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[Article]

Predicting Postrelease Survival in Large Pelagic Fish

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Abstract.—Sharks, turtles, billfish, and marine mammals are frequently caught accidentally in commercial fisheries. Although conservationists and fisheries managers encourage the release of these nontarget species, the long-term outcome of released animals is uncertain. Using blue sharks *Prionace glauca*, we developed a model to predict the long-term survival of released animals based on analysis of small blood samples. About 5% of the sharks were landed in obviously poor condition (lethargic and unresponsive to handling); these moribund sharks were sampled and euthanized. A subset of the remaining sharks was sampled and tagged with pop-up satellite archival tags (PSATs). Each of the PSATs that reported data (11 tags) showed that the sharks roamed at sea for at least 3 weeks postrelease. Five variables differentiated moribund sharks from survivors: plasma Mg^{2+} (moribund, 1.57 ± 0.08 mM; survivor, 0.98 ± 0.05 mM; $P < 0.00001$), plasma lactate (moribund, 27.7 ± 4.1 mM; survivor, 5.80 ± 2.96 mM; $P < 0.001$), erythrocyte heat shock protein 70 (Hsp70) mRNA (relative levels: moribund, 3.96 ± 0.53; survivor, 1.00 ± 0.29; $P < 0.005$), plasma Ca^{2+} (moribund, 3.70 ± 0.14 mM; survivor, 3.13 ± 0.11; $P < 0.005$), and plasma K^+ (moribund, 7.01 ± 0.66 mM; survivor, 5.12 ± 0.44 mM; $P < 0.05$). These analyses were used to develop logistic regression models that could "predict" the long-term survival of captured sharks, including a larger group of sharks that we sampled but did not tag. The best logistic model, which incorporated Mg^{2+} and lactate, successfully categorized 95% of fish of known outcome (19 of 20). These analyses suggest that sharks landed in an apparently healthy condition are likely to survive long term if released (95% survival based on biochemical analyses; 100% based on PSATs).

Commercial fishing activity has the potential to adversely affect the populations of large pelagic species, whether they are target species or bycatch. Though there is considerable disagreement about the current state of large pelagic fish populations (Hampton et al. 2005; Burgess et al. 2005), the animals at greatest risk are the large apex predators, particularly sharks (Baum et al. 2003; Baum and Myers 2004), scombrids (tuna and billfish) (Myers and Worm 2003), and turtles (Spotila et al. 2000). Substantial reductions in reproductive biomass of these long-lived, late-maturing predators could cause prolonged effects on the population; effects that are seen locally in predator hotspots (Worm et al. 2003) or ecosystem-wide (Jackson et al. 2001; Frank et al. 2005), and in extreme cases might threaten a species with extinction (Spotila et al. 2000).

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Sharks dominate the bycatch of many marine pelagic fisheries (Bonfil 1994; Rose 1996; Hurley 1998; Francis et al. 2001). Some fisheries have a very high mortality in shark bycatch (e.g., 75% in the Atlantic menhaden *Brevoortia tyrannus* purse seine fishery; de Silva et al. 2001). However, in the pelagic longline fisheries for tuna and billfishes, sharks are captured in good condition. For example, in a survey of the 1997–1998 New Zealand tuna longline fishery, about 87% of blue sharks *Prionace glauca* were alive at the time of gear recovery (Francis et al. 2001). Though unwanted bycatch is typically released from the fishing gear, it is unknown if these animals would survive long term. This uncertainty about postrelease survival is a management challenge in many fisheries for large pelagic species, from commercial longline to sports fisheries.

