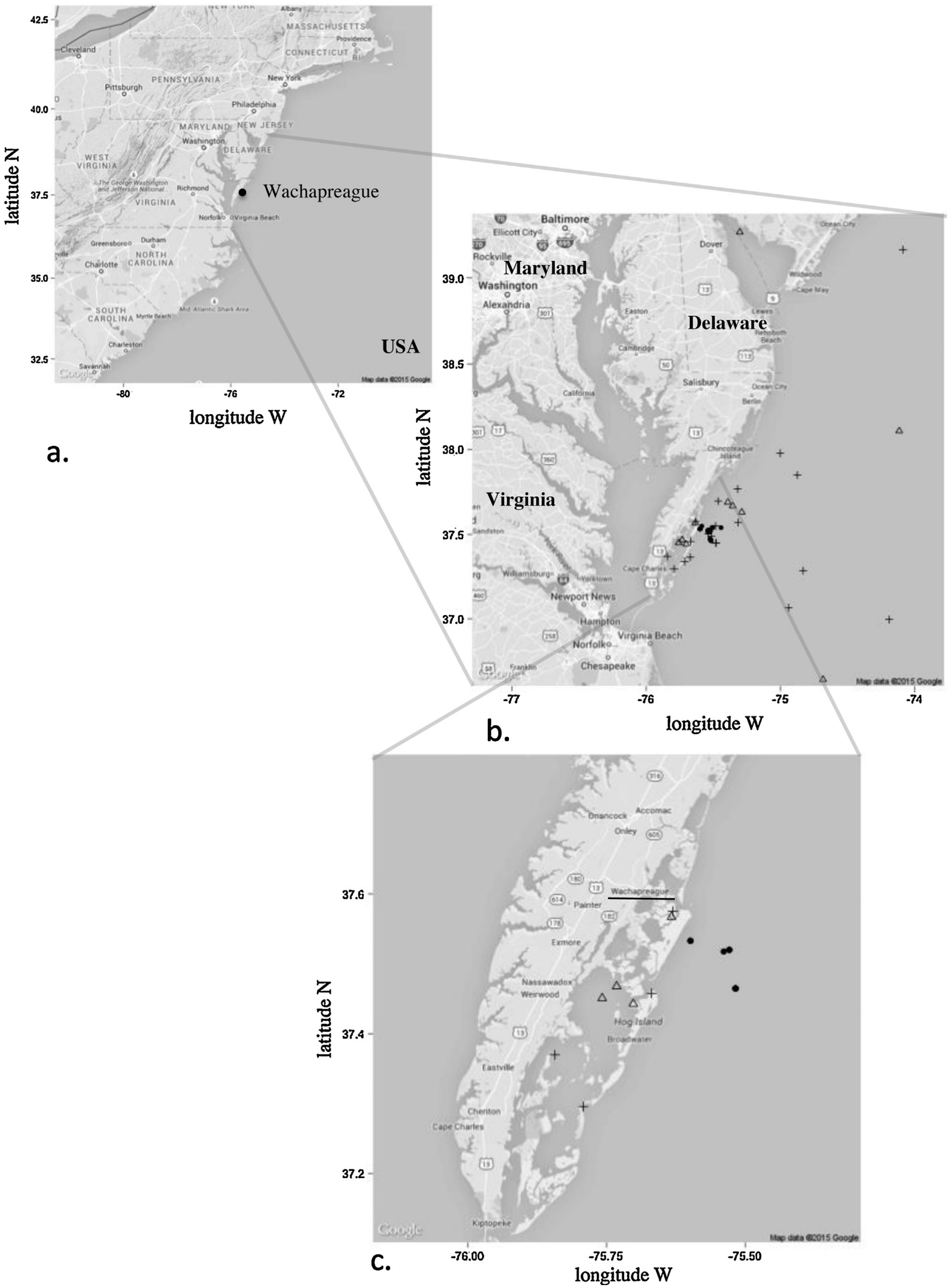

Fig. 1. Tagging (black circle) and pop-up locations of the PSAT tags for sandbar (black triangle) and dusky (black plus sign) sharks. (a) the general study location, (b) tagging and pop-up locations, (c) close up of the marsh where several PSAT pop-up locations occurred.

logit link function to determine possible predictor variables (i.e., TOL, soak-time, fork length, bottom temperature) of both at-vessel mortality and post-release mortality. Binomial response variables were set as live versus dead individuals and, because of low sample size, the predictor variable of time was grouped into 1.5-hour bins for this analysis only. The resulting logistic regression equation was used to determine explanatory variable probabilities. Sharks classified as 'moribund' were not fit to logistic models. Prior to running the regressions, a Levene's Test for homogeneity was used to ensure homoscedasticity between live and dead groups. All statistical analyses were conducted using RStudio (version 0.97.449) for R (version 3.0.2, r-project.org). Moving averages were calculated for the graphical representation of post-release mortalities using the R package zoo in RStudio. Regression analysis was used to assess the relationship between TOL and soak-time, and a Levene's Test was run before this analysis as well. For all statistical tests, significance was set at $\alpha < 0.05$. The tag deployment and pop-up locations were mapped using RStudio and the package ggmap.

3. Results

Thirty-four longline sets were conducted over seventeen days in June and July of 2011 (26 sets) and 2012 (8 sets) with soak-times ranging from ~0.5–12.5 h (~0.5–1 h = 14 sets, 1–1.5 h = 2 sets, 1.5–2 h = 3 sets, 2–2.5 h = 3 sets, 2.5–3 h = 2 sets, 3–4 h = 2 sets, 5 h = 5 sets, 7 h = 1 set, 8 h = 1 set, and 12.5 h = 1 set). A total of 50 dusky and 199 sandbar sharks (mean ± SD: 109 ± 21 cm FL and 99.5 ± 21 cm FL, respectively) were captured with TOL ranging from 8 to 660 min (Table 1). For all sets combined, ambient bottom water temperature (at hook depth) and water depth ranged from 15.7–21.5 °C and 5–19 m, respectively. Bottom water temperatures were significantly ($p < 0.05$) different between years, with temperatures averaging 17.3 ± 1.1 °C in 2011 and 20.6 ± 0.6 °C in 2012; however, temperature was not found to be a significant predictor of mortality (see below). All sharks were hooked cleanly, with the exception of a single dusky shark (119.4 cm FL) that exhibited a physical injury to one of its gill slits.

Table 1
Time-on-the-line for dusky and sandbar sharks caught on demersal longline gear. Hook times are listed by at-vessel condition, and sample size (n) for each group are provided (group *Alive with tetany* refers to swimming muscle tetany). Percentages listed are calculated from the total number of individuals within a species, with the exception of the percentage associated with the *Alive with tetany* condition, which is calculated out of the total number of *Alive* individuals.

			Time-on-the-Line (min)	
		n (%)	Range	Mean (±SD)
Dusky n = 50	Alive	30 (60)	16–449	152.5 ± 118.2
	Alive with tetany	9 (30)	53–449	214.7 ± 132.3
	Moribund	9 (18)	178–512	326.1 ± 119.8
	Dead	11 (22)	109–518	284.7 ± 157.8
Sandbar n = 119	Alive	111 (93)	8–660	168.1 ± 148.8
	Alive with tetany	7 (6)	116–642	306.4 ± 210.6
	Moribund	2 (2)	171–279	225 ± 76.4
	Dead	6 (5)	–	654

3.1. At-vessel mortality

For all sets pooled, at-vessel conditions of dusky sharks were 60% (n = 30) alive, 18% (n = 9) moribund, and 22% (n = 11) dead. Of the live dusky sharks 30% (n = 9) were exhibiting signs of muscle tetany. The at-vessel conditions of sandbar sharks were 93% (n = 111) alive, 2% (n = 2) moribund, and 5% (n = 6) dead. Of the live sandbar sharks, 6% (n = 7) were exhibiting muscle tetany and appeared exhausted (Table 1). Time-on-the-line (TOL), as determined by hook timers, for live at-vessel specimens ranged from 16 to 449 min for dusky sharks and from 8 to 660 min for sandbar sharks. Dusky sharks that experienced at-vessel mortality spent an average TOL of 284.7 ± 157.8 min (range: 109–518 min); the only successfully timed sandbar shark that experienced at-vessel mortality had a TOL of 654 min (Table 1). Both the number of sharks considered moribund and mortalities increased with TOL. For sharks caught in <3 h, 1.2% of sandbars were moribund and 21% of dusky sharks were moribund/dead. After 3–5 h, 5% of sandbars were moribund and 40% of dusky sharks were moribund/dead. After 5 h of capture, 33% of sandbars were dead, and 73% of dusky sharks were moribund/dead (Fig. 2gr).

