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At-vessel mortality and blood biochemical status of elasmobranchs caught in an Australian commercial longline fishery

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ABSTRACT

This study investigates mortality of sharks in a commercial longline fishery in Australia. To examine the rate and biological, environmental and technological factors contributing to at-vessel mortality, four setlines with 120 gangions possessing 'hook timers' were deployed daily (for 7h and 14h) using conventional gears from two commercial fishing vessels during 2013. A total of 689 animals across 22 species and including 18 elasmobranchs were landed. For the five species (*Carcharhinus* spp.), and one genus (*Sphyrna* spp) where there were sufficient numbers for analysis, generalised linear mixed models showed that species and the elapsed time spent on the line after hooking were the strongest predictors of at-vessel mortality, with spinner (*Carcharhinus brevipinna*), blacktip (*C. limbatus*) and hammerhead (*Sphyrna* spp) sharks exhibiting the highest death rates. The variables which best explained mortality, included: (i) sex of the caught sharks, and the interaction between species with (ii) capture depth, and (iii) the elapsed time spent on the line after hooking. For the subset of dusky (*C. obscurus*) and sandbar (*C. plumbeus*) sharks examined for physiological status at the point of capture, very few of the 13 chosen blood analytes varied significantly. Given the observed high mortality rates and stress associated with the time spent on the line after capture, operational changes to reduce these adverse impacts should be considered. Even simple changes such as shorter soak times could considerably mitigate these impacts.

1. Introduction

Globally, commercial fisheries are managed by (i) input controls such as gear restrictions and spatial or temporal closures to reduce the rates of exploitation, and (ii) output controls such as legal sizes and quotas, which permit effort to be maintained through the assumption of few impacts to released individuals (Kelleher, 2005). For sharks, the need to validate

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that assumption on a species-specific basis has seen an expanding field of research over the last decade to quantify physical trauma, physiological change and mortality associated with their capture (Skomal, 2007). Recently, many studies have also looked at gear and handling techniques that reduce negative impacts (i.e. capture, damage or stress) in these fisheries (Favaro and Côté, 2013; AFMA, 2014).

Global recognition of the need to comprehensively assess the mortality of sharks caught on commercial fishing gears has inspired many recent studies to address this issue (e.g. Beerkircher et al., 2002, Morgan and Burgess, 2007, Mandelman and Skomal, 2009, Macbeth et al., 2009, Marshall et al., 2012 and Gallagher et al., 2014a). Most of these studies examined 'at vessel' mortality and sub-lethal impacts, along with methods by which such impacts might be ameliorated. The general trends indicated that mortality rates were species specific and varied, ranging from 3% for tiger shark (*Galeocerdo cuvier*) to 100% in common blacktip (*Carcharhinus limbatus*), spinner (*C. brevipinna*), smooth hammerhead (*Sphyrna zygaena*) and scalloped hammerhead (*S. lewini*) sharks. More recently, the use of 'hook timers' has provided definitive measurements of the actual time of capture (Broadhurst et al., 2014) and, more importantly, provided evidence for the species-specific relationship between mortality and physiological changes associated with time spent on the line after initial hooking (Morgan and Carlson, 2010; Brooks et al., 2012).

While acute (i.e. immediate) mortality during capture is more easily quantified and applied to management, marine animals that are released alive after capture may experience latent sublethal consequences that negatively affect individuals and populations (Wilson et al., 2014). In fish, physiological effects from capture can progress to more chronic or whole-animal consequences (Skomal and Mandelman, 2012), such as impaired immune function (e.g. Lupes et al., 2006) and/or elevated predation risk (e.g. Raby et al., 2013). It is well established that sharks, like other fish, respond to the acute stressors of capture through a series of biochemical and physiological processes that manifest as measurable changes to their blood chemistry (Skomal and Bernal, 2010). Measuring the blood chemical status at the point of capture can therefore offer important insights into the relative interspecific and intraspecific responses to capture, as well as the influences of various other biological, physical and fishing/handling variables that might help explain any observed differences (Skomal and Mandelman, 2012). In turn, such data can help reveal strategies to attenuate stress and injury from capture, and provide valuable information for the purpose of ecological risk assessment in sharks (Gallagher et al., 2012). However, physiological responses to capture stressors appear to range widely between different species of shark, even varying between congeners, with various capture and handling factors also playing roles (e.g. Manire et al., 2001, Mandelman and Skomal, 2009, Marshall et al., 2012 and Gallagher et al., 2014b).

Similar to the international concerns for commercial fisheries targeting large sharks, there is alarm over the capture of sharks in the Ocean Trap and Line Fishery (OTLF) off New South Wales, Australia, (Macbeth et al., 2009). Historically, sharks formed a significant component of the OTLF, with the average annual catch of all shark species combined estimated at 173 t for years between 1998/99 and 2003/04 (Macbeth et al., 2009). However, the annual shark catch then increased, peaking at 457 t in 2005/06 (representing a ∼200% increase in two years), mainly due to an increase in fishers targeting 'large' sharks including bronze whaler (*C. brachyurus*), common blacktip, dusky (*C. obscurus*), sandbar (*C. plumbeus*), spinner and tiger sharks (Macbeth et al., 2009). Currently fishers are permitted to use up to 1200 hooks per day with a 500 kg (headed and gutted) weekly limit and a total allowable combined catch of 160 mt for large shark species (i.e. carcharhinids) (Macbeth et al., 2009). To prevent finning, all shark carcasses must brought to shore with the fins attached (Fischer et al., 2012).

Although there was grave concern that the annual catches of large sharks in the OTLF fishery may have been unsustainable, of equal concern was the high mortality rates measured for many of the targeted species and the consequences of output controls (such as the current weekly limits) to limit landed catches (Macbeth et al., 2009). Since that study, some of the species found to be targeted in the large shark fishery, such as great hammerhead (*S. mokarran*) and scalloped hammerhead, have been listed as threatened, endangered or protected (TEP) sharks under New South Wales (NSW) government legislation (NSW Government—part 7a, Fisheries Management Act, 1994). This listing highlights the requirement to ensure all possible measures are adapted to increase successful release of species that are incidentally caught or unwanted.

