Stress, post-release mortality, and recovery of commonly discarded deep-sea sharks caught on longlines

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ABSTRACT: Bycatch interactions with deep-sea elasmobranchs are increasingly common and can lead to dramatic declines in abundance over short time scales. Sharks hooked in the deep sea could face a higher likelihood of severe physiological disturbance, at-vessel mortality, and post-release mortality (PRM) than their shallower counterparts. Unfortunately, robust PRM rates have not yet been estimated for longline-caught deep-sea sharks, and as such are not currently incorporated into total fishery mortality estimates or bycatch assessments, limiting the effectiveness of current conservation or management initiatives. We empirically estimated PRM for 2 focal taxa of deep-sea shark, the Cuban dogfish *Squalus cubensis* and the gulper shark *Centrophorus* sp., using post-release enclosures deployed at-depth. We calculated 24 h PRM rates of 49.7 ± 8.5% (mean ± SE) for *S. cubensis* and 83 ± 16% for *Centrophorus* sp. and identified blood lactate, total length, glucose, and vitality scores as predictors of PRM in *S. cubensis*. We also observed all 24 h PRM within 11 h post-capture and demonstrated the effects of recovery depth and at-vessel blood chemistry metrics on post-release behavior. Our results suggest that PRM rates of deep-sea sharks are high and highlight the need for filling in this gap in fishery mortality estimates for other common discards in the future.

KEY WORDS: Post-release mortality · Bycatch · Stress physiology · Discard · *Squalus cubensis* · *Centrophorus* · Deep-sea · Elasmobranch

INTRODUCTION

In recent decades, commercial fisheries have expanded into the deep-sea (below 200 m) (Morato et al. 2006) due to advancements in fishing technology and declines in some coastal stocks (Cotton & Grubbs 2015). Unfortunately, deep-sea fishes are highly susceptible to overexploitation due to their very conservative life histories (Large et al. 2003, Simpfendorfer & Kyne 2009, Norse et al. 2012). García et al. (2008) suggested that the average fishing mortality rate that it would take to drive a deep-sea species extinct is only 58% of that for a continental shelf species and,

as would be expected, rapid depletion and abandonment of deep-sea fish stocks has been documented repeatedly (Koslow et al. 2000, Graham et al. 2001, Jones et al. 2005, Devine et al. 2006, Norse et al. 2012).

Deep-sea elasmobranchs are perhaps the least resilient fishes to exploitation as their maximum rates of population growth are among the lowest observed for any species (Kyne & Simpfendorfer 2007, Norse et al. 2012). Furthermore, the deeper a species' capture depth, the more vulnerable it is to capture-induced stress as a result of decreased metabolic capacity and energy stores (Koslow 1996, McClain et al. 2012), while large temperature, pressure, and light gradi-

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ents experienced during the forced and rapid ascent to the surface could impart additive stress on captured individuals. These technical, environmental, and biological factors can interact to increase the likelihood of at-vessel mortality or cryptic post-release mortality (PRM) after a capture event (Skomal & Mandelman 2012, Brooks et al. 2015).

At-vessel and PRM rates in elasmobranchs are species-specific and highly variable (Morgan & Burgess 2007, Enever et al. 2009, Hale et al. 2010, Braccini et al. 2012, Coelho et al. 2012, Gallagher et al. 2014a), depending on factors such as gear type, capture duration, respiratory mode, and metabolic capacity of the species in question (Davis 2002, Mandelman & Skomal 2009, Dapp et al. 2016). Similarly, the degree of physiological disturbance and/or physical injury experienced by a released individual can vary greatly, and may result in sub-lethal effects such as impaired behavior, growth, or immune function that can lead to reduced fitness or post-release predation (Davis 2002, Raby et al. 2014, Wilson et al. 2014).

There remains a lack of empirically estimated PRM rates for discarded deep-sea sharks (James et al. 2016), which are typically discarded due to low economic value or harvest prohibitions requiring their release, despite data that suggest that PRM of these discards can be common (Brooks et al. 2015). As deep-sea elasmobranchs are commonly caught as bycatch in fisheries targeting teleosts and crustaceans worldwide (Cotton & Grubbs 2015), there is the potential that total fishery mortality estimates for these species are underestimated as a result of not accounting for discard mortality, or conversely over-estimated by ignoring the potential for survivors, likely limiting the effectiveness of management efforts where they exist (depending on the fishery in question; Coggins et al. 2007, Molina & Cooke 2012).

This study sought to directly estimate the 24 h PRM rates of longline-caught deep-sea sharks, develop indirect methods to predict PRM using blood chemistry parameters and vitality scores, and shed light on the post-release behavior of individuals held in enclosures at the seafloor. Our primary species of interest was the Cuban dogfish *Squalus cubensis*, the most commonly encountered squalid in the deep reef fish and tilefish longline fisheries of the northern Gulf of Mexico (Hale et al. 2010, Jones et al. 2013), where over 95 % are discarded alive (Hale et al. 2010, Gulak et al. 2013). Our secondary taxon of interest was the gulper shark *Centrophorus* sp., which is part of one of the most highly exploited and most vulnerable species complexes of deep-sea sharks to date (Kyne & Simpfendorfer 2007, Kyne et al. 2012).

MATERIALS AND METHODS

Longline sampling

We conducted field work from July 2014 to June 2015 in northeastern Exuma Sound, approximately 2.5 km west of Powell Point on Eleuthera, The Bahamas (24.541° N, 76.121° W). Standard demersal longlines were set in 450 to 900 m of water during daylight hours only (Fig. 1). Mainline length was a minimum of 1.5 times the water depth. Longlines consisted of a grapnel anchor or weight to attach the mainline to the seafloor, 20 to 30 baited circle hooks (10/0 or 12/0) spaced 5 to 10 m apart, and an archival temperature and depth recorder (TDR) (LAT-1400; Lotek) that recorded depth and temperature every 4 s, placed 5 m from the last hook. Longline depths and temperatures were recorded as the deepest and coldest points measured for a given dataset, which in some instances may have been above the seafloor.

Hooks were baited with miscellaneous fish scraps and/or little tunny *Euthynnus alletteratus* and soak times were roughly 3.5 h (whereas commercial soak times are >12 h; Gulak et al. 2013). After the desired set duration, longlines were hauled using an electric pot hauler (Waterman Industries of Florida) at a rate of 0.3 m s^{-1}. Sharks were sequentially unhooked and placed in a water-filled cooler to minimize air exposure for the remaining workup, during which sharks were sampled for blood and then measured for pre-caudal, fork, and total lengths and assessed for maturity based on external morphology and/or published size-at-maturity data. Fin clips were taken for genetic analysis from a unique location to distinguish individuals while in the post-release enclosure during the subsequent 24 h of monitoring. The time between reaching the surface and being submerged in the enclosure was typically less than 5 min.