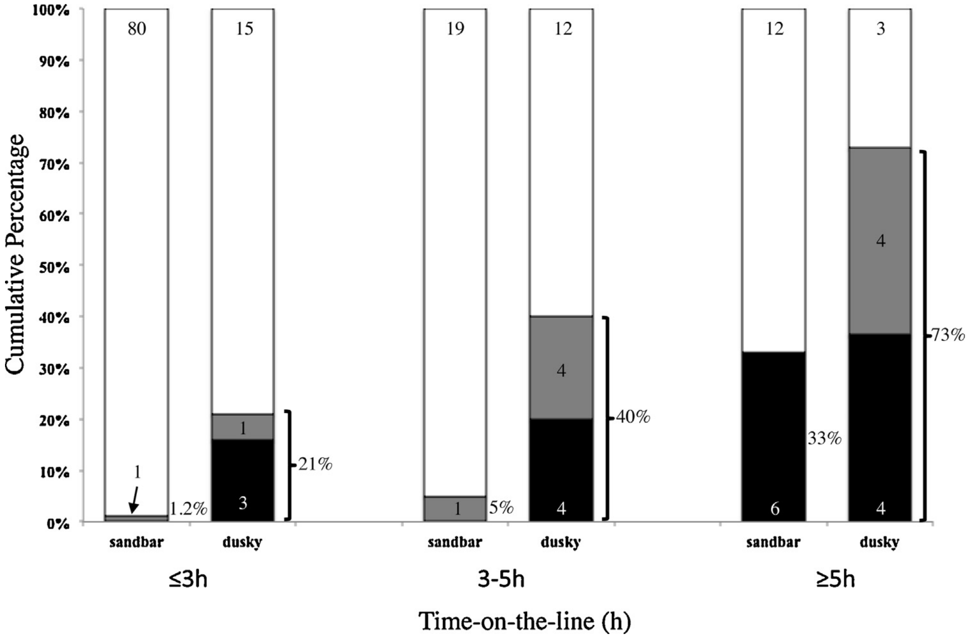

Fig. 2. At-vessel condition for sandbar and dusky sharks with different time-on-the-line (TOL). Columns show the cumulative percentages of alive (white), moribund (gray) and dead (black) sharks when the longline was hauled (sample sizes of each at-vessel category shown within the columns). Combined percentage of moribund and dead sharks for each species are shown next to each bar.

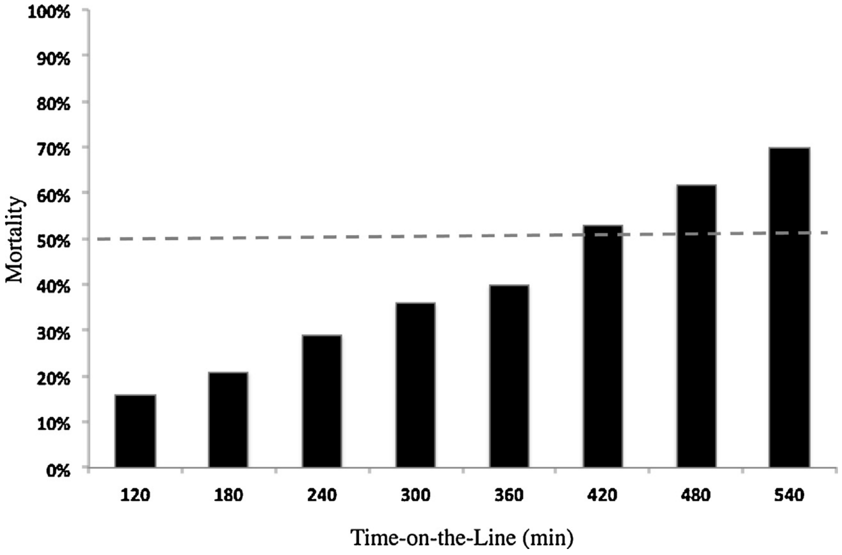

Fig. 3. Probability of mortality resulting from binomial logistic regression analysis (significant effect of time: $p = 0.04$, $z = 2.03$). Values shown are the predicted probabilities of occurrence of dusky shark mortality generated by analysis and dashed line indicates 50% mortality.

The logistic regression analysis of dusky sharks (captured either dead or alive) revealed that increasing TOL was a significant predictor of at-vessel mortality ($p = 0.042$, $z = 2.03$) (Fig. 3). Based on the regression model, the cumulative probabilities of dusky sharks exhibiting at-vessel mortality increased as a function of TOL (Fig. 3), increasing from 16% at 120 min to 70% at 540 min. There was no significant effect, as determined by the model, of soak-time, FL, or bottom water temperature on at-vessel mortality of dusky sharks. The effect of TOL for sandbar sharks could not be tested due to the low sample size ($n = 1$) of successfully timed animals with at-vessel mortality (i.e., hook-timer failures).

For the dusky sharks, soak-times of 1–3 h resulted in 76% alive, 8% moribund, and 16% dead, and soak-times of 3–8 h resulted in 39% alive, 22% moribund, and 39% dead. For the sandbar sharks, soak-times of 1–3 h resulted in 99% alive, 1% moribund, and none dead, and soak-times of 3–8 h resulted in 94% alive, 3% moribund, and 3% dead. The 12.5-hour soak-time resulted in the capture of no dusky sharks, and of the 10 sandbar sharks captured, 40% were alive and 60% were dead (Fig. 4). Regression analysis revealed that TOL and soak-time were significantly correlated ($y = 0.85x + 3.7$, $p < 2\mathrm{e}^{-16}$, $R^2 = 0.80$) (Fig. 5).

3.2. Post-release mortality

A total of 10 sandbar (102.3 ± 29.5 cm FL) and 21 dusky sharks (108.9 ± 19.4 cm FL) were tagged with PSAT tags (Table 2). Sharks