In any study that seeks to provide a comprehensive assessment of the fate of captured animals, it is desirable that in addition to quantifying mortalities (i.e. retained animals and those discarded dead), adequate measures of stress are recorded among survivors to assess the full extent of impacts that could result in delayed mortality, impaired welfare, or reduced fitness. Furthermore, this study uses 'hook timers' to enhance the accuracy of information relating to each shark. Based on this logic, our aims were to quantify (i) mortality and damage to all shark species, and (ii) the physiological responses of dusky and sandbar sharks (as representative species for carcharhinid sharks regularly targeted by commercial shark fishers worldwide) immediately following capture (i.e. hooking) on commercial longlines. This information will aid in determining which technical, environmental or biological factors contribute to mortality, damage and stress in carcharhinid species and will ultimately result in management outcomes that reduce the environmental impact of commercial fisheries targeting large sharks.

2. Methods

The research was completed during 17 daily fishing trips on board two commercial demersal longline vessels (14 and 19 m, respectively) off NSW, Australia in 2013. All sampling was opportunistically done within the spatial (Nambucca Heads —30°34′S 153°13′E and Wooli —29°56′S 153°26′E) and temporal ranges (January to July) of the northern NSW shark longline fishery (described by Macbeth et al., 2009).

2.1. Animal collection and fishing gear

The longline comprised a 9600 m, 3.2 mm diameter (Ø) monofilament polyamide (PA) mainline, separated into four 2400 m sections (termed 'lines') by weights (30 kg), and ropes (8 mm Ø, polypropylene) leading to floats (30 mm Ø; Broadhurst et al., 2014). Each of the four lines had 120 gangions (attached ∼20 m apart), each comprising a stainless-steel clip rigged with 3.6 m of 3.2 mm Ømonofilament PA separated with a 70 mm, 60 g swivel and terminating in a 16/0 stainless-steel, non-offset circle hook. All hooks were baited either with 0.3 kg of sea mullet (*Mugil cephalus*) or eastern Australian salmon (*Arripis trutta*). To determine the time spent on the line after hooking, each gangion was also fitted with a hook timer (HT 600, Lindgren-Pitman Inc.—following Sigler, 2000), which was activated when >4.53 kg of pressure was exerted on the hook (Broadhurst et al., 2014). To maintain bottom contact, weights (6–8 kg) were secured to the mainline between every 10 gangions. Eight water temperature (°C) loggers (Vemco Ltd, Nova Scotia, Canada) were attached to the mainline, along with one to the surface floats at each end of the longline, and set to record every 30 min.

Longlines were deployed on the seabed in depths of 50–100 m (∼3–10 nm offshore) between 1930 and 2330 on each of the 17 fishing days composing the study. To increase the probability of obtaining a range of hooking durations recorded by the hook timers, retrieval of the first two lines set (240 hooks) commenced after a minimum of 7 h deployment while retrieval of the remaining two lines (240 hooks) commenced after 14 h. During retrieval, data pertaining to each hook timer was recorded (line and hook number and time) as it came on board, irrespective of whether an animal was caught on its associated hook. Prior to on-board processing or release, all hooked animals were either brought on board or alongside the vessel, where their species, total length (TL to the nearest cm; or for sea turtles their curved carapace length—CCL), sex, and status (alive or dead) were recorded. In the case of each animal assessed, a condition index score for the likelihood of post-capture survival was estimated for each of four condition categories. These categories were (i) activity and stimuli, (ii) wounds and bleeding, (iii) sea lice, and, (iv) skin damage and bruising (Braccini et al., 2012). The condition index score for each category was selected from four classifications: high (1.00), moderate (0.66), low (0.33) or nil (0.00) likelihood of post-capture survival. Blood samples were collected from a subset of dusky and sandbar sharks caught (Section 2.2). Other technical and environmental data collected for each longline deployment included the date, times hooks were set and retrieved (to provide 'deployment duration'), GPS location and bottom depth, along with a range of other environmental variables (refer to Section 2.3).

2.2. Blood collection and analyses

To quantify the physiological stress response, 23 dusky and 42 sandbar sharks (of various sizes and sexes, and alive upon retrieval) were sampled for whole blood (∼8 ml) by caudal venipuncture using a 90 mm, 18 gauge needle and a 10 ml syringe, within 1 min of being brought onto the deck. Within 30 s of blood extraction from a shark, a subsample of approximately 10 μL of whole blood was placed into a hand-held 'Accutrend plus' field machine (Roche Diagnostics, Australia) to test for glucose (range of 1.1–33.3 mmol l^{-1}) and lactate (range of 0.8–22.0 mmol l^{-1}) (Wells and Pankhurst, 1999; Awruch et al., 2011). The remaining blood was transferred to a disposable 8 ml plasma separator tube containing lithium heparin (BD Vacutainer) and stored on wet ice for up to 6 h. Following this temporary storage the blood sample was centrifuged (at 5000 rpm for 5 min) and the plasma transferred into three 2-ml vials and frozen onboard at −15 °C. All frozen samples were transferred to a freezer (−80 °C) back at the laboratory before being analysed within seven days (see below) to minimise potential for change in blood biochemistry (Barton, 2002). The plasma samples were analysed at IDEXX laboratories (Brisbane, Australia) using a Beckman Coulter AU680 automated system for alkaline phosphatase – ALP (IU l^{-1}), aspartate aminotransferase – AST (IU l^{-1}), calcium (mmol l^{-1}), chloride (mmol l^{-1}), creatine kinase (IU l^{-1}), magnesium (mmol l^{-1}), phosphate (mmol l^{-1}), potassium (mmol l^{-1}), sodium (mmol l^{-1}), total protein (g l^{-1}) and urea (mmol l^{-1}).

2.3. Data and statistical analyses

Most of the general results describing the key biological (e.g. species, sex, size—TL, percentage sexually mature), environmental (e.g. water temperature, depth, moon phase) and technical (e.g. actual time of capture and total caught) factors relating to the actual capture of these animals are published in Broadhurst et al. (2014). This current paper, however, focuses directly on mortality, damage and any physiological changes attributable to hooking and the varying durations each animal spent on the line. For the mortality data, species with a sample size of ≤10 were used to describe the fishery but were excluded from any further statistical analysis. An exception to this were hammerhead sharks (scalloped, smooth and great hammerhead), as it was assumed that, in terms of their survival and relationships with any explanatory variables, the three species could be included as one at their genus level.