Blood sampling

Immediately upon reaching the boat, sharks were placed into tonic immobility and 3 to 4 ml of blood was taken by caudal venipuncture using a 25.4 mm, 22 gauge needle and either a 3 or 5 ml syringe rinsed with sodium heparin. Roughly 95 µl of blood was then inserted into an i-STAT CG4+ cartridge, which was analyzed by an i-STAT point-of-care analyzer (Heska Corporation) thermoset to 37°C to determine blood lactate and pH levels (Gallagher et al. 2010, Harter et al. 2015). Simultaneously, 1 ml of blood was transferred to a 1.5 ml Eppendorf tube and analyzed
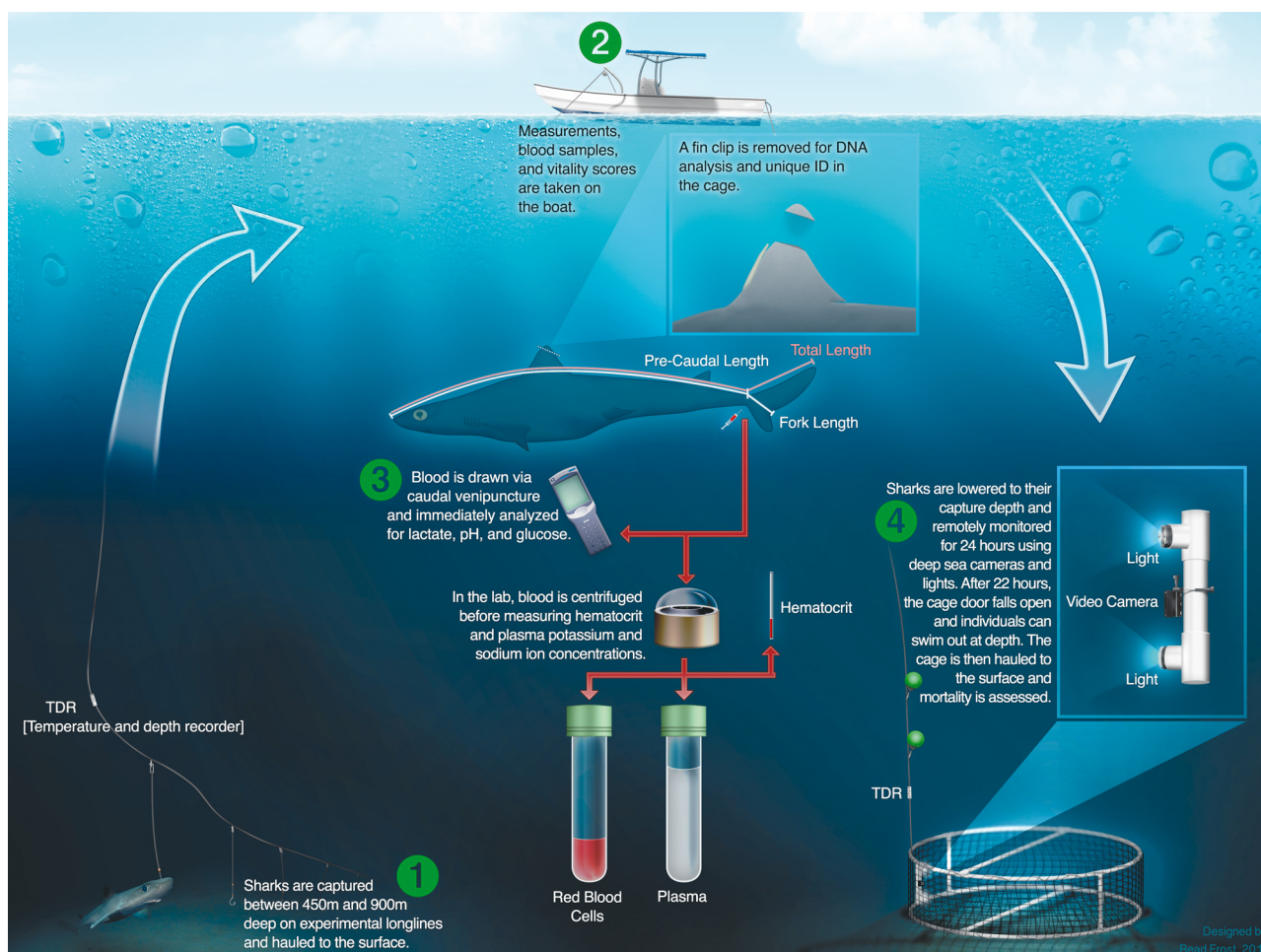
Fig. 1. Visual guide to the methods used in this study

by a waterproof pH meter (HI99161; Hanna Instruments) to determine blood temperature and pH (Talwar et al. 2017). Immediately following these analyses, one drop of blood was placed onto an Accu-Chek glucose meter strip (Roche Diagnostics) to determine blood glucose levels and one drop was placed onto a Lactate Plus Meter test strip (Nova Biomedical) to determine blood lactate levels in the event of an i-STAT error. Blood chemistry analysis typically occurred within 2 min following caudal venipuncture.

The remaining blood sample (~2 to 3 ml) was injected into a 10 ml vacutainer coated with dried lithium heparin (Becton, Dickinson and Co.) and placed on ice before being spun in a centrifuge (Clay Adams Compact II Centrifuge) for 5 min at $10\,000 \times g$ to separate plasma from red blood cells. Similarly, a micro-hematocrit tube (Drummond Scientific) was filled with a sample of whole blood and sealed with Critoseal (McCormick Scientific) before it was spun in a micro-hematocrit centrifuge (LW Scientific

Zippocrit) at $4400 \times g$ for 4.5 min. Hematocrit was calculated as the percentage of total blood volume made up of red blood cells. Plasma was frozen at $-20°C$ and transported in liquid nitrogen to the University of New England, where plasma sodium and potassium ion concentrations were quantified using atomic emission spectrometry (Cole-Parmer Single-Channel Digital Flame Photometer Model 02655-00). Each sample was measured in triplicate and samples were analyzed in groups of 5; the standard curve was repeatedly measured between each group.

Enclosures

After a complete workup, animals were placed into a submerged, circular post-release enclosure and assigned a vitality score (Table 1). The enclosure was constructed of 3.8×3.8 cm PVC-coated wire mesh reinforced with PVC struts and measured roughly

Table 1. Vitality scores assigned to sharks placed in the post-release enclosure before being lowered to the sea floor

Vitality score	Description
Excellent	Vigorous body movement, no apparent injuries, strong swimming behavior
Fair	Inconsistent body movement, responds to stimulation, possible minor injuries, moderate swimming behavior
Poor	Weak body movement, little response to stimulation, possible minor injuries, weak or absent swimming behavior

2.5 m in diameter and 4 m^3 in volume. After all individuals from a given longline set were added, the enclosure's door was tied shut with a galvanic timed release (Neptune Marine Products), allowing it to fall open after 20 to 22 h so that surviving sharks could swim out. The maximum number of sharks placed in a single enclosure was 6, but was more commonly 1 to 3 animals enclosure^{-1}. The enclosure was then lowered to the seafloor as close to the capture location as possible. A TDR was attached 5 m above the enclosure's bridle and 2 floats were attached to the mainline with stainless longline snaps at 50 and 100 m from the enclosure to prevent the mainline from tangling with the mesh material. Two programmable white LED lights ('Lanternfish', Blue Turtle Engineering) and a GoPro Hero 3 White Edition camera programmed with a Time Lapse Intervalometer (Cam-Do) in a Scout Pro H3 deep-sea housing (Group B Distribution) were attached to the inside of the enclosure before deployment and synced to record for 4 continuous minutes every half hour for 24 h. Depth and temperature were calculated as discussed previously. After reaching the sea floor, the enclosure was pulled onto its side by the drag of the boat and surface buoys and hauled 24 h later (chosen primarily for logistical reasons). Any surviving sharks remaining in the enclosure were released at the surface after the cage haulback.