Long-term postrelease survival is typically estimated by means of tagging programs. Historically, large-scale conventional tagging programs were employed but these yielded low return rates. For example, in a 30-year study of Atlantic blue sharks, only about 5% of the tags were recovered (Kohler et al. 1998). Such

results are consistent with a high postrelease mortality, but could also be attributed to large population sizes, dispersal, tag loss, or uncooperative fishers. Short duration studies using ultrasonic telemetry have shown that large pelagic fish usually survive for at least 24–48 h following release from sportfishing or longline gear (Holland et al. 1990; Block et al. 1992; Brill et al. 1993; Lutcavage et al. 2000). More recently, pop-up satellite archival tags (PSATs) have been used to assess postrelease behavior, which secondarily provides information about long-term survival of released animals. Due to the high cost of the tags, such studies have focused on high-profile species such as blue marlin *Makaira nigricans* (Graves et al. 2002), white sharks *Carcharodon carcharias* (Boustang et al. 2002) and bluefin tuna *Thunnus thynnus* (Block et al. 2005; Wilson et al. 2005).

We combine a PSAT tagging approach with biochemical analysis to assess the survival of blue sharks, a species that dominates the bycatch of most pelagic fisheries (e.g., the Atlantic menhaden purse seine fishery [Francis et al. 2001], the New Zealand tuna longline fishery [de Silva et al. 2001], and the Pacific swordfish *Xyphias gladius* and tuna longline fisheries [Ward et al. 2004]). Such biochemical profiling can be an inexpensive alternative to large-scale tagging programs, making it feasible for fisheries managers to conduct intensive sampling programs to assess the consequences of fishing practices.

Methods

Capture, tagging, and sampling of sharks.—Scientific longline cruises were conducted from the National Oceanic and Atmospheric Administration (NOAA) research vessels *Townsend Cromwell* and *Oscar Elton Sette* in the central Pacific Ocean near the Hawaiian archipelago. Sharks were caught by conventional longline fishing gear, with shallow night-time sets of less than 100 m (as determined by attached Time Depth Recorders from Wildlife Computers, Redmond, Washington). Each basket had about 4–5 hooks per basket, with the 15/0 circle hooks typically baited with squid (*Illex* spp.). A green chemical light stick was affixed above each dropper. Generally between 400 and 600 hooks were set per night and soak times ranged from 10 to 18 (average ~12) h. This fishing strategy approximated the typical Hawaiian "swordfish" style of fishing employed by commercial longliners in the region (Ito et al. 1998; Bigelow et al. 2006). In a commercial fishing setting, lines with unwanted shark bycatch are cut, releasing the animal without bringing it onboard. In our study, sharks were brought on board in a sling and were restrained by crew with mattresses. Thus, the additional handling in our study could have induced a degree of stress beyond that seen in the commercial fishery. Had we seen significant postrelease mortality, sampling and tagging steps might have led to an overestimation of postrelease mortality.

Model PTT-100 PSATs, from Microwave Telemetry (MT; Columbia, Maryland) were affixed to each shark's dorsal fin by drilling a hole 10–15 mm in diameter near the base of the fin and threading 49-braid stainless steel wire encased in Tygon tubing, which acted as the harness. Stainless steel crimps were used to attach the harness to a tether made of 122-kg fluorocarbon that was crimped to the nose cone of the PSAT.

The PSATs deployed on sharks were programmed to acquire temperature and pressure (depth) readings every hour. Depth and temperature data were measured as 8-bit numbers. Depth resolution was ~5.4 m and temperature resolution was ~0.176°C. Tags were programmed to detach either 6 or 13 months after deployment. Two "fail-safe" options were programmed into the PSAT. If the shark died with the tag affixed, the negative buoyancy of the shark would cause the tag to sink; once the PSAT registered a pressure corresponding to a depth of 1,200 m, a corrosional link was activated, jettisoning the tag from the shark, allowing it to float to the surface to transmit acquired data to an Advanced Research and Global Observation Satellite (ARGOS). Alternatively, if the tag experienced no significant pressure change within four consecutive days, it automatically initiated data recovery procedures. This might occur if the tag was shed, causing it to float at the surface, or if the tag was otherwise stationary at a depth less than 1,200 m. For the PSATs, estimates for dawn and dusk were automatically calculated in the tag by a proprietary algorithm.