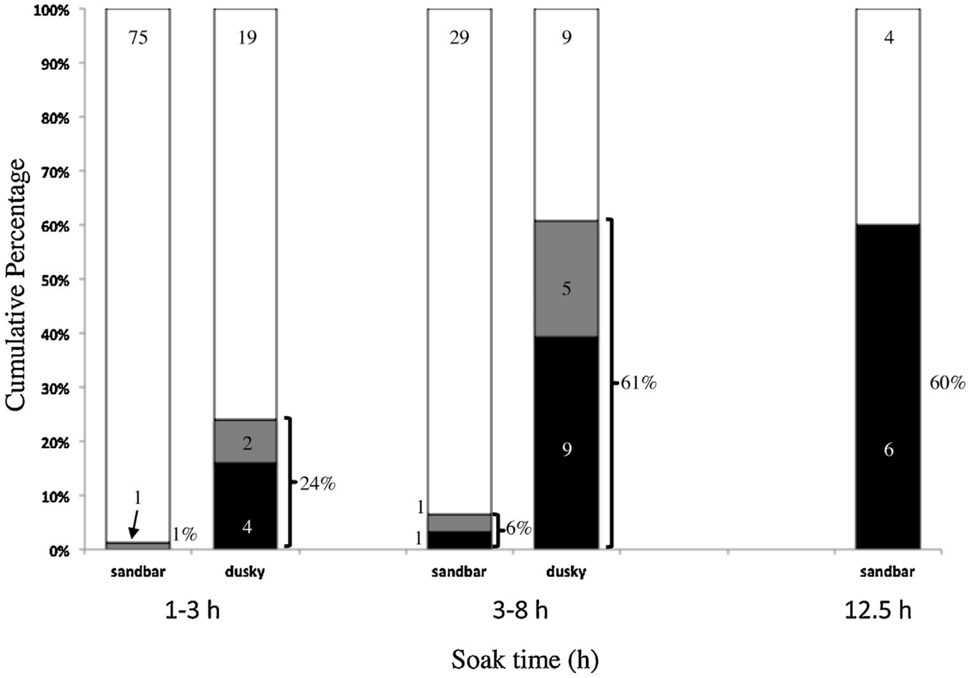

Fig. 4. At-vessel condition for sandbar and dusky sharks with different soak times. Columns are cumulative percentages of alive (white), moribund (gray) and dead (black) sharks. Sample size for each at-vessel category are shown within the columns and the combined percentage of moribund and dead sharks for each species shown next to each bar.

Table 2
Biological, tag-deployment, and post-release outcomes for sharks captured by demersal longline gear.

Shark	ID	FL (cm)	Sex	PSAT type	TOL (min)	Date tagged	Tag latitude N	Tag longitude W	At liberty (days)	Pop-up latitude N	Pop-up longitude W	Recovery period (hours)	Release condition	Outcome
1	VD1	115	F	Mk10	<195	6/21/11	37.52	75.52	30	39.16	74.08	–	A	Survival
2	VD3	90	M	Mini	<235	6/21/11	37.52	75.52	17	37.97	75.00	–	A	Survival
3	VD5	126	F	Mk10	<247	6/21/11	37.46	75.51	–	37.49	75.51	–	A	Mortality
4	VD7	130	M	Mk10	80	6/21/11	37.46	75.51	–	37.56	75.31	–	A	Mortality
5	VD8	81	M	Mini	16	6/22/11	37.52	75.54	9	37.54	75.48	–	A	Survival
6	VD9	92	M	Mini	46	6/22/11	37.52	75.54	19	37.84	74.87	–	A	Survival
7	VD10	–	F	Mk10	65	6/22/11	37.52	75.54	16	37.69	75.46	–	A	Survival
8	VD17	116.8	M	Mk10	<150	6/28/11	37.53	75.59	7	37.34	75.71	–	A	Survival
9	VD18	134.6	M	Mk10	141	6/28/11	37.53	75.59	4	37.36	75.67	3.9	A	Survival
10	VD19	101.6	F	Mk10	166	6/28/11	37.53	75.59	30	37.45	75.66	–	A	Survival
11	VD21	100.3	M	Mk10	187	6/30/11	37.52	75.52	13	37.29	75.79	1.8	A	Survival
12	VD23	141	F	Mk10	193	6/30/11	37.52	75.52	–	37.52	75.52	–	A	Mortality
13	VD24	119.4	M	Mk10	187	6/30/11	37.52	75.52	3	37.36	75.84	1.5	A	Survival
14	VD25	139.7	F	Mini	241	6/30/11	37.52	75.52	4	37.76	75.31	–	A	Survival
15	VD35	90	F	Mini	286	6/19/12	37.47	75.52	–	37.47	75.52	–	M	Mortality
16	VD37	100.5	F	Mini	370	6/19/12	37.52	75.53	–	37.52	75.53	–	M	Mortality
17	VD39	85	M	Mini	401	6/20/12	37.52	75.53	3	37.52	75.53	10.7	A	Survival
18	VD40	108.5	F	Mk10	512	6/20/12	37.52	75.53	5	37.52	75.53	35.3	M	Survival
19	VD45	84	M	Mk10	190	6/28/12	37.54	75.44	–	37.54	75.44	–	A	Mortality
20	VD47	125	F	Mk10	217	7/2/12	37.51	75.53	30	37.51	75.53	153.0	A	Survival
21	VD48	97	M	Mk10	304	7/2/12	37.51	75.53	28	37.51	75.53	–	A	Survival
22	VSB30	96	M	Mini	<224	6/21/11	37.52	75.52	12	37.68	75.39	5.0	A	Survival
23	VSB31	–	M	Mk10	153	6/21/11	37.46	75.51	30	37.45	75.75	–	A	Survival
24	VSB32	101	F	Mini	249	6/21/11	37.46	75.51	30	37.46	75.73	–	A	Survival
25	VSB33	103	F	Mini	263	6/21/11	37.46	75.51	3	37.56	75.63	1.6	A	Survival
26	VSB34	55	–	Mk10	113	6/27/11	37.54	75.50	10	38.10	74.11	–	A	Survival
27	VSB35	96.5	M	Mini	121	6/28/11	37.53	75.59	3	37.44	75.70	–	A	Survival
28	VSB60	110.5	F	Mk10	402	6/19/12	37.52	75.53	–	37.52	75.53	–	A	Mortality
29	VSB61	97	F	Mk10	475	6/20/12	37.52	75.53	–	37.52	75.53	–	A	Mortality
30	VSB65	93	F	Mini	583	6/20/12	37.52	75.53	30	37.52	75.53	6.5	A	Survival
31	VSB66	169	F	Mk10	660	6/22/12	37.54	75.58	5	37.54	75.58	–	A	Survival

FL = fork length, Sex is M = male and F = female, PSAT = pop-up satellite archival tag, TOL = time-on-the-line, Release Condition is A = alive and M = moribund.

were processed and returned to the water as quickly as possible (average out of water handling time 7.3 ± 4.3 min). Of the 31 deployed PSATs, 9 tags were physically recovered, and data from these tags were preferentially used over transmitted data from Argos. Tag data showed shark survival for both species (average days-at-liberty: dusky 13.7 ± 10.9; sandbar 15.4 ± 12.5) (Table 2) with several tags being released prematurely. Of those tagged sharks that were considered moribund at-vessel, 66.7% died post-release. Overall, dusky sharks exhibited 29% ($n = 6$) post-release mortality, with 11% of sharks dying after time-on-the-line ≤3-hours and 42% >3-hours (Fig. 6, Fig. 7). However, time was not a significant predictor ($p = 0.6$) of post-release mortality with logistic regression analysis. Sandbar sharks exhibited 20% ($n = 2$) post-release mortality, with 100% survival if captured up to 3 h on the longline, but showing mortalities at ~7–8 h (Fig. 7).

Based on PSAT tag data, 9 sharks (6 dusky and 3 sandbar sharks) exhibited limited vertical post-release behavior that included moving at a near constant depth (swimming in close proximity to the bottom) for time periods ranging from 1.5 to 35 h; one dusky shark maintained constant depth and temperature for 153 h. After these periods, they resumed extensive use of the water column (Fig. 8). Only a single individual of the nine exhibiting a recovery period had a release condition of "moribund". One of the dusky sharks captured had a physical injury to one of its gill slits when released, but exhibited a recovery period of 1.5 h.

4. Discussion

Although the assessment of at-vessel mortality for sharks is easily quantifiable (e.g., Morgan and Burgess, 2007), this is one of the first studies to quantify the impacts of TOL on at-vessel condition and post-release survival. In this study, we identified a 3-hour hook-time threshold, after which at-vessel and post-release mortality markedly increased. In addition, although both species were vulnerable to longline capture, we found interspecific differences in mortality rates between sandbar and dusky sharks, with the dusky shark being more sensitive to capture.