Data analysis

At-vessel mortality rates for all shark species were calculated as the percentage of the total catch of a species found to be dead upon first handling. Twenty-four hour PRM rates and standard errors (SE) were calculated using Eqs. (1) and (2), which use each enclosure deployment as the unit of replication (M = mortality rate; r = number of enclosures; Pollock & Pine 2007):

$$M = \frac{\sum_1^r M_i}{r} \qquad (1)$$

$$\mathrm{SE}(M) = \sqrt{\frac{\sum_1^r (M_i - M)^2}{r(r-1)}} \qquad (2)$$

Blood chemistry parameter values were evaluated post-hoc using the Shapiro-Wilk test for normality, and outliers identified and removed using diagnostic plots in R programming language (R Development Core Team 2008). Blood pH values for both *Centrophorus* sp. and *Squalus cubensis* were converted to laboratory quality values based on equations developed for *S. cubensis*, which include temperature correction and laboratory correction factors (Harter et al. 2015, Talwar et al. 2017).

In-cage videos were analyzed for time of first swimming (TOFS; defined as time of first observable, sustained forward movement) and time of death (defined as the last time an animal was observed ventilating) for each individual, and total seconds swimming was recorded for the first minute of each 4 min video segment for each animal. Percent time swimming was then calculated for each animal by dividing its total time swimming by the total time during which that animal was alive and observed across the first minute of all video segments up to 900 m in a given 24 h period. This metric was then binned into active (>20% swimming) and inactive (<20% swimming) categories for analysis. Similarly, time of death and TOFS were binned into early (<120 min post-capture) and late (>120 min post-capture) categories. These decisions were based on the shape and properties of the data (non-normally distributed, semi-categorical) and the median values.

All further statistical analyses were conducted only for *S. cubensis* due to low sample sizes for other species. To predict PRM, generalized linear models (GLMs) with a binomial probability distribution and a logit link function were fitted to the data using maximum likelihood estimation. Blood chemistry parameters and total lengths were re-scaled into measurements of deviation from the mean for use in these models. The full model described the relationship between 24 h mortality as a binary response variable and 5 potential explanatory variables as well as interaction terms. A random effect to account for enclosure deployment was initially included, but as it accounted for <1% of the deviance in the full model, it was removed. The possible main effects that were included were the continuous variables of blood pH, blood lactate, blood glucose, hematocrit, and total length, as well as the interaction terms for lactate and

total length, lactate and glucose, pH and lactate, and pH and total length. Potassium and sodium ion concentrations were excluded from this model as they significantly reduced the sample size and had little predictive value of PRM in other analyses. Nonsignificant factors were removed in backwards stepwise fashion while evaluating the increases in deviance and Akaike's information criterion (AIC) with each removal. The model was reduced until the minimal adequate model remained, which included only significant terms or terms that, once removed, caused an increase in AIC or deviance (see Crawley 2007). These models were then used to estimate the likelihood of mortality for animals with a known fate. An individual with an estimated likelihood of mortality higher than 50% was classified as a mortality; survivors were 50% or below. These predicted outcomes were then compared to the experimentally observed outcomes for these individuals which allowed for the selection of the model that best predicted mortality.

To understand the effect of capture characteristics on mortality, GLMs were used to describe the relationship between 24 h mortality as a binary response variable and sea surface temperature, time at the surface (the time between reaching the surface and release of the cage from the boat), and their interaction term as explanatory variables. The same model selection process was used as described above.

Pearson's chi-squared tests were then used to test the null hypothesis that the distribution of survivors and mortalities was equal across vitality scores. Vitality scores were also examined to identify blood chemistry parameters that differed between groups using 1-way ANOVAs and Tukey's tests. Further, the relationship between time post-caging and mean time swimming (pooled across all animals for each 1 min video segment) was examined with linear regressions and compared between groups of survivors and mortalities as well as within survivors for

those at shallow (<625 m) and deep (>625 m) enclosure depths (625 m was chosen because it was the mean enclosure depth and because cage depths were bimodally distributed, with clusters between 550–600 m and 700–750 m). The rate of increase in mean time swimming was compared among these groups using ANCOVA. Lastly, binned swimming behaviors and times of death were compared with t-tests and/or Mann-Whitney U-tests, as were blood chemistry parameters between species, depending on whether or not data were normally distributed. All analyses were performed using JMP v.7.0.1 (SAS Institute) and R programming language (R Development Core Team 2008); the level of significance for all tests was $\alpha < 0.05$. Graphs were created using SigmaPlot v.11.0 (SYSTAT Software).

RESULTS

Capture characteristics

A total of 108 sharks from 6 species were captured over 72 longline sets fishing at a mean depth of 628 m and a mean temperature of 11.95°C (Table 2). Of these individuals, 66 were penned over 37 trials, with post-release enclosures resting at a mean depth of 641 m (range 456 to 846 m) and a mean temperature of 11.73°C (range 7.7 to 16.2°C) after descending at a mean rate of 0.49 m s^{-1} (range 0.28 to 0.59 m s^{-1}). The sea surface temperature over the study period ranged from 24 to 30°C.

Sharks were hooked in the jaw or soft palate except for one instance where an animal was hooked through the right spiracle. Physical injury at-vessel was documented in only 1 *Squalus cubensis* (broken jaw) and 1 *Mustelus canis insularis* (secondary hooking in the pectoral fin). These individuals were not included in post-release caging trials. We saw no evidence of barotrauma.