Analysis of blood samples.—Blood samples (~10 mL) were collected from the caudal vein using heparinized (sodium salt) syringes. A sample was centrifuged to provide hematocrit values. Blood was centrifuged to separate red blood cells from plasma, with each fraction frozen in liquid nitrogen for later analysis.

RNA was extracted from frozen erythrocyte pellets and analyzed as described by Currie et al. (1999). The frozen pellet was powdered in liquid nitrogen, homogenized in guanidinium thiocynate, and the RNA extracted using a phenol-chloroform method. The quality of the RNA sample was verified using the ratio of absorbance at 260 versus 280 nm (ratio 1.8–2.0). Samples of RNA were examined by means of electrophoresis using formaldehyde denatured agarose gels, then transferred to nylon membranes for northern blot analysis. A cDNA probe was prepared encoding

a shark heat shock protein 70 (Hsp70) mRNA fragment (GenBank accession number AF502441). The probe was labeled using ^{32}P-2′-deoxycytidine 5′-triphosphate (^{32}P-dCTP) and hybridized as previously described (Currie et al. 1999). The radioactivity was measured using a Molecular Devices phosphoimager. A second hybridization with alpha-tubulin cDNA was used to correct for loading differences. A single RNA sample was included on all blots to allow direct comparisons between blots. The data are in arbitrary units, with the mean of the survivors set to a value of 0.

Plasma metabolites (glucose, lactate, and urea), ions (Mg^{2+}, K^+, Ca^{2+}, Cl^-, and Na^+), and proteins (alanine aminotransferase, aspartate aminotransferase, creatine kinase, alkaline phosphatase, lactate dehydrogenase, total protein, and albumin) were analyzed using a Roche Modular Systems PPE Serial 903. Osmolarity was measured using a vapor-pressure osmometer (Advanced Instruments, Logan, Utah).

Statistical analysis.—About 50% of the tags failed to send data to the ARGOS satellite. Though the reasons for the tag failures are not known, there is no reason to ascribe any particular outcome to sharks tagged with PSATs that failed to report. These "nonreporter" sharks are therefore treated as unknowns in the analysis. Where analysis yielded a value below the detection threshold, the value for the detection threshold itself was used in analyses. For each variable, the data for survivors and moribund sharks were compared by means of a two-tailed *t*-test. The analytical approach was to identify variables that distinguished the survivors from the moribund sharks, then use the best of these variables to develop a logistic regression model to assign individuals to a survivor or moribund group. The logistic regression model is, thus, a predictor of survival validated by the tagging successes.

The model was then applied to the entire data set (survivors, moribund fish, and unknowns). For each model, R^2 (U) was used to evaluate its ability to predict outcome. For each model the probability that each individual (survivor, moribund, or unknown) survived [P(s)] was then calculated; an individual was categorized as a survivor if P(s) was less than 0.50.

Results

Catch Data and Tagging Observations

Of the 522 large pelagic fish captured, 211 were sharks, of which 172 were blue sharks. Thus, blue sharks constituted 82% of captured sharks and 33% of the total catch.

About half of the PSATs deployed in this study (11 of 23) successfully reported their data to the satellite, but only 4 of the 11 reached their pop-off date. The remaining seven tags were shed prematurely, a common phenomenon in PSAT studies (e.g., in a comprehensive study of PSAT performance containing 662 tags, only 87 (17%) hit their preprogrammed pop-off dates [M. K. M., unpublished data]). The reasons for premature release are unknown, but even these tags yielded useful data until the pop-off occurred. It is important to emphasize that a premature release was not due to death of the shark. Sharks are negatively buoyant and sink when swimming activity ceases. An example of a PSAT recording for a dead shark is shown in Figure 1. This shark, tagged in preliminary studies, ranged locally with regular vertical movements for about 5 d before the tag sank to 1,200 m and jettisoned. Unfortunately, no blood sample was collected from this shark, which is the only example of delayed postrelease mortality.