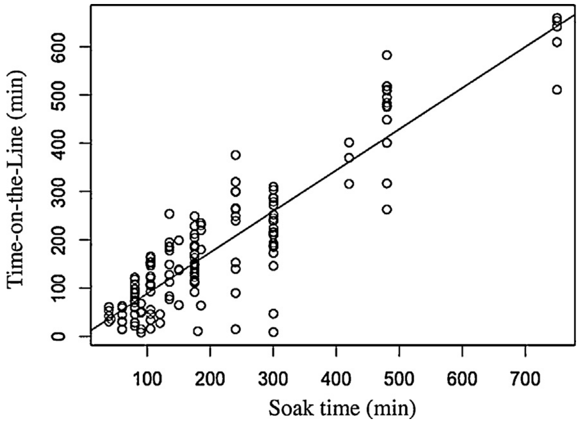

Fig. 5. Relationship between time-on-the-line (TOL) and soak-time for dusky sharks caught on the longline. Line represents the significant relationship: TOL = 0.85(Soak time) + 3.7, $p < 2 \times 10^{-16}$, $R^2 = 0.8$.

Recent work has documented the physiological consequences associated with fish capture on commercial fishing gear and how they may affect short-term (i.e., hours-days) and long-term (i.e., weeks-months) survival (e.g., Campana et al., 2009; Davis et al., 2001; Gallagher et al., 2014; Gingerich et al., 2007; Kneebone et al., 2013; Mandelman and Farrington, 2007; Mandelman and Skomal, 2009; Marshall et al., 2012; Skomal, 2007). There are only a few methods for assessing post-release survival and there are limita-

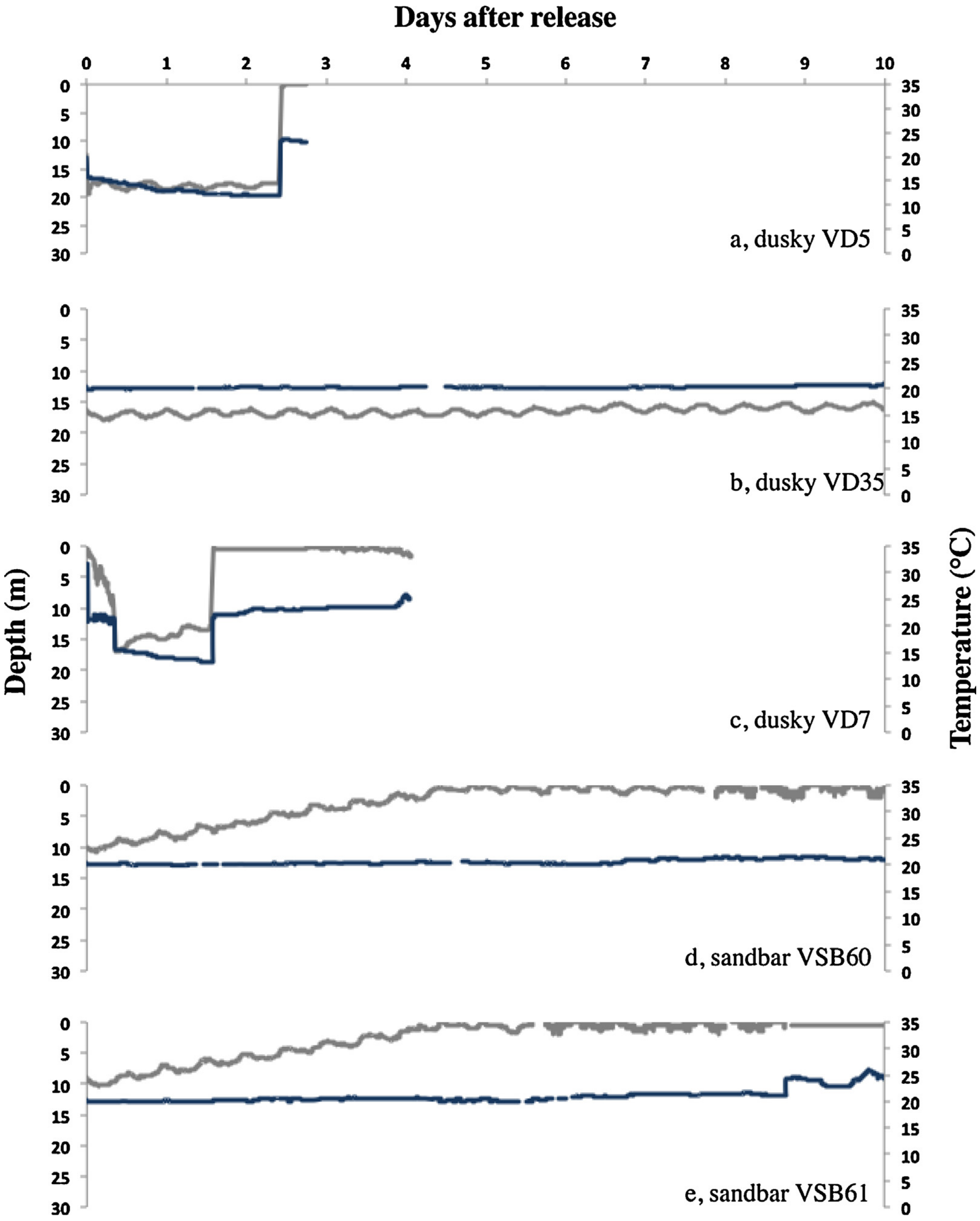

Fig. 6. Depth (light gray line) and ambient water temperature (blue line) for five sharks that experienced post-release mortality. a–c: dusky sharks, d–e: sandbar sharks. The dusky shark in c is the only individual that exhibited delayed post-release mortality in this study. The incremental change in depth seen in d and e are an artifact of the PSAT tags and the absence of a change in depth was verified by consistent temperature seen during the same time period.

tions associated with all of them (Musyl et al., 2011; reviewed by Skomal and Bernal, 2010). To date, it remains difficult to generalize on the fate of released sharks, as there are many confounding variables affecting survival (e.g., hook type and size, leader material, fight time, vessel, fish size, handling and discard practices) (Campana et al., 2009; Horodysky and Graves, 2005; Musyl, 2009; reviewed in Musyl 2011). However, there is a growing body of evidence that increased levels of exhaustive exercise associated with struggling on a line are correlated with higher post-release mortality and total mortality rates (Campana et al., 2009; Wood et al., 1983). This source of mortality, previously unaccounted for, may also contribute to overall population declines and is important information for stock assessments (Hueter et al., 2006). While it is difficult to control gear specifications (e.g., gear length, material, hook times) that can impact mortality rates during routine commercial fishing operations (Musyl et al., 2011), we made every effort to control confounding factors by standardizing our gear (hook type, leader, handling practices) so as to test the effects of soak-time and TOL on mortality rates. Given that gear specifications were modeled after commercial bottom longline fisheries, at-vessel and post-release mortalities should be representative of the fishery.