The first approach for analysis of the survival data used a generalised linear mixed model (GLMM) that incorporated terms that were commensurate with the experimental design. These terms included the fixed effects of 'treatment' (i.e. 7 h/14 h deployment), 'species' and their interaction, along with random effects for 'day' and the nested interactions of 'treatment and day' and 'day and line'.

The second approach involved fitting a number of GLMMs aimed at determining the key variables affecting mortality (aim #1) and each of the blood parameters (aim #2). These analyses included the random effect of day and fixed effects for species,

Table 1
Scientific and common names, total numbers caught, total length or curved carapace length (mean ± SD cm—TL/CCL), and minimum (min.) and maximum (max.) times (h:m—from on the hook timers) that animals were found alive or dead on the line after initial hooking for all species caught over the 17 days. '–' no data.

Scientific name	Common name	No	TL/CCL	Alive		Dead	
				min.	max.	min.	max.
Elasmobranchs							
Aptychotrema rostrata	Eastern shovelnose ray	2	75 ± 7	–	–	–	–
Carcharhinus plumbeus	Sandbar shark	160	191 ± 27	0:53	18:56	2:59	20:23
C. limbatus	Common blacktip shark	113	197 ± 31	0:25	6:18	1:18	19:00
C. obscurus	Dusky shark	74	310 ± 71	1:33	18:12	3:27	19:37
C. brevipinna	Spinner shark	50	206 ± 59	1:10	2:33	3:15	16:44
C. brachyurus	Bronze whaler shark	6	259 ± 42	6:15	15:45	5:34	14:27
C. leucas	Bull shark	1	311	14:10	14:10	–	–
Carcharias taurus	Grey nurse shark	12	236 ± 51	3:31	12:07	–	–
Dasyatis brevicaudata	Smooth stingray	18	173 ± 55	1:32	14:15	–	–
Galeocerdo cuvier	Tiger shark	123	185 ± 50	0:01	17:15	3:02	13:12
Mustelus antarcticus	Gummy shark	22	98 ± 12	–	–	–	–
Orectolobus maculatus	Spotted wobbegong	10	122 ± 22	–	–	–	–
O. ornatus	Ornate wobbegong	5	108 ± 18	–	–	–	–
O. halei	Banded wobbegong	3	134 ± 51	–	–	–	–
Rhynchobatus australiae	White-spotted guitarfish	8	203 ± 20	7:54	14:25	9:59	9:59
Sphyrna lewini	Scalloped hammerhead	52	182 ± 31	0:14	2:00	1:20	16:56
S. zygaena	Smooth hammerhead	2	173 ± 18	–	–	6:56	16:10
S. mokarran	Great hammerhead	11	302 ± 30	–	–	5:47	14:06
Teleosts							
Neoarius graeffei	Blue catfish	3	–	–	–	–	–
Pagrus auratus	Pink snapper	1	83	–	–	–	–
Rachycentron canadum	Cobia	7	97 ± 13	2:24	3:15	6:58	10:24
Reptiles							
Caretta caretta	Loggerhead turtle	1	100	–	–	–	–

along with a number of environmental and biological variables and first order interactions between species and each of the environmental variables. Specifically, the variables included were hooking depth (m), sea height (m), wind (kn), surface current speed (kn), surface current direction, moon phase and percentage visible, surface and bottom water temperature (°C), air temperature (°C), hooking duration (h:min), TL (cm), sex and the condition index score for 'wounds and bleeding'. Bottom water temperature was converted to a factor version (i.e. categories), with level one for those sharks caught in less than 20° and level two otherwise, due to high bimodality of the original data. Sea swell was highly confounded with sea height and hence not considered in the analyses, while condition index scores for 'activity and stimuli' were confounded within status (dead/alive) and therefore not appropriate as an explanatory variable. Lastly, the 'presence of lice' and 'skin damage and bruising' had insufficient range to be included in the analyses.

The third model contained only informative terms (i.e. those achieving statistical significance or obeying marginality) and was obtained using a backward elimination process with two linked stages: elimination of non-significant interactions and then main effects. A conservative threshold of $p = 0.05$ was used for both stages to determine the minimal interaction and main effect model.

All models were fitted using the ASReml-R package (Butler et al., 2009) within the R statistical environment (R Core Team, 2012). All GLMMs were fitted with a logit link. Inferences concerning fixed effects for the first approach were undertaken using a pseudo Wald-type test based on the asymptotic distribution of the Wald pivot computed for each model term in the GLMM. In the second group of analyses, since the penalised quasi-likelihood estimate of the variance component for the only random effect was fitted and a generalised linear model (GLM) used, model selection for the fixed effects was undertaken using the asymptotic distribution of the change in deviance (McCullagh and Nelder, 1994). For some blood variables the relationship between the response variable and duration of hooking was considered on the log-linear or log–log scale.

3. Results

Six hundred and eighty-four individuals encompassing 22 species (18 elasmobranch, three teleost and one reptile species) were caught from 8160 hook deployments (8.3 individuals per 100 hooks) over the 17 days of fishing (Table 1). Hooks were deployed across a variety (mean ± SD, range) of depths (67.8 ± 10.7 m, 50–105 m), water temperatures (surface: 24.2 ± 1.0 °C, 22.5–25.0 °C; bottom: 20.6 ± 3.3, 16.4–21.5 °C), water currents (0.9 ± 0.5 kn, 0.3–2.0 kn), seas (0.7 ± 0.2 m, 0.5–2.0 m), swells (0.8 ± 0.5 m, 0.5–2.0 m) and moon phases (waxing and waning).