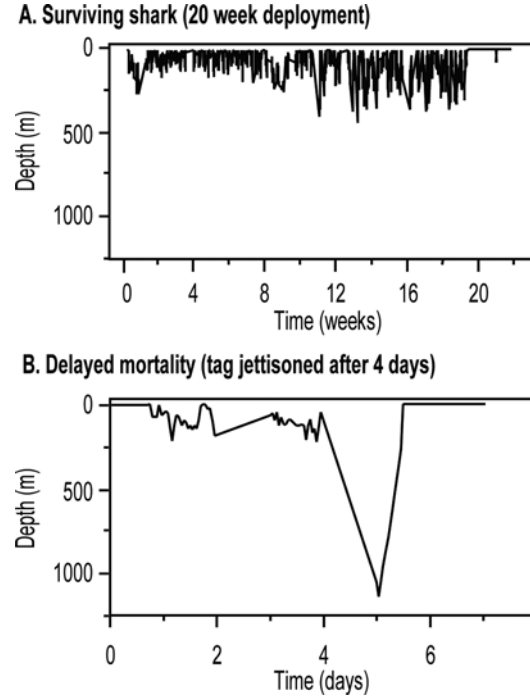

FIGURE 1.—Time–depth profiles from pop-up satellite archival tags (PSATs) affixed to two blue sharks. Panel **(A)** shows a representative profile with the shark ranging in the upper 100 m until the tag reached its pop-off date. Panel **(B)** represents a shark shown in preliminary studies to die 4 d after release. This shark was tagged but no blood sample was collected; it remains the only example of a PSAT signature of postrelease mortality in this species.

Data from the successful tags were transmitted and downloaded via the ARGOS satellites, contributing 1,841 aggregate days of data with a mean ± SD of 116 ± 96 d. The horizontal movement patterns throughout

TABLE 1.—Summary of tagging and sampling of blue sharks.

Category	Number
Blue sharks captured	172
Moribund sharks	9
Sharks tagged but not sampled	1
Sharks tagged and sampled	23
Survivors	11
Nonreporters[a]	12
Sharks sampled but not tagged[a]	10

[a] Included in "unknowns."

the Hawaiian waters were similar to those reported previously by Strasburg (1958) and Nakano (1994). The vertical data suggest that blue shark exhibit "typical" pelagic fish diving patterns with "W" movements traversing from near the surface to those below the mixed layer during the day to a baseline depth of around 400 m; an example of a depth profile is shown in Figure 1. Most shark movements were within the upper 220 m, but a few sharks made occasional forays into depths of 500–600 m. Night movements were almost exclusively contained within the uniform surface layer. About 90% of movements were in water temperatures between 11 and 25°C and 75% of all movements were between 20 and 25°C.

Predicting Outcome of Released Blue Sharks

The tagging and sampling process generated three treatment groups: moribund, survivor, and unknown (Table 1). Moribund sharks were landed in a lethargic state in which they were minimally responsive to handling. These sharks were sampled and euthanized without tagging. Of the 172 blue sharks captured, only nine were classed as moribund (5%) and the remaining 163 sharks (95%) were in apparently healthy condition. There were 11 sharks that yielded tagging data; these survivors roamed at sea for more than 3 weeks with no signs of postrelease mortality. Of the remaining 152 captured sharks, 22 were sampled but had an uncertain outcome; these unknowns included sharks that were sampled but not tagged ($n = 10$) and sharks with tags that failed to report ($n = 12$).

The first analyses compared only surviving and moribund fish, which were two groups presumed to be of homogeneous condition. (The unknowns, in contrast, were a collection of individuals sharing only an uncertain outcome; thus, it is not meaningful to compare this group as a whole to either the survivor group or moribund group.)