4.1. At-vessel mortality

The overall at-vessel mortality rates that we observed in sandbar and dusky sharks after capture on demersal longline were markedly lower than those previously reported (Morgan and Burgess, 2007) (dusky: 22% this study vs. 81% published, and sandbar: 5% this study vs. 36% published). A key difference between these findings is that soak-times in the current study were consistently shorter (with

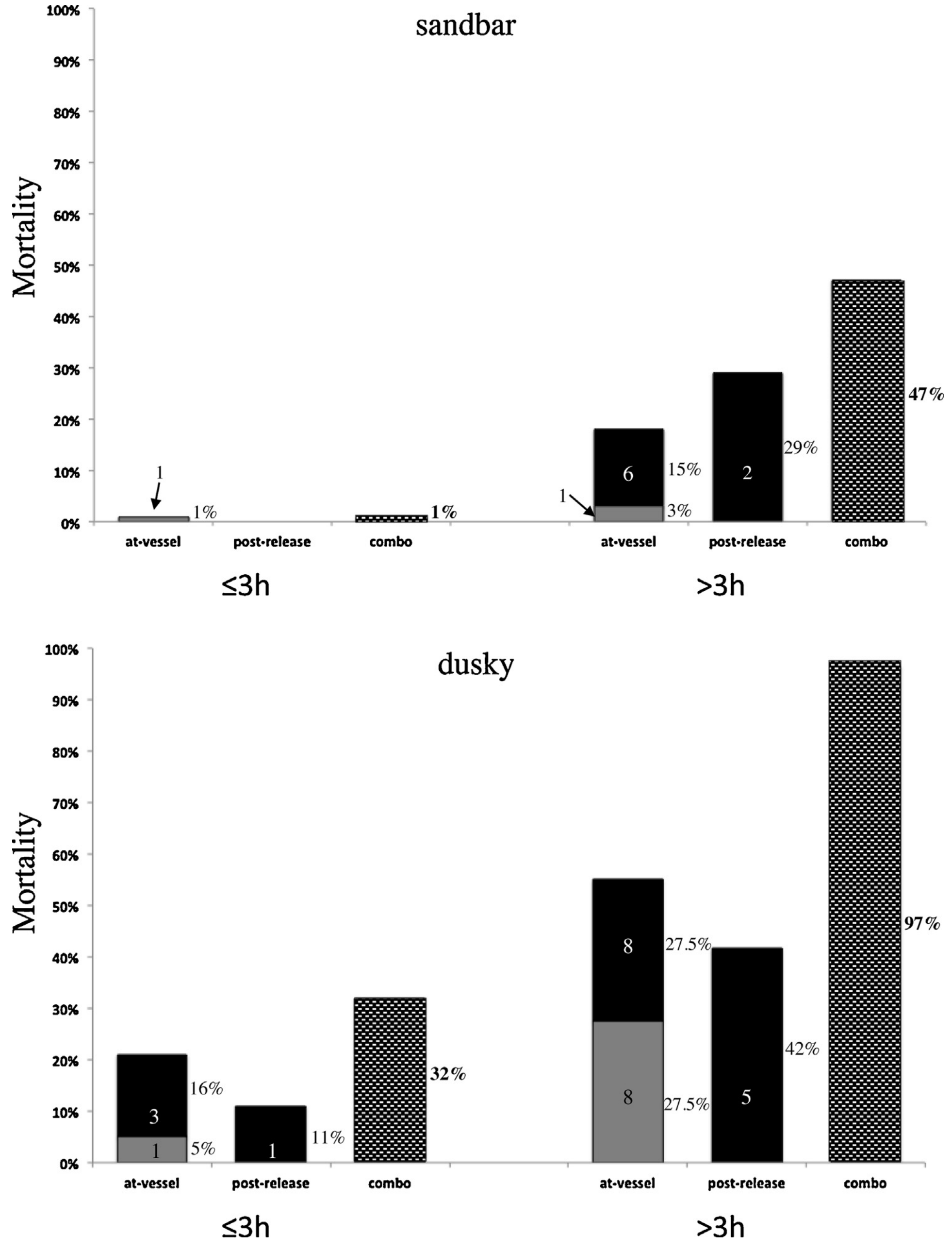

Fig. 7. Post-release and at-vessel condition for sandbar (top plot) and dusky (bottom plot) sharks after capture for less than and greater than 3-hours on the longline; gray = moribund, black = dead, hatched = sum of moribund and dead. Sample size is shown within columns, and the percent for each condition is shown next to the columns.

91% at 5 h or shorter) than typically used by commercial longliners (~12 h). Nonetheless, dusky sharks began showing evidence of muscular tetany after ~1 h, and at-vessel mortality was observed as early as 109 min TOL. In contrast, sandbar sharks did not show signs of muscle tetany until about 2 h TOL, and, in general, were able to survive on the line for up to 11 h (Table 1).

Recent work on sharks shows that there are species-specific physiological responses to interactions with fishing gear (e.g., Beerkircher et al., 2000; Mandelman and Skomal, 2009; Marshall et al., 2012; Morgan and Burgess, 2007; Morgan and Carlson, 2009; Gallagher et al., 2014) and that the magnitude of the stress response may be linked to: (1) metabolic scope, (2) the ability to physiologically respond to stress, and (3) the capacity to recover from the stressor (Skomal and Bernal, 2010). The at-vessel mortality observed in dusky sharks (22%) in this study suggests that, relative to sandbar sharks (5%), they experience greater physiological disruptions and may have a reduced ability to recover from capture by longline. Our results suggest that the probability of dying on the line more than doubled for dusky sharks between hook times of 3 h (21% predicted mortality) and 6 h (44% predicted mortality) (Fig. 3). In addition, of the dusky sharks caught, none were alive when time on the experimental longline gear exceeded 7.5 h. In contrast, the at-vessel mortality of sandbar sharks was minimal, even after being hooked for 11 h (Fig. 2, Table 1). Taken together, our results show that an increase in soak-time elevates the likelihood of capture-related mortality, a finding similar to that of blue sharks (Campana et al., 2009).

Surprisingly, we found that the time at which dusky sharks become moribund varied greatly. This resulted in a longer average TOL for moribund dusky sharks than that observed in the sandbar shark, which exhibited less intraspecific variation (326.1 ± 119.8 vs. 225 ± 76.4 min, respectively) (Table 1). The variable responses