Table 2. Capture composition and characteristics of sharks caught on deep-sea longlines throughout this study as well as at-vessel and 24 h post-release mortality rates. N/A: not applicable

| Species	No. captured	Total length (mean ± SD) (cm)	Capture depth (mean ± SD) (m)	Capture temp. (mean ± SD) (°C)	No. Penned	At-vessel mortality rate (%)	24 h post-release mortality rate (mean ± SE)(%)
Squalus cubensis	72	58.1 ± 11.6	622.3 ± 71.9	12.0 ± 1.8	54	8.3	49.7 ± 8.5
Centrophorus sp.	13	88.7 ± 11.5	769.5 ± 42.8	8.8 ± 0.8	8	30.8	83.0 ± 16.0
Mustelus canis insularis	14	88.6 ± 11.1	539.6 ± 65.0	14.1 ± 2.0	4	7.1	75.0 ± 25.0
Hexanchus nakamurai	6	129.3 ± 12.0	582.1 ± 43.9	13.1 ± 1.2	0	16.7	N/A
Heptranchias perlo	2	75.0 ± 17.0	631.5 ± 34.7	12.0 ± 0.4	0	100	N/A
Hexanchus griseus	1	227	772	10	0	0	N/A
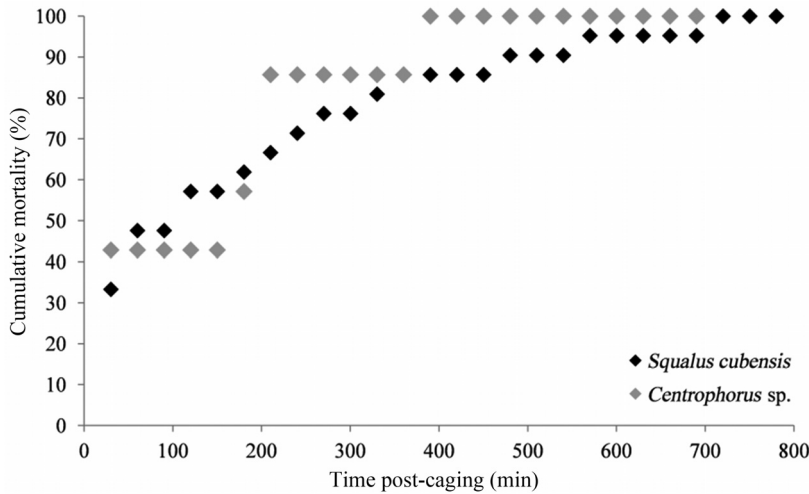
Fig. 2. Time of death of *Squalus cubensis* and *Centrophorus* sp. that died within the 24 h video monitoring period in post-release enclosures at depth

Mortality and blood chemistry

At-vessel mortality rates were highly variable across 6 species, while 24 h PRM rates for *S. cubensis*, *Centrophorus* sp., and *M. canis insularis* ranged from 49.7 to 83%, although sample sizes were limited for *Centrophorus* sp. and *M. canis insularis* (Table 2). The mean (±SE) time of death was 190 ± 43.8 min post-capture for *S. cubensis* and 260 ± 65.6 min post-capture for *Centrophorus* sp. that died within the 24 h caging period (Fig. 2). All mortalities were observed within 690 min post-caging.

Blood glucose levels were significantly lower in *Centrophorus* sp. compared to those in *S. cubensis* (Student's *t*-test, p < 0.05). There were no significant interspecific differences in blood pH, lactate, hematocrit, plasma potassium, or plasma sodium levels (Table 3).

Predicting post-release mortality: *S. cubensis*

The GLM analysis determined that a model including glucose, hematocrit, lactate, and total length provided the best fit to binary 24 h mortality data

($AIC_{Full\ Model} = 34.50$, $AIC_{Reduced\ Model} = 29.30$). Only lactate and total length, however, were significant predictors of mortality (Table 4).

Using the reduced models from this analysis, data from animals with a known fate were substituted into the generated predictive equations to estimate probabilities of mortality. The model including total length, lactate, and glucose correctly assigned 82% of individuals into the appropriate category, which was the highest of any reduced model (Table 4). As such, a logistic regression model including these terms was used to predict 24 h mortality for practical use in a fishery context. To obtain the probability of mortality (*M*) for an individual with known at-vessel blood lactate, total length, and blood glucose values, the maximum likelihood estimates ($b_0 = -4.93578$, $b_1 = -0.75226$, $b_2 = 0.14598$, $b_3 = 1.08897$) for the mortality curve were substituted into the response function in Eq. (3):

$$M = 1 - \frac{\exp(b_0 + b_1X_1 + b_2X_2 + b_3X_3)}{1 + \exp(b_0 + b_1X_1 + b_2X_2 + b_3X_3)} \quad (3)$$

Based on this model, a probability of mortality of 0.5 was found at a lactate value of 10.5 mmol l^{-1} (X_1) and a glucose value of 4 mmol l^{-1} (X_3) for a shark of average total length (58 cm, X_2). The probability of mortality then increased with higher blood lactate levels, lower glucose levels, and smaller total lengths.

A parallel GLM analysis determined that there was no significant effect of sea surface temperature or time at the surface on 24 h binary mortality data for this species. The reduced model, after backwards stepwise elimination, included only time at the surface ($AIC_{Full\ Model} = 78.8$, $AIC_{Reduced\ Model} = 76.1$; Table 5).

Vitality scores were distributed differently than expected (Pearson's $\chi^2 = 11.78$, df = 2, p = 0.001). Of those individuals assigned a score of 'excellent', 21% died, whereas a score of 'fair' resulted in 42% mortality and a score of 'poor' resulted in 100% mortality (Fig. 3).

Table 3. Blood chemistry parameters and corresponding sample sizes for *Squalus cubensis* and *Centrophorus* sp. captured during this study

		pH		Lactate (mmol l^{-1})		Hematocrit (%)		Glucose (mmol l^{-1})		Na$^+$ (mmol l^{-1})		K$^+$ (mmol l^{-1})
	n	Mean ± SE	n	Mean ± SE	n	Mean ± SE	n	Mean ± SE	n	Mean ± SE	n	Mean ± SE
S. cubensis	51	7.27 ± 0.02	41	9.80 ± 0.59	53	25.4 ± 0.52	51	4.72 ± 0.12	26	282.2 ± 3.31	26	3.57 ± 0.12
Centrophorus sp.	8	7.14 ± 0.05	4	9.29 ± 1.90	9	25.0 ± 1.64	9	3.39 ± 4.69	3	271.1 ± 35.60	2	3.11 ± 0.02

Table 4. Full model and minimal adequate model parameter values and Akaike's information criterion (AIC) values for each generalized linear model (GLM) derived from backwards stepwise GLM analysis to describe 24 h mortality in *Squalus cubensis* based on 5 initial model parameters and 4 interaction terms, as well as Akaike weights (w_i) and percent correct assignments for the mortality of animals with a known fate (probabilities of 50% or greater were considered mortality events). Estimates and standard errors (SE) are on a logit scale; *p ≤ 0.05

Parameter	Estimate	SE	z-value	Pr(>|z|)	Model	AIC	w_i	% Correctly assigned
Full model					Full model	34.50	0.02	
Intercept	2.15	1.85	1.16	0.24				
Lactate × total length	0.07	1.57	0.05	0.96	– Lactate × total length	32.50	0.06	
Hematocrit	0.23	1.37	0.17	0.87				
pH × total length	0.38	2.15	0.18	0.86	– pH × total length	30.53	0.15	
pH	2.16	2.57	0.84	0.40	– pH	30.38	0.16	
pH × lactate	−2.27	2.55	−0.93	0.35	– pH × lactate	29.53	0.25	
Lactate × glucose	−1.85	1.64	−1.13	0.26	– Lactate × glucose	29.30	0.28	
Total length	2.23	1.79	1.24	0.21				
Glucose	1.58	1.24	1.28	0.20				
Lactate	−0.39	2.26	−1.74	0.08				
Most parsimonious model					Most parsimonious model	29.30	0.28	74
Intercept	1.17	0.90	1.30	0.19				
Hematocrit	0.39	0.71	0.55	0.58	– Hematocrit	31.84	0.08	82
Glucose	0.99	0.68	1.44	0.15	– Glucose	47.20	0.00	72
Total length	2.12	0.93	2.29	*	– Total length	51.41	0.00	64
Lactate	−2.88	1.31	−2.21	*	– Lactate	76.56	0.00	