Condition indices for the probability of survival for (i) wounds and bleeding (mean ± SE of 0.98 ± 0.01), (ii) skin damage and bruising (0.98 ± 0.01), and (iii) damage from lice (0.99 ± 0.00)were generally high for all individuals (combined). Specifically, only six animals (0.8% of all individuals) representing four shark species (dusky, sandbar, scalloped hammerhead and spinner sharks) had any signs of damage from lice, while 2.6% (19 individuals from eight species) had skin damage and

Table 2
Scientific and common names and mean condition index scores (based on Braccini et al., 2012) as (i) activity and stimuli, (ii) wounds and bleeding and (iii) skin damage and bruising and % survival after the 7 or 14 h deployments for all species caught over the 17 days. '–' no data. Condition index scores for the likely hood of post-capture survival are classified as high (1.000), moderate (0.666), low (0.333) or nil (0.00).

Scientific name	Common name	Activity and stimuli	Wounds and bleeding	Skin damage and bruising	Survival (%)	
					7 h	14 h
Elasmobranchs						
Aptychotrema rostrata	Eastern shovelnose ray	1.000	1.000	1.000	–	100
Carcharhinus plumbeus	Sandbar shark	0.502	0.975	0.975	57.0	37.3
C. limbatus	Common blacktip shark	0.088	0.980	0.980	14	4.5
C. obscurus	Dusky shark	0.369	0.954	0.968	46.7	20.5
C. brevipinna	Spinner shark	0.047	0.946	0.973	5.56	3.1
C. brachyurus	Bronze whaler shark	0.333	0.777	0.888	–	33.3
C. leucas	Bull shark	0.660	1.000	1.000	–	100
Carcharias taurus	Grey nurse shark	1.000	1.000	1.000	100	100
Dasyatis brevicaudata	Smooth stingray	1.000	1.000	1.000	100	100
Galeocerdo cuvier	Tiger shark	0.946	0.970	0.995	95.7	93.4
Mustelus antarcticus	Gummy shark	0.773	1.000	1.000	75	80
Orectolobus maculatus	Spotted wobbegong	1.000	1.000	1.000	100	100
O. ornatus	Ornate wobbegong	1.000	1.000	1.000	100	100
O. halei	Banded wobbegong	1.000	1.000	1.000	100	100
Rhynchobatus australiae	White-spotted guitarfish	0.833	1.000	1.000	100	75
Sphyrna lewini	Scalloped hammerhead	0.096	0.928	0.961	12.5	9.9
S. zygaena	Smooth hammerhead	0.000	1.000	1.000	0	0
S. mokarran	Great hammerhead	0.000	0.969	0.877	0	0
Teleosts						
Neoarius graeffei	Blue catfish	1.000	1.000	1.000	–	100
Pagrus auratus	Pink snapper	1.000	1.000	1.000	–	100
Rachycentron canadum	Cobia	0.571	1.000	1.000	50	60
Reptiles						
Caretta caretta	Loggerhead turtle	1.000	1.000	1.000	–	100

bruising and 6.4% (44 individuals from eight species) had wounds and bleeding (Table 2). In contrast, the mean condition index score for activity and stimuli across all individuals was 0.65 ± 0.08 (Table 2). Specifically, 55.0% of the captured animals were rated as having medium (11 individuals, score of 0.66), low (32 individuals, score of 0.33), or no (336 individuals, score of 0.00) activity or response to stimuli (Table 2). These values were highly correlated with status (i.e. dead—53.8%) and subsequently removed from any further models.

Mortality varied significantly overall, with individuals from only seven species of elasmobranchs – the three wobbegongs (*Orectolobus maculatus*, *O. ornatus* and *O. halei*), bull shark (*C. leucas*), grey nurse shark (*Carcharias taurus*), eastern shovelnose ray (*Aptychotrema rostrata*) and smooth stingray (*Dasyatis brevicaudata*) – all surviving the capture process (Table 2). There were seven species (common blacktip, dusky, grey nurse, sandbar, spinner, and tiger sharks and smooth stingray) and one genus (great-, smooth- and scalloped hammerheads combined) contributing sufficient data (>10 individuals) for inclusion in analyses to describe the factors influencing mortality. Non-target species grey nurse shark and smooth stingray were removed from the models as they all survived being on the line for between 3.5 and 12.0 h and between 1.5 and 14.3 h respectively (Table 1). For the remaining six species/groups, the first model revealed highly significant main effects of treatment (GLMM, $p < 0.01$) and species (GLMM, $p < 0.01$) but not for their interaction (GLMM, $p = 0.85$). Specifically, the overall mortality rate was significantly lower in animals caught during the 7 h (46.6%) than the 14 h (58.4%) deployment irrespective of species, while mortality rates among species varied from 96.9% (spinner shark) to 5.7% (tiger shark).

The most parsimonious model to determine the key variables that influenced mortality included the main effect of sex (GLMM, $p < 0.01$) and interactions between species and hooking depth (GLMM, $p < 0.01$), and between species and elapsed time spent on the line after hooking (GLMM, $p < 0.01$). Specifically, log odds ratios revealed that mortality was 2.25 times more likely to occur in males than females, irrespective of species. For sandbar sharks, there was a significant and strong negative relationship between mortality and hooking depth, with the probability of mortality decreasing from approximately 69% at 50 m to 18% at 100 m (Fig. 1). Albeit lower overall, the probability of mortality in common blacktips decreased from 100% to 85% across their range of capture depths, especially below 70 m. In contrast, strong positive relationships between mortality and hooking depth existed for dusky and tiger sharks, with the probability of mortality increasing from 55% to 84% and one to 28% respectively, with increasing depth across their respective ranges of capture depths. The probability of mortality in spinner and hammerhead sharks was estimated at close to 100% across all capture depths (Fig. 1).

With the exception of eastern shovelnose rays, wobbegong and gummy sharks (which did not trip the hook timers) and smooth and great hammerheads (where none survived), individuals of all the remaining species survived at least 78 min after initial hooking (Table 1). The first signs of mortality occurred after approx. 1 h 20 min in common blacktip and scalloped

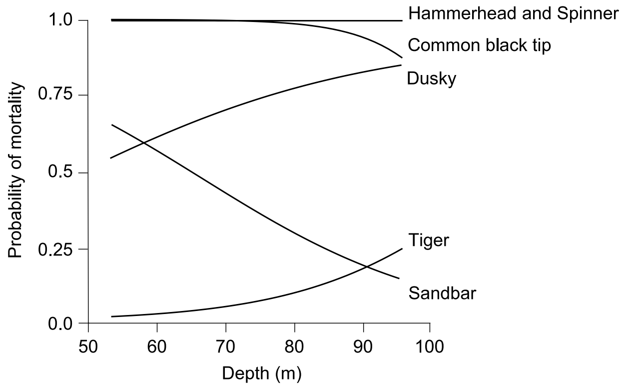

Fig. 1. Fitted lines from the GLMMs for the probability of mortality against depth (m) of capture for tiger ($n = 123$), sandbar ($n = 160$), dusky ($n = 74$), common blacktip ($n = 113$), spinner ($n = 50$) and hammerhead ($n = 65$) sharks that were caught over the 17 days of fishing.