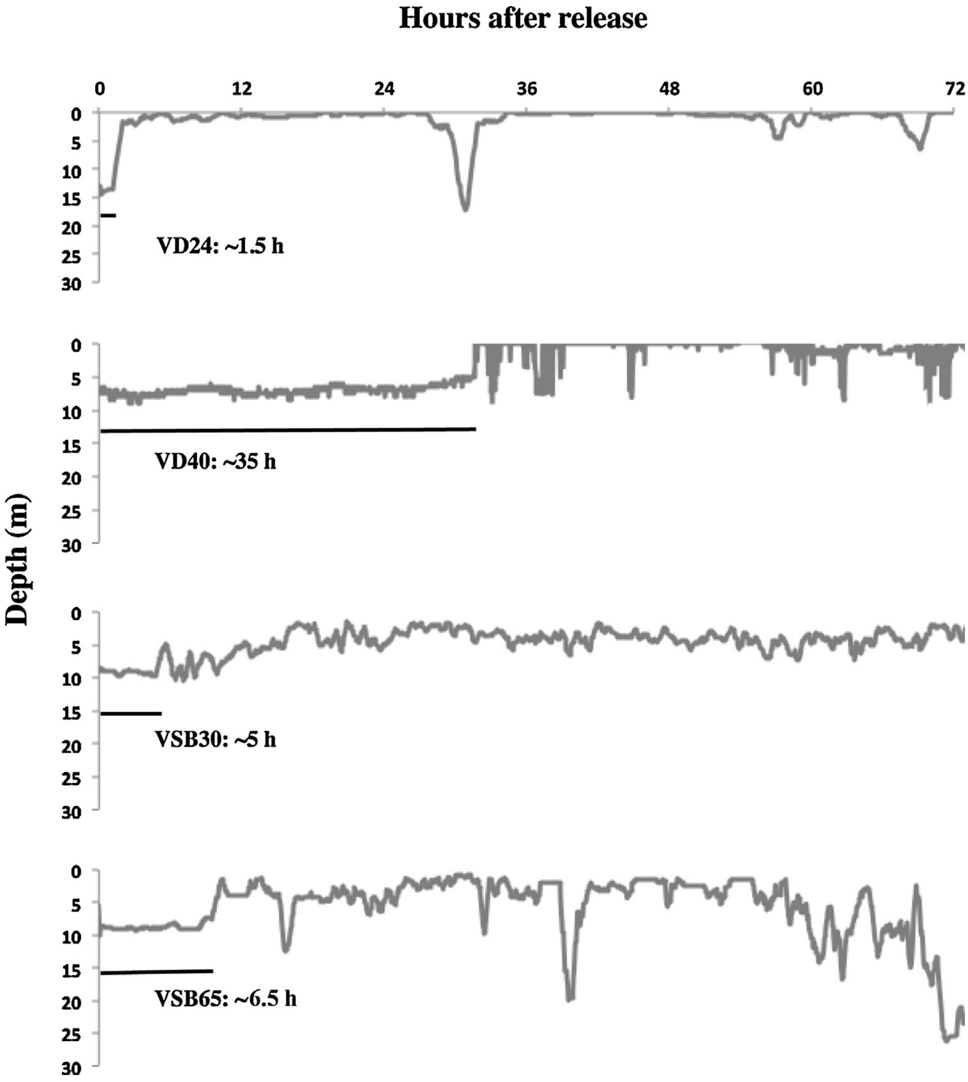

Fig. 8. Depth plots representing four individuals from this study that showed a recovery period after release, during which the sharks maintained a fairly constant depth before resuming the use of the water column. The top two figures are from dusky sharks, and the bottom two are from sandbar sharks. Corresponding recovery period durations (indicated by black lines) are written in each figure next to the shark ID.

among dusky sharks suggest that both the behavioral response (i.e., struggling on the line) to an acute stressor and subsequent physiological disruptions vary intraspecifically, a scenario documented in other fish (Horodysky and Graves, 2005; Van Raaij et al., 1996). Such information should be considered in future work investigating interspecific sensitivity of sharks to capture stress.

Based on the logistic regression analysis, there was a significant effect of TOL, but not soak-time, on at-vessel mortality. However, given the high correlation between soak-time and TOL, larger sample sizes will likely show that soak-time is a significant predictor of mortality as well. At the 3–4-hour window of soak-time, there appears to be a shift from live to moribund/dead dusky sharks (Figure 4). This correlates well with the TOL data, which indicate that the 3–4-hour period may be a tipping point for dusky sharks, after which survival is greatly reduced. Although sandbar sharks exhibited higher mortality with longer soak-times, this window is much longer than that of the dusky shark. Soak-times of 1–8 h resulted in minimal numbers of moribund and dead sandbar sharks, while the soak-time of 12.5 h produced more dead sandbars than live ones. Hence, the typical ~12 h soak-time used by commercial fisheries (Hale et al., 2011) may well be the threshold for the sandbar shark at which time survival appears to be significantly reduced.

4.2. Post-release mortality

To date, the number of post-release mortality studies conducted on sharks captured in longline fisheries is limited. Available evidence indicates that post-release mortality in sharks varies from relatively low (19%) in the blue shark to higher (29%) rates in the spiny dogfish (*Squalus acanthias*) (Campana et al., 2009; Mandelman and Farrington, 2007), depending on gear type and the duration and severity of the handling practice. Furthermore, a shark that is removed from the water after capture will encounter a bout of air exposure that impedes respiratory gas exchange and results in respiratory acidosis (Cooke et al., 2002) and, potentially, acute hyperthermia (overheating), which may exacerbate the stress response (Gingerich et al., 2007). The combination of these external conditions and the physiological costs associated with exhaustive exercise (fighting on the line) during capture, can lead to post-release mortality.

Our results show that post-release mortality rates in dusky (29%) and sandbar sharks (20%) (Table 2) after longline capture, is similar to the post-release mortality rate observed for longline-captured blue sharks (19%, Campana et al., 2009). To estimate rates of post-release mortality for the sandbar and dusky sharks, managers have historically used data available for other species (i.e., the blue shark, Campana et al., 2009), and applied a "6%" rule (i.e., post-release mortality is estimated by adding 6% to at-vessel mortality rates, NMFS, 2011). Specifically, Campana et al. (2009) found that post-release mortality was 6% higher than at-vessel mortality in the blue shark. Acknowledging the limitations of using this relationship, NMFS (2011) used the 6% rule to estimate dusky shark post-release mortality, a value that is very similar to the results from the current study (6.6% above at-vessel mortality). However, the markedly different findings for the sandbar shark suggest that post-release mortality levels are up to 15% higher than the at-vessel rate, highlighting that sandbars may experience more post-release mortality than previously thought.

Our at-vessel mortality data showed that the number of moribund and dead sharks increased with TOL. Given that 66.7% of the moribund sharks that we tagged and released subsequently died, it can be assumed that the importance of TOL for at-vessel catch will carry over to the post-release scenario. However, logistic regression analysis found that TOL was not a significant predictor of post-release mortality for both species, a result found in other studies (e.g., Horodysky and Graves, 2005). Given the trends in at-vessel condition, it is possible that the results of the post-release logistic regression are influenced by the low sample size. For this reason, we examined the data for a 3-hour threshold (as seen in the at-vessel data) and found that post-release mortality did increase in sharks that were hooked for more than 3 h (42% for dusky and 29% for sandbars). Despite low at-vessel mortality rates in sandbar sharks (5%), it appears that they experience elevated post-release mortality, which suggests that delayed and irreversible physiological damage may occur as a result from being captured on demersal longline gear. Similarly, the longer dusky sharks are hooked, the higher the levels of post-release mortality (Fig. 7).

The post-release mortality levels observed in this study, which have been lacking for the dusky shark (Romine et al., 2009), indicate that post-release mortality is also a significant source of total mortality after longline capture in the dusky shark. First, of the dusky sharks that were considered moribund upon gear haulback and were subsequently tagged and released, 66.7% of these individuals died post-release. Because these sharks were still showing signs of life (i.e., eye and jaw response), they may be classified as "alive" upon release within the fishery, when in reality there is a much reduced chance of recovery. In addition, the combined effects of at-vessel and post-release mortality observed in dusky sharks captured on the line for ≥3 h results in a total mortality rate of 97% when exposed to demersal longline gear. This high rate confirms previous assessments that dusky sharks are highly vulnerable to longline fishing practices (Romine et al., 2009). The combined rate for sandbar sharks is lower at 47%, again highlighting the differences in response to longline gear by these congeneric species.

With the exception of one dusky shark, which died ~8.5 h after release, post-release mortality occurred immediately (within 60 min) after release, regardless of whether an individual was considered alive or moribund at the time of tag deployment (Fig. 6). The high incidence of immediate post-release mortality in these sharks is similar to that found in other fish such as white marlin (*Tetrapturus albidus*), which experienced 71% post-release mortality of which 80% died within 60 min of being released (Horodysky and Graves, 2005).

It is possible that the physiological consequences associated with the stress of capture and handling (e.g., lactate reuptake, restoring intracellular redox potentials – reviewed by Skomal and Bernal, 2010) result in behavior that requires a reduction in swimming after release, as fish may need to allocate energy to restore homeostasis. Some of the surviving sandbar and dusky sharks in this study remained at a constant depth for a period of time immediately after release (Fig. 8, Table 2), a result similar to that observed in blue and porbeagle (*Lamna nasus*) sharks (Hoolihan et al., 2011). This period of time may correlate to a post-release recovery period, which appears to vary between species (e.g., Arendt and Lucy, 2002; Campana et al., 2009; Hoolihan et al., 2011; reviewed by Skomal, 2007). For example, blue sharks can exhibit an average recovery period of 4 days (Campana et al., 2009), while other fish species may range from ≤2 h (Skomal and Chase, 2002) up to 3–60 days (Hoolihan et al., 2011) post-release. The results of our study are markedly shorter (1.5–35 h, with one dusky shark maintaining constant depth and temperature for ~6.5 days, Fig. 8) than the recovery periods observed in Hoolihan et al. (2011), but similar to those of white marlin (20 h recovery) after capture on rod and reel (Horodysky and Graves, 2005). More dusky sharks exhibited swimming behavior suggestive of a recovery period in this study (6 dusky sharks versus 3 sandbar sharks), again highlighting that this species appears to be more sensitive to capture on longline gear. Just one of the nine sharks that exhibited a recovery period was considered moribund at the time of release, and it is easy to extrapolate that longer soak times would exacerbate the need for recovery and increase chances of post-release mortality.