Table 5. Full model and minimal adequate model parameter values and Akaike's information criterion (AIC) values for each generalized linear model (GLM) derived from backwards stepwise GLM analysis to describe 24 h mortality in *Squalus cubensis* based on select capture characteristics, as well as Akaike weights (w_i). SST: sea surface temperature

Parameter	Estimate	SE	z-value	Pr(>|z|)	Model	AIC	w_i
Full model					Full model	78.80	0.09
Intercept	6.13	8.23	0.75	0.46			
Time at the surface	−0.27	0.99	−0.28	0.78			
SST × time at the surface	0.01	0.04	0.38	0.71	– SST × time at the surface	76.94	0.24
SST	−0.25	0.30	−0.82	0.41	– SST	76.06	0.37
Most parsimonious model					Most parsimonious model	76.06	0.37
Intercept	−0.58	0.56	−1.05	0.30			
Time at the surface	0.09	0.06	1.46	0.14	– Time at the surface	76.56	0.29

One-way ANOVAs revealed differences in at-vessel blood pH and lactate levels among *S. cubensis* assigned vitality scores from poor to excellent (pH: $F_{2,56} = 3.42$, p < 0.05; lactate: $F_{2,39} = 4.52$, p < 0.05). Those assigned a vitality score of poor had a significantly lower at-vessel blood pH (mean ± SE = 7.14 ± 0.03) and significantly higher at-vessel blood lactate level (13.97 ± 1.51 mmol l^{-1}) than those assigned a vitality score of fair (pH: 7.25 ± 0.02; lactate: 8.95 ± 0.72 mmol l^{-1}) according to Tukey's test, although there was no significant difference between pH or lactate values for excellent (pH: 7.26 ± 0.03; lactate: 9.71 ± 0.94 mmol l^{-1}) and poor categories.

Post-release behavior: *S. cubensis*

S. cubensis swimming behaviors were normal (e.g. correct orientation, resting on the bottom, exploring the enclosure) for survivors, which often swam in circles around the enclosure's perimeter (Fig. 4). The mean (±SE) TOFS was 113 ± 17.8 min post-caging for *S. cubensis* that survived the 24 h caging period, while for those that died it was 172.5 ± 74.8 min post-capture. All sharks began swimming by the 420 min post-capture video segment (Fig. 5). Only 19% of sharks that died swam.

The mean time swimming during the first minute of each video segment increased over time for surviving
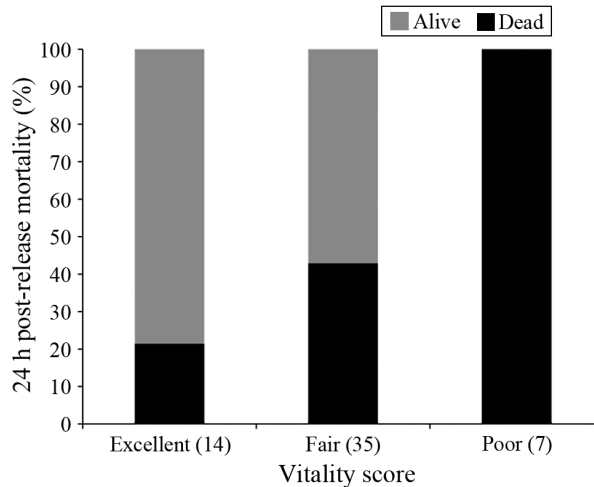
Fig. 3. Post-release mortality of *Squalus cubensis* placed in 24 h post-release enclosures by vitality score (no. penned). The distribution of sharks that survived or died after 24 h post-release was significantly different between groups of sharks assigned excellent, fair, and poor vitality scores (Pearson's χ^2 = 11.78, df = 2, p = 0.001)

S. cubensis (r^2 = 0.37, p < 0.01) from roughly 5 s during the 30 min post-capture video segment to over 20 s during the 900 min post-capture segment (Fig. 6). For those that died, mean time swimming reached a peak during the 210 min post-capture segment (Fig. 6).

Mean time swimming for surviving *S. cubensis* was higher within enclosures that were shallower than 625 m compared to within enclosures set deeper than 625 m (t = 3.72, p < 0.05). The rate of increase in swimming behavior (i.e. recovery) was marginally faster for sharks in shallower enclosures as well (slope$_{shallow}$ = 0.02; slope$_{deep}$ = 0.01; ANCOVA interaction term, p = 0.06; Fig. 7). Further, the mean (±SE) TOFS was significantly earlier for sharks in shallow enclosures (<625 m; 73.13 ± 12.84 min) compared to deep enclosures (>625 m; 167.50 ± 32.71 min) (Mann-Whitney U-test, $n_{shallow}$ = 16, n_{deep} = 12, p < 0.05).

At-vessel blood glucose levels were significantly higher for *S. cubensis* that had a TOFS more than 120 min post-caging (late: 5.22 ± 0.19 mmol l^{-1}) compared to those that had a TOFS less than 120 min post-caging (early: 4.66 ± 0.17 mmol l^{-1}; t = 2.19, p < 0.05). There were no other differences between early and late TOFS when examining its relationship with other at-vessel blood chemistry metrics (e.g. blood lactate, blood pH). However, at-vessel *S. cubensis* blood lactate levels were significantly lower and at-vessel blood pH levels significantly higher for active (lactate: 6.7 ± 1.73 mmol l^{-1}; pH: 7.32 ± 0.03) compared to inactive (lactate: 10.42 ± 0.98 mmol l^{-1}; pH:
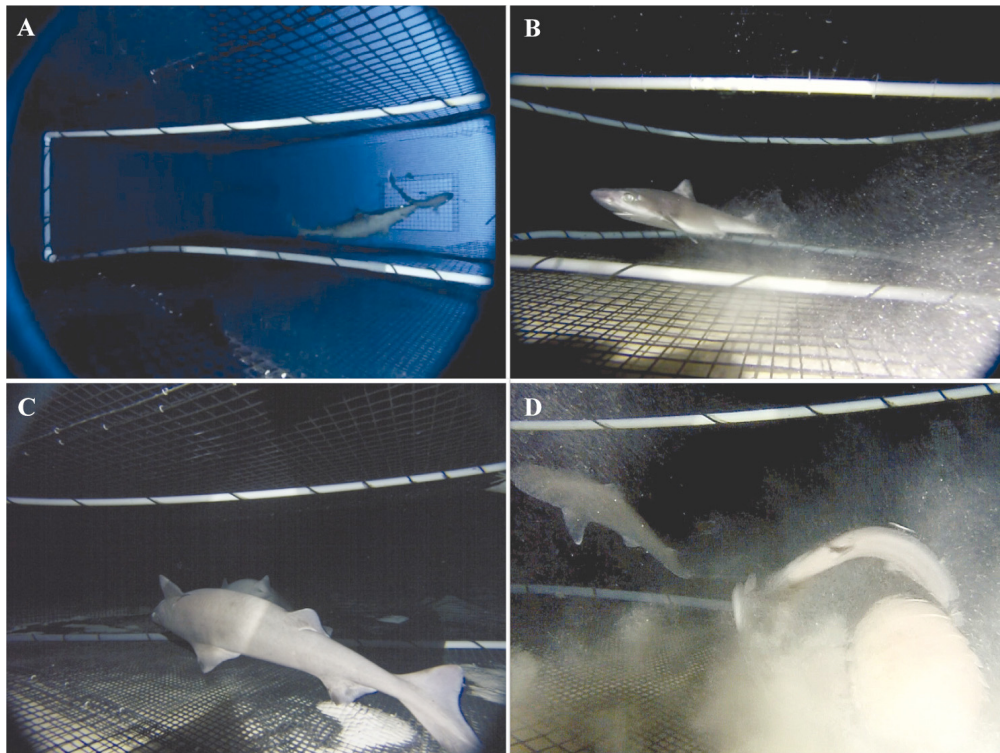