Table 3
Descriptive results (means ± SE and range) of blood-chemistry variables for sandbar ($n = 42$) and dusky ($n = 23$) sharks after capture from demersal long lines off south-eastern Australia between January and July 2013.

Blood variable	Sandbar		Dusky	
	Mean (±SE)	Range	Mean (±SE)	Range
Sodium (mmol l^{-1})	291.8 ± 1.9	258–326	282.5 ± 2.0	251–295
Potassium (mmol l^{-1})	5.4 ± 0.3	2.5–10.4	6.3 ± 0.7	3.4–14.6
Chloride (mmol l^{-1})	258.0 ± 2.4	222–311	257.0 ± 3.4	215–278
Urea (mmol l^{-1})	324.2 ± 9.5	128.7–423.6	345.9 ± 15.1	258.2–578.2
Calcium (mmol l^{-1})	4.2 ± 0.1	3.6–7.1	3.8 ± 0.1	3.3–4.9
Magnesium (mmol l^{-1})	2.4 ± 0.2	1.4–8.5	2.2 ± 0.1	1.5–4.1
Lactate (mmol l^{-1})	16.1 ± 0.7	2.1–20.1	14.3 ± 1.1	2.3–19.4
Glucose (mmol l^{-1})	4.4 ± 0.3	1.7–12.6	5.9 ± 0.5	1.9–12.3
Phosphate (mmol l^{-1})	5.1 ± 0.4	1.9–11.8	4.0 ± 0.7	1.4–13.1
Total protein (g l^{-1})	29.3 ± 0.9	18–43	25.6 ± 1.3	16–35
Creatine Kinase (IU l^{-1})	62.1 ± 6.2	1–198	47.2 ± 5.3	1–97
ALP (IU l^{-1})	3.2 ± 0.2	1.5–7	3.9 ± 2.2	1.5–53
AST (IU l^{-1})	3.0 ± 1.0	1.5–41	8.4 ± 4.3	1.5–88

ALP—alkaline phosphatase; AST—aspartate aminotransferase; Phosphate—total inorganic phosphate; Calcium—unionised calcium. Potassium, calcium, magnesium, AST and phosphate were considered on the log-linear or log–log scale in each GLMM. Samples below the minimum detectable limits for ALP and AST were recorded as 50% of the lowest value.

hammerhead sharks and between approx. 3–6 h in most other species caught. Many individuals were, however, still alive up to 12–18 h after hooking, depending on species (Table 1). The significant interaction between species and time spent on the line after hooking with respect to influencing mortality is represented by hammerheads and tiger sharks as the two extremes. More specifically, a small proportion of the former showed relatively brief periods of survival following hooking, while the latter showed a high survival rate irrespective of the length of time on the hook (Fig. 2). Along with hammerhead sharks, the rates of survival of common blacktip and spinner sharks was very low for even relatively short (<3 h) periods following hooking and, with the exception of one common blacktip, all sharks from these species were dead within 5 h of being hooked. The time spent on the line had a less marked effect on mortality in the cases of dusky and sandbar sharks, although mortality rates did increase significantly 5–6 h following hooking for both species (Fig. 2).

Descriptive results (mean ± SE and ranges) of the thirteen blood variables collected from sandbar and dusky sharks are shown in Table 3. Very few of the environmental, biological and technical factors were significant in the most parsimonious GLMMs describing any differences (Fig. 3). However, the mean concentration of total protein was significantly higher in sandbar (29.3 ± 0.9 g l^{-1}) than dusky (25.6 ± 1.3) sharks (GLMM, $p < 0.05$). Although not particularly strong, there was a significant positive relationship between capture depth and aspirate aminotransferase (GLMM, $p < 0.05$, Fig. 3(A)), and between the elapsed time spent on the line after hooking and mean concentrations of potassium and lactate (GLMM, $p < 0.01$, Fig. 3(B) and (C)). In contrast, there was a negative relationship between hooking duration and mean concentration of chloride (GLMM, $p < 0.05$, Fig. 3(D)). Notably, all animals retained alive and quantified as having a low condition index score for activity and stimuli had mean potassium concentrations of >8.7 mmol l^{-1} (Fig. 3(C)).

4. Discussion

The species-specific variation in mortality and stress quantified during this study was similar to that recorded in many previous studies (Beerkircher et al., 2002; Morgan and Burgess, 2007; Macbeth et al., 2009; Brooks et al., 2012; Gallagher