4.3. Management implications

For any study that attempts to correlate the at-vessel condition or the post-release fate of a captured shark to the fishing event, it is critically important to determine how closely the experimental fishing technique matches the real-world commercial fishing methods. Moreover, it is imperative that the analysis considers how other abiotic (e.g., ambient temperature) and biotic (e.g., shark size) factors compare to the commercial conditions. For example, in blue sharks, mortality after capture on pelagic longlines can vary between 5 and 35% depending on fish size and condition, gear specifications, and boatside handling practices (Campana et al., 2009; Moyes et al., 2006; Musyl et al., 2009). For this reason, the fishing methods (e.g., gear specification, fishing season) of the current study closely reflected those used by the NMFS research fishery using bottom-longline to target sandbar sharks (Personal communication, Lori Hale, NOAA), as well as the Large Coastal Shark longline commercial fishery, although the latter tends to use longer soak times (~15 h) (Hale et al., 2011). Thus, our finding that TOL increases at-vessel mortality and decreases post-release survival for dusky sharks relative to sandbar sharks supports the decision by ASMFC/NMFS to manage these two species separately in the western North Atlantic.

The most recent stock assessment for sandbar sharks indicates that this species is still overfished, but overfishing is not occurring (NMFS, 2013a). Therefore, recent changes to the HMS FMP may be beginning to benefit the sandbar shark stock in the northwestern Atlantic (NMFS, 2013a). Although this is positive news, our results indicate that sandbar sharks are still vulnerable to capture on bottom longline gear, particularly when exposed to soak times of ~12-hour (Fig. 4). It is indeed plausible that large reductions in fishing effort resulting from recent regulations have stopped overfishing, but continued interactions with gear have not allowed for significant stock rebuilding (i.e., stock remains overfished). Therefore, additional measures may be needed to limit interactions with this gear type and, perhaps, reduce soak-times. In addition, our results show that post-release mortality plays a higher role in capture-related mortality for the sandbar shark, relative to at-vessel condition, and needs to be factored into future stock assessment models.

Our findings provide additional evidence that the dusky shark is one of the most vulnerable shark species to fishing effort studied to date, with a very high (97%) combined at-vessel and post-release moribund/mortality rate after capture times of ≥3-hours. When combined with the life-history characteristics of this species, specifically the 3-year reproductive cycle and low intrinsic rate of annual population growth (∼2%), this study highlights the management challenges associated with trying to rebuild the population in the northwestern Atlantic (Musick et al., 1993; Natanson et al., 2013; Romine et al., 2009). This project demonstrates that the reduction in longline soak time reduces both at-vessel and post-release mortality not only for the dusky, but for the sandbar shark as well.

This study was unique, however, in that hook timers were used to quantify TOL, which was correlated with soak-time ($R^2 = 0.80$, Fig. 5). Therefore, this work can be directly translated into fisheries management for these species. For example, keeping soak times <3 h will reduce total mortality (at-vessel mortality + at-vessel moribund + post-release mortality) by ∼46% for sandbars and ∼60% for dusky sharks. This close correlation between hook-time and soak-time also indicates that sharks are taking bait earlier in the longline set and, hence, reducing soak times may not greatly impact the overall catch of desired species.

5. Conclusions

This project was able to demonstrate that dusky sharks have a high incidence of at-vessel and post-release mortality after capture on bottom longline gear, with mortality occurring more frequently after 3 h on the line. Although dusky sharks seem to have an exacerbated physiological response to longlining that leads to higher rates of total mortality, both species are vulnerable when compared to other species, such as the blue shark or tiger shark, after longline capture (reviewed in Marshall et al., 2012). This study indicates that sandbar and dusky sharks are at risk when caught on longline sets for standard soak-times (∼12 h). The reasons for this higher vulnerability are unclear, warranting a directed physiological response assessment for these species to determine what internal disruptions (as a secondary stress response) may be causing death.

As to why dusky sharks are more sensitive to longline gear, perhaps this species fights harder, struggling more intensively after capture, and disrupting homeostasis to the extent that they are unable to recover; such interspecific behavioral variations have been reported (Gallagher et al., 2014). One other possibility is that interspecific variation may be due to variation in the physiological stress response between species, even if closely related (Gallagher et al., 2014). However, it seems more likely to see such physiological differences between sharks of differing swimming modes (e.g., the active sharks versus more sluggish species), as opposed to congeneric species (Marshall et al., 2012). More physiological research is needed to elucidate such answers. Regardless, taking into account the cumulative levels of at-vessel and post-release moribundity/mortality for dusky sharks, we found a 97% chance of total mortality in this species after capture for 3-hour soak period or longer. Given the dismal population status of this species, such information should be carefully considered by NOAA/NMFS.

Acknowledgements

This work would not have been possible without funding by the NOAA Saltonstall-Kennedy Grant # NA9NMF-4270076. Special thanks to Lori Hale and Dr. John Carlson of the NOAA Southeast Fisheries Science Center who advised and provided the exact gear specifications of the longline for this project. Thanks to Dr. Lisa Natanson, who provided advice and longline gear. This project was hugely facilitated by the support and enthusiasm of the entire VIMS ESL staff, interns, and volunteers, and in particular, Edward Smith, Sean Fate, Reade Bonniwell, and Linda Ward, without whom this project would have been much more complicated. Dr. John Graves from VIMS provided the equipment for retrieval of our PSAT tags and, along with Dr. Andrij Horodysky, provided advice on how to find them. Megan Winton provided extremely helpful advice and coding regarding the statistical analysis of the data, with which the manuscript was greatly improved. This paper is Contribution No. 3475 of the Virginia Institute of Marine Science, College of William & Mary. This is Massachusetts Division of Marine Fisheries Contribution No. 59.

References

Arendt, M.D., Lucy, J.A., 2002. Intermediate-term (6 month) survival of adult tautog following catch and release, determined by ultrasonic telemetry. In: Lucy, J.A., Studholme, A.L. (Eds.), Catch and Release in Marine Recreational Fisheries. American Fisheries Society, Symposium 30, Bethesda, Maryland, pp. 184–188.

Beerkircher, L., Cortes, E., Shivji, M., 2000. Characteristics of shark bycatch on pelagic longlines off the southeastern United States, 1992-2000. Mar. Fish. Rev. 64, 40–49.

Campana, S.E., Joyce, W., Manning, M.J., 2009. Bycatch and discard mortality in commercially caught blue sharks Prionace glauca assessed using archival satellite pop-up tags. Mar. Eco. Prog. Ser. 387, 241–253.

Carwardine, M., Watterson, K., 2002. The Shark Watchers Handbook: A Guide to Sharks and Where to See Them. Princeton University Press, Princeton.

Cooke, S., Schreer, J., Dunmall, K., Philipp, D., 2002. Strategies for quantifying sublethal effects of marine catch-and-release angling: Insights from novel freshwater applications. In: Lucy, J.A., Studholme, A.L. (Eds.), Catch and Release in Marine Recreational Fisheries. American Fisheries Society, Symposium 30, Bethesda, Maryland, pp. 121–134.

Davis, M., Olla, B., Schreck, C., 2001. Stress induced by hooking, net towing, elevated sea water temperature and air in sablefish: lack of concordance between mortality and physiological measures of stress. J. Fish. Biol. 58, 1–15.