Fig. 4. Photo panel showing (A) a gulper shark and a Cuban dogfish during descent, (B) a Cuban dogfish swimming around the enclosure, (C) 2 gulper sharks unable to orient effectively while still alive, and (D) post-release predation of a Cuban dogfish by a giant isopod after over 20 h in the enclosure
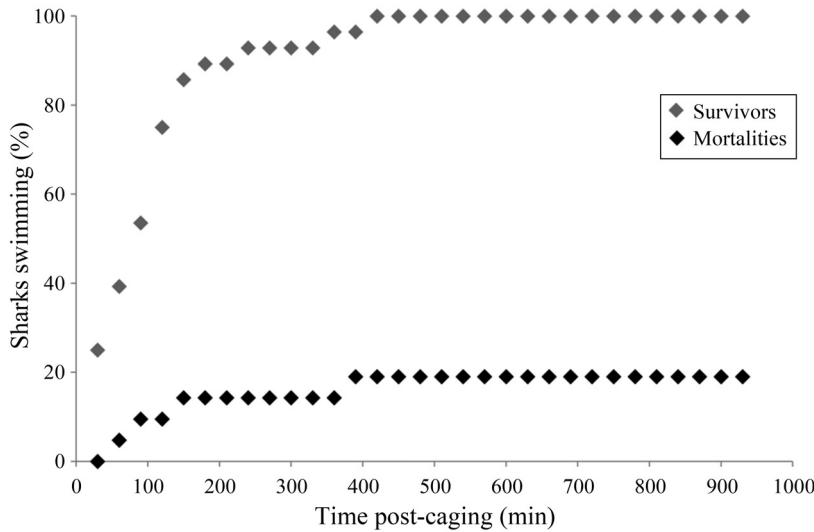
Fig. 5. Percent of all *Squalus cubensis* exhibiting swimming behavior during the 24 h video monitoring period in post-release enclosures at depth

7.22 ± 0.03) sharks observed during the 24 h post-release caging period as calculated by percent time swimming (<20% inactive, >20% active; lactate: $t = 2.56$, $p < 0.05$; pH: $t = -2.41$, $p < 0.05$).

S. cubensis that had a time of death after 120 min post-capture were significantly larger (late: 61.99 ± 3.39 cm) compared to those that had a time of death before 120 min post-capture (early: 50.32 ± 3.56 cm; Mann-Whitney *U*-test, $p < 0.05$). No other variables (e.g. enclosure depth, blood chemistry metrics) could differentiate between groups of sharks with early and late times of death.

Post-release behavior: *Centrophorus* sp.

While only 1 *Centrophorus* sp. survived the entire 24 h caging period, some individuals did survive for multiple hours after capture and were monitored for post-release behavior. None of these sharks, including the individual that survived, exhibited correct orientation or regular, sustained swimming behaviors. Instead, even while alive, they hovered inverted while respiring primarily through their spiracles and only moved with very brief (<5 s), irregular, slow tail movements (Fig. 4). These periods of activity were often the result of scavenging isopods climbing onto an animal and eliciting a twitch or single tail beat. The mean time of death was 260 ± 65.6 min post-capture for this species.

DISCUSSION

Although PRM rates have been estimated for multiple shark species captured in coastal waters (e.g. Heupel & Simpfendorfer 2002, Hueter et al. 2006), this is one of the first studies to estimate a PRM rate for any deep-sea shark despite their prevalence as fisheries bycatch (Cotton & Grubbs 2015). We found
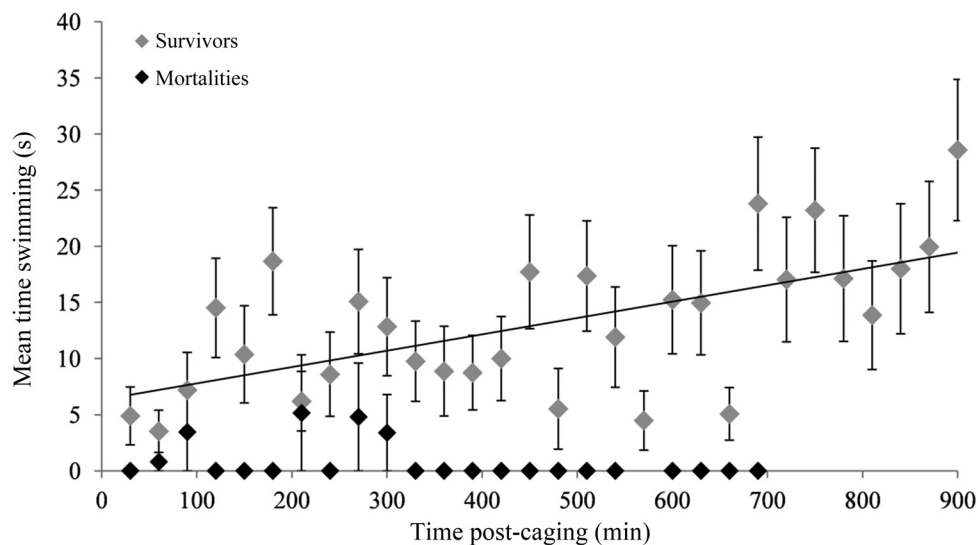