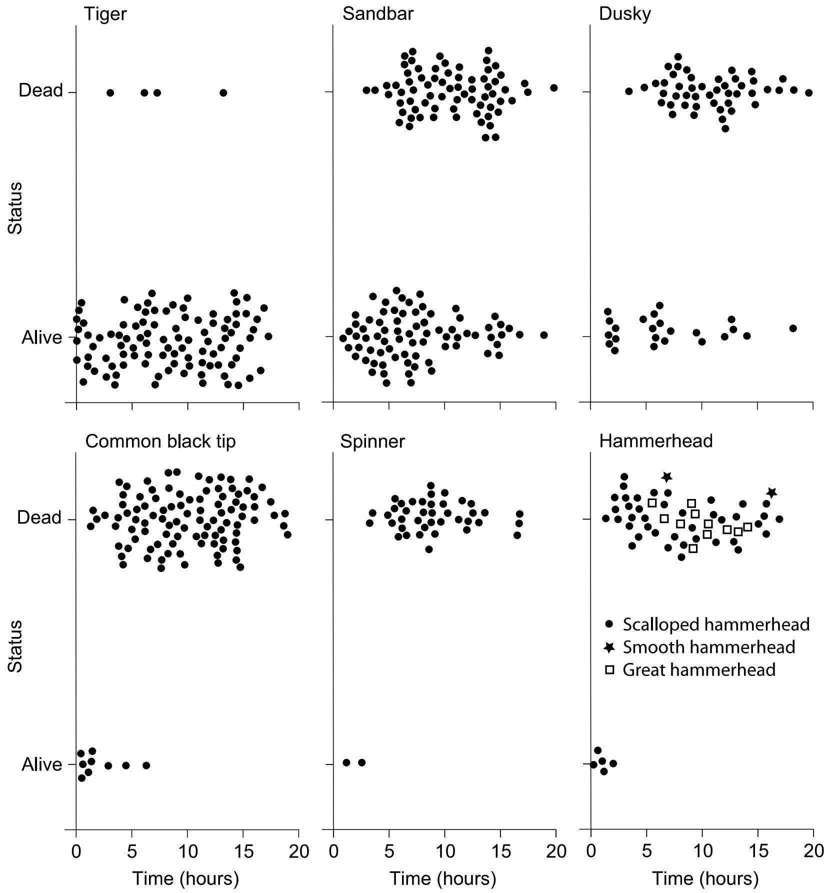

Fig. 2. Scatter plots of mortality and survival against the duration of time (h) spent on the line after initial hooking for tiger ($n = 123$), sandbar ($n = 160$), dusky ($n = 74$), common blacktip ($n = 113$), spinner ($n = 50$) and hammerhead (scalloped: $n = 52$, smooth: $n = 2$, and great: $n = 11$) sharks that were caught over the 17 days of fishing.

et al., 2014a). Although the long-term impact on physiological health and survivorship of sharks released is unknown, it is evident that a large proportion of the deaths during the capture process could be reduced via simple changes to address some of the significant causal effects, identified here as (i) sex, (ii) depth of capture, and (iii) duration of hooking. Although these changes may be unviable in the commercial fisheries environment, the potential benefits of any such changes can be discussed by considering the underlying mechanisms by which these key factors produced negative impacts, and their relative importance.

Very few animals exhibited signs of damage after capture, which is consistent with trends for many other species (Braccini et al., 2012). The relatively benign effects in the current fishery probably reflect the longline gear being used and lack of depredation on captured sharks. However, the assessment for 'activity and stimuli' was highly correlated with fate and explained by the time spent on the line after being hooked. For example, some species were relatively tolerant (e.g. all rays, wobbegongs and grey nurse sharks survived) or minimally affected (e.g. tiger shark) by capture, while others such as dusky and sandbar sharks started to die 4–5 h after hooking. This trend was also evident in Braccini et al. (2012), who indicated that increased soak times significantly decreased the post-capture survival score for over 25 chondrichthyan species. Of greatest concern in the current study is the susceptibility of hammerheads (scalloped, smooth and great), spinner and common blacktip sharks to mortality, with all individuals (with the exception of one common blacktip shark) dead within 5 h of capture. For all of these susceptible species, mortality started to occur after 60 min of being hooked. While similar trends and variability in mortality rates among species have been previously recorded in many other comparable studies, the hook timers used here recorded data concerning the temporal progression of any mortality in individual species and provided valuable additional information that many of those other studies lacked.

The contrasting differences among species in mortality rates of hooked sharks are potentially linked to differences in their ventilation morphology and physiology (Last and Stevens, 2009). Specifically, the ability of species such as grey nurse and wobbegong sharks to ventilate via buccal pumping, whereby water is drawn into the buccal cavity and passed over the gills probably contributed in part to their high survival rates, as they do not need to constantly swim (Carlson et al., 2004). By contrast, hammerheads, common blacktip and spinner sharks are obligate ram ventilators, requiring constant movement to push water through the buccal cavity and over their gills (Carlson et al., 2004). In addition to the injuries

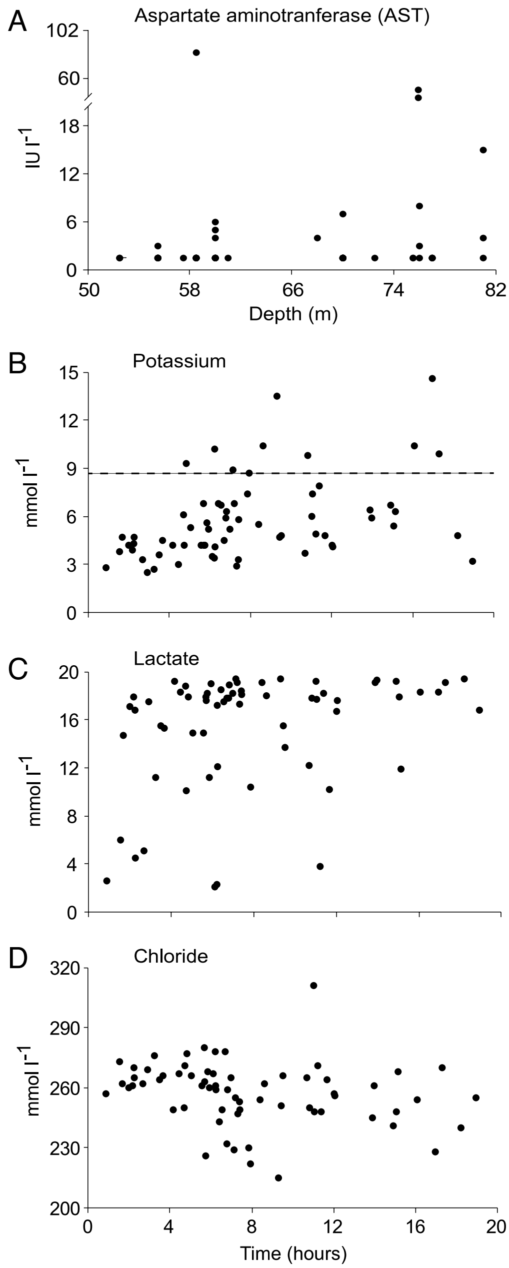

Fig. 3. Plots showing the significant relationships found in the most parsimonious GLMMs between the (A) capture depth and the concentration of aspartate aminotransferase (IU l^{-1}) in dusky and sandbar sharks (pooled) and (B–D) elapsed time (h) after hooking and the concentrations of potassium (mmol l^{-1}), lactate (mmol l^{-1}), and chloride (mmol l^{-1}). All sharks with mean potassium concentrations of >8.7 mmol l^{-1} were quantified as having a low condition index score for activity and stimuli and unlikely to survive. Data were pooled together for dusky and sandbar sharks due to no significant effect being found for the main effect of 'species' in the most parsimonious models.