Gallagher, A.J., Serafy, J.E., Cooke, S.J., Hammerschlag, N., 2014. Physiological stress response, reflex impairment, and survival of five sympatric shark species following experimental capture and release. Mar. Eco. Prog. Ser. 496, 207–218.

Gingerich, A.J., Cooke, S.J., Hanson, K.C., Donaldson, M.R., Hasler, C.T., Suski, C.D., Arlinghaus, R., 2007. Evaluation of the interactive effects of air exposure duration and water temperature on the condition and survival of angled and released fish. Fish. Res. 86, 169–178.

Graves, J.E., Horodysky, A.Z., Latour, R.J., 2009. Use of pop-up satellite archival tag technology to study postrelease survival of and habitat use by estuarine and coastal fishes: an application to striped bass. Fish Bull. 107, 373–383.

Hale, L.F., Gulak, S.J.B., Napier, A.M., Carlson, J.K., 2011. Characterization of the shark bottom longline fishery, 2010. In: NOAA Technical Memorandum. NMFS-SEFSC-611, 35p.

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.

Hoolihan, J.P., Luo, J., Abascal, F.J., Campana, S.E., De Metrio, G., Dewar, H., Domeier, M.L., Howey, L.A., Lutcavage, M.E., Musyl, M.K., Neilson, J.D., Orbesen, E.S., Prince, E.D., Rooker, J.R., 2011. Evaluating post-release behavior modification in large pelagic fish deployed with pop-up satellite archival tags. ICES J. Mar. Sci. 68, 880–889.

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.

Hueter, R., Huepel, M., Heist, E., Keeney, D., 2004. Evidence of philopatry in sharks and implications for the management of shark species. J. Northwest Atl. Fish. Sci. 35, 239–247.

Hueter, R.E., Manire, C.A., Tyminski, J.P., Hoenig, J.M., Hepworth, D.A., 2006. Assessing mortality of released or discardedfish using a logistic model of relative survival derived from tagging data. T. Am. Fish. Soc. 135, 500–508.

Hussey, N.E., McCarthy, I.D., Dudley, S.F.J., Mann, B.Q., 2009. Nursery grounds, movement patterns and growth rates of dusky sharks, *Carcharhinus obscurus*: a long-term tag and release study in South African waters. Mar. Freshwater Res. 60, 571–583.

Kneebone, J., Chisholm, J., Bernal, D., Skomal, G., 2013. The physiological effects of capture stress, recovery, and post-release survivorship of juvenile sand tigers (*Carcharias taurus*) caught on rod and reel. Fish. Res. 147, 103–114.

Kohler, N.E., Turner, P.A., 2001. Shark tagging: a review of conventional methods and studies. Environ. Biol. Fish 60, 191–223.

Mandelman, J.W., Farrington, M.A., 2007. The physiological status and mortality associated with otter-trawl capture, transport, and captivity of an exploited elasmobranch, Squalus acanthias. ICES J. Mar. Sci. 64, 122–130.

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.

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

Morgan, A., Burgess, G.H., 2007. At-vessel fishing mortality for six species of sharks caught in the northwest Atlantic and Gulf of Mexico. Proceedings of the 59th Annual Conference of the Gulf and Caribbean Fisheries Institute 19, 123–130.

Morgan, A., Carlson, J., 2009. Capture time, size and hooking mortality of bottom longline-caught sharks. Fish. Res. 101, 32–37.

Moyes, C.D., Fragoso, N., Musyl, M.K., Brill, R.W., 2006. Predicting postrelease survival in large pelagic fish. T. Am. Fish. Soc. 135, 1389–1397.

Musick, J.A., Branstetter, S., Colvocoresses, J.A., 1993. Trends in shark abundance from 1974 to 1991 for the Chesapeake Bight region of the U.S. Mid-Atlantic coast. NOAA Technical Report NMFS 115.

Musyl, M.K., Moyes, C.D., Brill, R.W., Fragoso, N.M., 2009. Factors influencing mortality estimates in post-release survival studies. Mar. Eco. Prog. Ser. 396, 157–159.

Musyl, M.K., Brill, R.W., Curran, D.S., Fragoso, N.M., McNaughton, L.M., Nielsen, A., Kikkawa, B.S., Moyes, C.D., 2011. Postrelease survival, vertical and horizontal movements, and thermal habitats of five species of pelagic sharks in the central Pacific Ocean. Fish. Bull. 109, 341–368.

Natanson, L.J., Gervelis, B.J., Winton, M.V., Hamady, L.L., Gulak, S.J.B., Carlson, J.K., 2013. Validated age and growth estimates for Carcharhinus obscurus in the northwestern Atlantic Ocean, with pre- and post management growth comparisons. Environ. Biol. Fish. 97, 881–896.

NMFS. 2006. Final Consolidated Atlantic Highly Migratory Species Fishery Management Plan. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Office of Sustainable Fisheries, Highly Migratory Species Management Division, Silver Spring, MD. Public.

NMFS. 2008. Final Amendment 2 to the Consolidated Atlantic Highly Migratory Species Fishery Management Plan. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Office of Sustainable Fisheries, Highly Migratory Species Management Division, Silver Spring, MD. Public Document. pp. 726.

NMFS, 2011. SEDAR 21 Stock Assessment Report. HMS Dusky Shark. SEDAR, 4055 Faber Place Drive, Suite 20, North Charleston, SC 29,405.

NMFS. 2013a. Final Amendment 5a to the 2006Consolidated Atlantic Highly Migratory Species Fishery Management Plan. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Office of Sustainable Fisheries, Highly Migratory Species Management Division, Silver Spring, MD. Public Document. pp. 410.

NMFS. 2013b. U.S. National Bycatch Report First Edition Update 1 (L.R. Benaka, C. Rilling, E.E. Seney, and H. Winarsoo, Editors. U.S. Department of Commerce, 57 p.

NMFS. 2014. Dusky shark (*Carcharhinus obscurus*), online: http://www.nmfs.noaa.gov/pr/species/fish/duskyshark.htm

Rechisky, E.L., Wetherbee, B.M., 2003. Short-term movements of juvenile and neonate sandbar sharks, Carcharhinus plumbeus, on their nursery grounds in Delaware Bay. Environ. Biol. Fish 68, 113–128.

Romine, J.G., Musick, J.A., Burgess, G.H., 2009. Demographic analysis of the dusky shark, Carcharhinus obscurus, in the Northwest Atlantic incorporating hooking mortality estimates and revised reproductive parameters. Environ. Biol. Fish 84, 277–289.

Skomal, G.B., Chase, B.C., 2002. The physiological effects of angling on post- release survivorship in tunas, sharks, and marlin. In: Lucy, J.A., Studholme, A.L. (Eds.), Catch and Release in Marine Recreational Fisheries. American Fisheries Society, Symposium 30, Bethesda, Maryland, pp. 135–138.

Skomal, G.B., 2007. Evaluating the physiological and physical consequences of capture on post-release survivorship in large pelagic fishes. Fisheries. Manag. Ecol. 14, 81–89.

Skomal, G., Bernal, D., 2010. Physiological responses to stress in sharks. In: Carrier, J., Musick, J., Heithaus, M. (Eds.), Sharks and Their Relatives II: Biodiversity, Adaptive Physiology, and Conservation. CRC Press, Boca Raton, pp. 459–490.

Van Raaij, M.T.M., Pit, D.S.S., Balm, P.H.M., Steffens, A.B., van den Thillart, G.E.E.J.M., 1996. Behavioral strategy and the physiological response in rainbow trout exposed to sever hypoxia. Horm. Behav. 30, 85–92.

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

Yokota, K., Kiyota, M., Minami, H., 2006. Shark catch in a pelagic longline fishery: comparison of circle and tuna hooks. Fish. Res. 81, 337–341.