Fig. 6. *Squalus cubensis* mean time swimming (calculated for the first minute of each video segment only) during the first 900 min following enclosure deployment by post-release fate. Mean time swimming of survivors increased significantly with duration in the enclosure ($r^2 = 0.37$, $p < 0.01$)
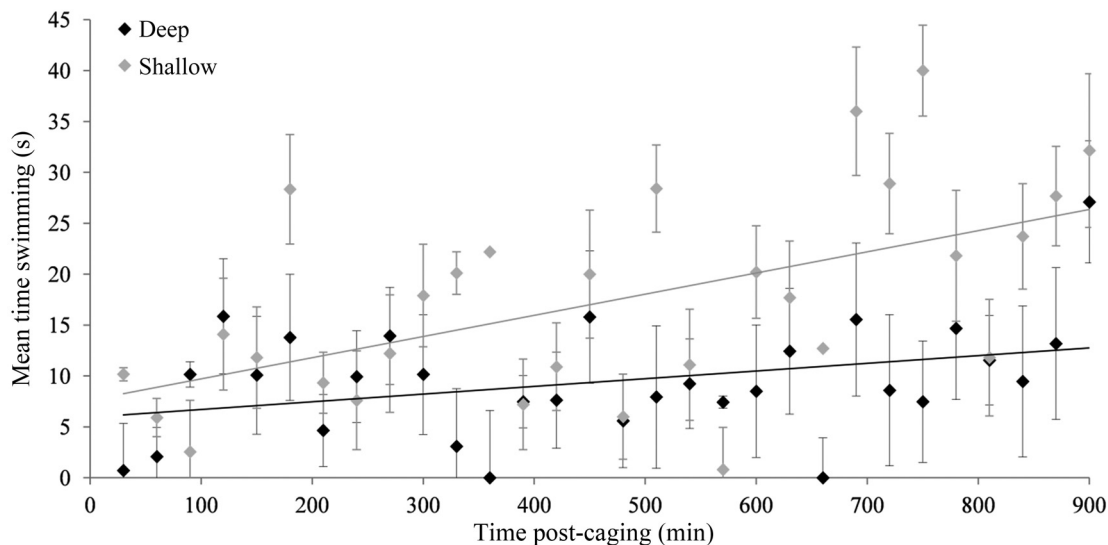
Fig. 7. *Squalus cubensis* mean time swimming (calculated for the first minute of each video segment only) for those that survived in either shallow (<625 m) or deep (>625 m) enclosures during the first 900 min following deployment. Mean time swimming increased significantly over time for both shallow and deep groups of survivors (shallow: $r^2 = 0.30$, $p < 0.05$; deep: $r^2 = 0.12$, $p = 0.05$), and the rate of increase was marginally higher for the sharks in shallow enclosures (ANCOVA interaction term, $p = 0.06$)

that even following short soak times (up to 3.5 h), PRM rates for longline-caught deep-sea sharks were high, ranging from 49.7 to 83%.

At-vessel and post-release mortality

At-vessel mortality rates reported here are nearly identical to those reported by Brooks et al. (2015) at the same study site for *Squalus cubensis* (9%), *Centrophorus* sp. (29%), and *Hexanchus griseus* (0%), although we documented higher rates of mortality for *Hexanchus nakamurai* (16% here vs. 7% previously) and *Mustelus canis insularis* (7% here vs. 0% previously). These slight discrepancies are probably due to low catch rates for these species, as longline protocols were similar. Hale et al. (2010) reported slightly lower at-vessel mortality rates for *S. cubensis* (2.9%) in the bottom longline fishery targeting sharks in the Gulf of Mexico, whereas Gulak et al. (2013) reported a 9 and 4.6% dead discard rate for this species in the deepwater reef fish and tilefish bottom longline fisheries, respectively, in that region.

While our PRM estimate for *S. cubensis* (49.7%) excludes mortality past 24 h, the majority of PRM seems to occur rapidly following release, with roughly 60% of both *Centrophorus* sp. and *S. cubensis* mortality occurring within 200 min post-capture. Further, post-release behavioral data show that *S. cubensis* swimming activity increased within our observation

period, implying some degree of recovery. Research on teleosts, however, has shown that mortality can take place weeks post-capture (Davis & Olla 2001), although as time elapses it becomes increasingly difficult to distinguish capture-induced mortality from other sources.

Our data also suggest that PRM rates for *Centrophorus* sp. are high (83%) and agree with previous satellite telemetry data from *Centrophorus* sp. released from longline gear, where 8 out of 11 tags did not report and 3 suggested immediate predation in a study at the same subtropical location (Brooks et al. 2015). Conversely, Daley et al. (2015) reported extremely high survivorship for longline-caught *C. zeehani* in temperate waters in southern Australia. An important note on these discrepancies is that animals in Daley et al. (2015) were captured with the intent to maximize survivorship by fishing during cool winter nights (sea surface temperatures between 15 and 25°C), whereas both this study and Brooks et al. (2015) took place when sea surface temperatures reached 30°C during the day. Interestingly, *Centrophorus* sp. in both our study and those in southern Australia responded to caging by hovering upside down during the post-release monitoring period (R. K. Daley pers. comm.). However, when released without an enclosure in the cooler surface waters of southern Australia, *Centrophorus* sp. swam away with little apparent behavioral impairment (R. K. Daley pers. comm.), whereas those in warmer

Bahamian waters exhibited little movement upon release at the surface. As such, temperature and/or enclosure effects on this species group could be substantial, although what causes these sharks to lose their ability to orient is unknown. One potential mechanism could be related to the high oil content of *Centrophorus* livers (Deprez et al. 1990), as liver oil can be sensitive to changes in pressure (Phleger 1998, Pethybridge et al. 2010, Daley et al. 2015).

Impaired swimming behavior in *Centrophorus* sp., *S. cubensis* and *H. nakamurai* released at the surface suggests that post-release predation could be high for deep-sea sharks, particularly when considering the propensity for pelagic sharks to circle the longline during retrieval, a common occurrence in commercial fisheries (Stevens et al. 2000, Raby et al. 2014). Post-release predation was observed for 2 *S. cubensis*: one released at the surface, which was eaten by a silky shark *Carcharhinus falciformis* as it approached 130 m (as determined by a trailing TDR; B. Talwar unpubl. data) and one that was attacked by a giant isopod *Bathynomus giganteus* while in the enclosure at depth (Fig. 4). The attacked shark was resting on the bottom in seemingly good condition; it vigorously tried to detach itself from the isopod without success. Predators and scavengers were also observed during video monitoring at the seafloor, including *H. griseus* and unidentified deep-sea groupers which attempted to access the penned occupants. Ultimately, post-release predation could inflate the experimentally derived PRM rates reported here.

Sub-lethal effects of capture

Our data show that post-release swimming activity increased over time for *S. cubensis*, and that the rate of increase was slower at deeper depths, presumably due to lower metabolic rates associated with colder temperatures (up to a 6°C difference between shallow and deep enclosures). Similarly, TOFS was significantly later. It is possible that with a depressed metabolic rate, the return to physiological homeostasis could be delayed at deeper depths (Skomal & Mandelman 2012).