and/or lethal physiological stress from struggling to break free after capture, the restricted mobility while hooked causes ram ventilators to be subjected to hypoxia or anoxia, and commonly death, after prolonged periods (Renshaw et al., 2011). However, mortality rates across species of ram ventilators have been found to vary significantly among studies. For example, survival rates for dusky and sandbar sharks ranged from 72.1 and 73.3% (Gallagher et al., 2014b), 18.9 and 63.9% (Morgan and Burgess, 2007), and 20.5 and 37.3% during the current study. Specifically, their association with oxygen-poor benthic waters (Compagno, 1984), and slower ambient swimming speeds might make them more robust to hypoxia and able to survive longer after hooking than their congeners (Morgan and Burgess, 2007). Similarly, the high survival rates in tiger sharks were expected as they possess the ability to switch between buccal pumping and ram ventilation, and have typically been found by other studies to have high (>90%) survival rates after hooking (Morgan and Burgess, 2007; Morgan et al., 2009; Marshall et al., 2012).

The greatest benefits for increasing survivorship of captured sharks in commercial fisheries could be derived by addressing some of the operational (fishing) variables that might contribute to longer times on the hook. The most obvious of these would be to shorten the duration of line deployment (i.e. soak time). However, to ensure the majority of individuals survive in this case, the soak time would need to be <2 h (conservative) or, more realistically, no more than 5 h before significant numbers of all species started to die. These time frames are, however, considerably less than the 7–27 h regularly observed in the NSW large shark fishery during 2008/09 (Macbeth et al., 2009). While shorter times could ideally be achieved by using fewer hooks per line, the time taken to set and retrieve a given length of line could vary considerably according to inter-vessel operational differences, variability in prevailing weather conditions and depending on the number of sharks hooked on the line. The average time taken to retrieve 120 hooks during the current study was 104 min, but varied between 60 and 180 min depending on the number of animals hooked on the line and 'bust offs' associated with the mainline breaking due to entanglement with sharks or reef. To compensate for the loss of catch associated with reduced deployment durations, more targeted fishing during peak periods of shark capture might be beneficial (i.e. between midnight and dawn, Broadhurst et al., 2014). Such improvements in efficacy would be more economically viable (less fuel and bait) and potentially result in fewer surplus sharks being discarded dead under any trip limits imposed by relevant management arrangements for shark fisheries.

In addition to the obvious relationship between mortality rate and the elapsed time spent on the line after hooking, hooking depth was also a significant predictor of mortality; especially for sandbar and dusky sharks. However, no definitive rationale exists as to why the trends observed here occurred, especially for sandbar sharks, for which there was a 40% decrease in the probability of mortality occurring between the 50 and 100 m depth ranges. Any causal effects were possibly attributed to factors not measured during the current study (i.e. other physiological and/or environmental variables such as bottom water currents) or, more likely, the cumulative impacts of the variables tested which were not detected in the models. Support for their ability to survive across the depths seen in the current study is provided by the basic biology of both species. For example, both species are closely associated with the sea floor and at depths to 300 m (Compagno, 1984; Last and Stevens, 2009; Barnes et al., in preparation), and spend the majority of time in waters to 120 m deep (Barnes et al., in preparation). As sandbar sharks are the main target species in many carcharhinid shark fisheries globally, any future protection or need to limit mortalities could be attained by limiting the depths at which gears can be deployed.

Sex also significantly influenced mortality rates in the sharks hooked, with males twice as likely to die as females, irrespective of species. Although we could not identify any specific reasons as to why this may have occurred, sex-related disparities in shark mortality have also been reported elsewhere. Lotti (2011) found that the probability of mortality was greater in male scalloped hammerheads caught on demersal longlines in the Gulf of Mexico and western North Atlantic, and suggested that low dissolved oxygen concentrations found specifically where males were caught may have contributed to their higher mortality rate. Similarly, Coelho et al. (2013) found that male blue sharks caught on pelagic longlines in the Atlantic Ocean were more likely to die than females, although there was considerable variation between fishing seasons and capture locations. Sex-specific differences in fish physiology have previously been documented, but may seasonally vary as a result of reproductive activity (Cooke, 2004). Although gender-driven variation in mortality at extreme hypoxia has been recorded for fishes as small as the mosquitofish (*Gambusia affinis*) (Cech et al., 1985), it is clear that the main influences on mortality rate of hooked sharks are generally poorly understood and need further consideration. In any case, it is probable that any overriding effect that hooking depth or sex may have on mortality rates would be relatively insignificant if mortalities are reduced by minimising the time spent on the line after hooking. This in turn would also reduce any negative physiological changes discussed below.

Changes in physiology of sandbar and dusky sharks attributed to being hooked on commercial longlines have been discussed in a number of studies (e.g. Mandelman and Skomal, 2009 and Marshall et al., 2012). Based on previous studies reporting at-vessel mortality rates and/or acute physiological status following fishing capture (Morgan and Burgess, 2007; Mandelman and Skomal, 2009; Marshall et al., 2012), dusky sharks are less resilient to withstanding capture and handling stressors than many other large shark species. Consequently, dusky sharks in the present study were generally expected to exhibit more disrupted blood chemical values relative to sandbar sharks. When accounting for other physical, biological, and fishing-practice predictor variables, however, blood chemistry was not informative in distinguishing the physiological status between the two species. In fact, only total protein concentrations differed, with sandbar sharks exhibiting higher levels at the point of retrieval than dusky sharks. In response to the stress-induced loss of plasma water or cell/organ damage incited by hooking and capture, elevated total plasma protein levels have previously been reported in both elasmobranchs (e.g. Mandelman and Farrington, 2007) and teleosts (e.g. Fletcher, 1975). While there could have been a distinct response explaining higher levels in sandbar sharks, the magnitude of difference between species has little, if any, physiological significance. Based on other analytes examined in the present study, there is no other indication of overall osmotic differences, or any other pure species effect on blood chemistry.

Based on blood chemical findings, none of the environmental or biological factors considered had a clear effect on intraspecific physiology. This is likely attributable to relatively limited sample sizes for each species, along with the potential influence of the broad array of hooking durations interacting with various other explanatory variables. Moreover, as previously surmised, based on blood data from another carcharhinid (Brooks et al., 2012), physiological recovery as indicated by changes in concentrations of certain analytes, could have commenced while individuals were still hooked, further adding to the intraspecific variability evident in this study. However, while some individuals might have begun to resolve any acute physiological disturbances while still hooked, it is also possible that some analytes were not expressing the full extent of change at the point of capture, particularly for animals only recently caught. It is also plausible that individual variation occurred in the period of time elapsed since most recent food intake may have influenced the values for some analytes (Manire et al., 2001). Finally, as evidenced by similarities in concentrations of some analytes among individuals (within a species) despite wide disparities in hooking durations, it is apparent that behavioural and/or physiological responses to longline hooking ranged widely among individuals. This may have been due to individuality in the form of some sharks being particularly disturbed, while others were not. Alternatively, acute stress associated with longline capture may simply not have translated into measurable differences in certain analytes. One unavoidable limitation in this study and others like it (e.g., Brooks et al., 2012) is the inability to repeatedly sample individual sharks across the course of the time on the hook. Without the ability to trace blood chemical changes from the onset of stress through the start of recovery within individuals, it may conceal more nuanced effects on some of these blood analytes.

Despite the general lack of interspecific differences, some general patterns emerged when dusky and sandbar sharks were examined in aggregate. For example, the longer sharks were hooked, the more elevated were plasma potassium, lactate and chloride concentrations. Numerous studies have reported a positive relationship between the duration or intensity of capture stress, and elevations in the former two analytes in sharks (e.g. Cliff and Thurman, 1984 and Frick et al., 2010). Acutely elevated potassium (i.e. hyperkalemia; a probable function of leakage from damaged muscle cells due to an intracellular acidosis) in particular has been shown to inhibit cardiac output at levels exceeding $\sim$7 mmol l^{-1} in piked dogfish, (*Squalus acanthias*), and has been surmised as a possible precursor to lethal endpoints in sharks subjected to capture and handling stress (Martini, 1974). This is supported in the current study, where all sandbar ($n = 5$) and dusky ($n = 5$) sharks with potassium concentrations >8.7 and >9.3 mmol l^{-1} respectively, had low condition index scores for activity and stimuli and were unlikely to survive.

In addition to the obvious trends and changes in physiology which may be apparent in all species as a response to hooking, the capture of species listed as Threatened or Vulnerable by the International Union for the Conservation of Nature (http://www.iucnredlist.org) (i.e. scalloped and great hammerheads, grey nurse sharks and a loggerhead turtle) is concerning. Although all grey nurse sharks survived, the majority of hammerheads died, even after short periods of time on the line following hooking. Although their capture in the OTLF has been documented via a scientific observer study (Macbeth et al., 2009), management measures to further minimise negative impacts on these species are required. For example, in addition to recommending short deployments to reduce the time spent on the line after hooking and increasing the probability of survival, it would also be necessary to reduce their capture all together by fishing at night when they are less likely to be hooked (Broadhurst et al., 2014). These data support the use of defined spatial and temporal fishing areas/closures combined with compulsory vessel-monitoring and logging systems as management tools in shark fisheries.

Although the results of this study have quantified the status (alive or dead), damage and stress in various species of targeted and non-target sharks captured specifically on demersal longlines, other gears such as handlines, droplines and mid-water setlines are also used to target sharks in various fisheries worldwide, including in the NSW OTLF (Macbeth et al., 2009). While these methods potentially constitute relatively smaller subcomponents of the global targeted shark fishing fleets, they should nonetheless be included in all further research into reducing unwanted mortalities. Furthermore, although we have not discussed the fate of those individuals released alive during our study, acoustic and satellite telemetry research on some of the sandbar and dusky sharks (as the main target species) released was done to investigate their post-release fate and wider movements (Barnes et al., in preparation). Given the species-specific differences in mortality, it is clear that this should be done on a wider number of species impacted by commercial shark fishing pressure (Skomal, 2007; Hammerschlag et al., 2011). As evidenced by blood analyte values in this study relative to previous work examining capture stress in elasmobranchs, sandbar and dusky sharks were only moderately physiologically impaired by being hooked. The species-specific differences in mortality rates highlight that it would be pertinent to repeat the blood chemistry research across all targeted shark species to assist managers in developing suitable strategies for sustainable use of shark stocks. Finally, more research looking at establishing whether wire traces or monofilament line should be used on the gangions is required; as previous work has suggested that catch rates of sharks on monofilament lines are variable among fisheries (Branstetter and Musick, 1993; Ward et al., 2008). Addressing the need for all or at least some of the above information would facilitate a more comprehensive assessment of shark fisheries and how they can reduce their impact on unwanted catch.

The high mortality rates across many shark species resulting from the hooking and gear retrieval process associated with the targeted shark longlining component of the OTLF revealed here and by Macbeth et al. (2009) provides sufficient justification for managers (and fishers) to refine the management of the fishery. Although our results clearly show that sex (males) and hooking depth affect the survival rates of sharks (depending on species), of greatest utility for developing appropriate management strategies is the significant positive relationship between the time spent on the line after hooking and probability of mortality (especially for common blacktip, hammerhead and spinner sharks). Combining a reduction in permissible soak times with nocturnal deployment and retrieval practices (to minimise the capture of protected hammerheads—Broadhurst et al., 2014) will aid in attempts to minimise negative impacts associated with discarding unwanted individuals. However, the maximum deployment durations recommended for significantly reducing mortalities (1–5 h) may not be commercially viable.

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