Post-release swimming activity of *S. cubensis* was lower in individuals with higher at-vessel blood lactate levels and lower pH levels, and TOFS was later (>120 min) for sharks with significantly higher at-vessel blood glucose levels. Lactate accumulation as a result of exhaustive exercise (Skomal & Bernal 2010) can contribute to high levels of stress, blood

acidosis, and/or mortality (Frick et al. 2010, Danylchuk et al. 2014, Gallagher et al. 2014b, Hutchinson et al. 2015), while elevated blood glucose is a common response to capture stress as hormones mobilize hepatic glycogen to fuel active muscle tissue (Hoffmayer & Parsons 2001, Mandelman & Farrington 2007, Skomal & Bernal 2010). These disturbances can be related to long fight times and on-hook fight behaviors which can affect post-release recovery and predator evasion (Olla et al. 1992, 1995, Ryer 2004, Wilson et al. 2014), as evidenced by the behavioral impairments seen here.

Predicting post-release mortality: *S. cubensis*

Incorporating cryptic discard mortality into total fishery mortality estimates is of vital importance to fisheries management, but direct estimation of PRM across fisheries is often unrealistic. Instead, predicting PRM with indirect methods can be more practical. While Renshaw et al. (2012) highlight the limitations of blood chemistry in forecasting long-term discard mortality in elasmobranchs, other studies have successfully used both blood chemistry (Moyes et al. 2006, Skomal 2006, 2007, Heberer et al. 2010, Gallagher et al. 2014b, Hutchinson et al. 2015) and vitality scores (Manire et al. 2001, Hueter et al. 2006) to predict PRM in sharks and teleost fishes. While physical injury should be incorporated into future models (Renshaw et al. 2012), it was very rare in this study and thus injured animals were omitted. The predictive models reported here should prove useful for capture scenarios other than our own as blood chemistry and vitality scores can reflect the magnitude of stress experienced by an individual regardless of the type of stressor. Further, these methods can be applied in a field setting rapidly and cost effectively by fishery observers or others (Benoît et al. 2010, Stoot et al. 2014).

Our first predictive model of *S. cubensis* PRM included total length, at-vessel blood lactate, and at-vessel blood glucose concentrations. This model showed that the probability of 24 h PRM increased with higher lactate levels, lower blood glucose levels, and lower total lengths, and identified a greater than 50% probability of mortality at blood lactate concentrations exceeding 10.5 mmol l^{-1} and blood glucose concentrations below 4 mmol l^{-1} for an individual of average total length (58 cm). For comparison, lactate concentrations for moribund sharks have been reported between 15 and 20 mmol l^{-1} for blue *Prionace glauca*, thresher *Alopias vulpinus*, and shortfin

mako *Isurus oxyrinchus* sharks (Hight et al. 2007), and over 10.2 mmol l^{-1} for moribund gulper *Centrophorus* sp. sharks (B. Talwar unpubl. data) while unstressed values are typically less than 5 mmol l^{-1} (Cliff & Thurman 1984, Spargo 2001, Mandelman & Farrington 2007). Although lactate is often predictive of mortality (Moyes et al. 2006, Hight et al. 2007, Marshall et al. 2012, Hutchinson et al. 2015), it is unlikely to be the singular cause of death in stressed sharks (Wood et al. 1983, Frick et al. 2010), and its value as a predictor of PRM is likely species-specific (Renshaw et al. 2012).

The effect of total length (the second significant predictor in this model) could be related to a size-specific ability to cope with physiological insults and/or related to a reduction in fight intensity in larger sharks, ultimately reducing the chances of mortality. Other studies have indeed shown that the probability of mortality is lower for large size classes of discards (Neilson et al. 1989, Sangster et al. 1996, Milliken et al. 1999, Davis 2002), although Morgan & Carlson (2010) documented the opposite relationship for sandbar *Carcharhinus plumbeus* sharks. Large size could also act as a thermal buffer to the drastic temperature changes experienced by a deep-sea shark during capture (over 15°C here). The core temperature of smaller sharks warms faster than large sharks, leading to greater thermal stress, as seen in some teleosts (Davis et al. 2001, Davis & Olla 2001, Davis 2002). While this study did not establish a link between thermal stress and mortality, previous studies have for marine fishes (Muoneke & Childress 1994, Davis & Olla 2001), and the effects of temperature change on deepwater sharks deserves further research.

Blood glucose levels had a smaller effect than either total length or blood lactate in this predictive model, where lower glucose levels resulted in a higher likelihood of mortality. As mentioned previously, glucose levels may increase with prolonged stress (Skomal & Bernal 2010, Skomal & Mandelman 2012, Marshall et al. 2012), and as such higher glucose levels may be predictive of mortality, contrary to our model's predictions. Other studies do agree with the relationship reported here, however (e.g. Cliff & Thurman 1984, Marshall et al. 2012).

Vitality scores also predicted mortality for *S. cubensis* although scores of release condition are very rough and can be subjective (Benoît et al. 2010). They are shown here to relate with blood chemistry (Hyatt et al. 2016), although there was overlap between pH and lactate levels across 'excellent' and 'poor' groupings. This overlap suggests that these

scores indeed reflect more than just the blood chemistry metrics analyzed here. Reflex impairment indices may be a better choice to provide an indirect method (Benoît et al. 2015) for predicting PRM in the future (as in Braccini et al. 2012, Danylchuk et al. 2014, Gallagher et al. 2014b).

Limitations

Post-release enclosures are commonly used to estimate PRM in a field setting (Mandelman & Farrington 2007, Stewart 2008, Mandelman et al. 2013, Weltersbach & Strehlow 2013, Campbell et al. 2014), although their semi-artificial holding conditions do not mimic true post-release conditions (e.g. exclusion of predators, altered descent rate; Weltersbach & Strehlow 2013, Shipley et al. 2017). Enclosures can also impart additive stress and/or cause physical injury, although in our study we saw no evidence of either. We also found no effect of enclosure density on mortality in exploratory GLMs, and our circular enclosure design allowed for sharks to swim continuously. Including control groups to separate out the effects of caging from capture and release could alleviate some of these concerns (Pollock & Pine 2007, Weltersbach & Strehlow 2013), but would have been impossible for this study given the constraints of working in deep water.

The PRM rates reported here could also be underestimated due to differences in handling practices between our study and those in a commercial setting. As *S. cubensis* and *Centrophorus* sp. have dorsal fin spines, fishers often discard them immediately to avoid personal injury, but in doing so they sometimes break an animal's jaw during the de-hooking process (S. Gulak pers. comm.). Although we tried to mimic commercial sorting practices by limiting air exposure and releasing animals quickly, we intentionally minimized animal injury by removing hooks by hand.

CONCLUSIONS

Considering the current trends for fishing deeper (Morato et al. 2006), the magnitude of commercial discards worldwide (estimated at 25% of total catches; Pascoe 1997, Davis 2002, Kelleher 2005), and the disproportionate contribution of elasmobranchs to these figures (Molina & Cooke 2012, James et al. 2016), data deficient and highly vulnerable deep-sea sharks are likely at greater risk for bycatch-induced population declines than ever

before, particularly when considering the high PRM rates reported here. Incorporating predicted or estimated PRM rates into total fishery mortality estimates is recommended to improve the management of commonly discarded deep-sea sharks.

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