Blood and plasma analyses are summarized in Table 2. A number of variables showed very little variation among animals, with no obvious distinction between survivor and moribund groups. For example, glucose, Na^+, Cl^-, urea, and osmolarity each varied among individuals by less than 5% of the mean. Other variables showed considerable differences among individuals, but differed little between survivors and moribund fish (e.g., hematocrit, creatine kinase, and lactate dehydrogenase). Only five variables were significantly different between survivors and moribund sharks: plasma Mg^{2+}, plasma lactate, erythrocyte Hsp70 mRNA, plasma K^+, and plasma Ca^{2+} (Figure 2). These variables were used to develop a logistic regression model that could be used to predict the outcome of all captured sharks with outcome as the dependent variable (0 = moribund, 1 = survived), and different physiological measures, alone and in combination, as independent variables. We focused on the two most divergent variables (Mg^{2+} and lactate) but also considered Hsp70 mRNA because of its use as an index of stress at the cellular level.

The logistic model using only plasma Mg^{2+}correctly assigned 8 of 9 as moribund sharks and 10 of 11 as

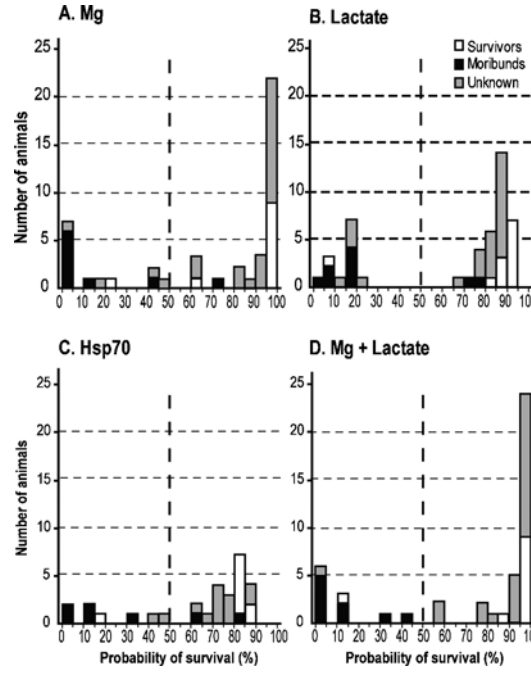

FIGURE 2.—Logistic regression analysis of survivors, moribund sharks, and unknowns based on **(A)** Mg^{2+} alone ($\chi^2 = 18.6$, df = 1, $P < 0.0001$, $R^2 = 0.71$), **(B)** lactate alone ($\chi^2 = 11.35$, df = 1, $P = 0.0008$, $R^2 = 0.43$), **(C)** Hsp70 mRNA ($\chi^2 = 7.53$, df = 1, $P = 0.006$, $R^2 = 0.36$), or **(D)** both Mg^{2+} and lactate ($\chi^2 = 19.7$, df = 2, $P < 0.0001$, $R^2 = 0.75$). For each model, R^2 (U) was used to evaluate predictive ability. The probability that each individual (survivor, moribund, or unknown) survived (P[s]) was then calculated for each model; an individual was categorized as a survivor if P(s) was greater than 0.50.

survivors (Figure 2a). Similar results were seen with lactate (Figure 2b): correct assignment of 8 of 9 as moribund sharks and 10 of 11 as survivors. A model with Hsp70 mRNA as the independent variable (Figure 2c) misassigned 2 moribund sharks and 1 survivor, although some samples were missing from the analysis due to sample limitations. A logistic regression incorporating both Mg^{2+} and lactate (Figure 2d) was the best predictor (log-likelihood ratio chi-square = 20.9, $P < 0.0001$, df = 2). In this model, only one individual (a survivor) was misclassified (95% correctly categorized).

It is important to recognize that the consequences of a misassignment differ between survivors and moribund sharks. If a moribund fish was misassigned as a survivor, this presents the possibility that it might have survived despite its lethargic appearance. In such a case, the model results in an overestimation of mortality. In contrast, if a shark that was known to survive is predicted to be moribund by the model, this suggests a false negative, a potential weakness in the use of the model as a predictor of survival.

When the different logistic models were applied to the blood profiles of the unknowns, most of the sharks of unknown outcome were biochemically distinct from moribund sharks and indistinguishable from the sharks known to survive. Most of the unknown sharks fit the profile of a survivor: 18 of 22 (82%) using the Mg^{2+} model, 17 of 22 (77%) using lactate, and 21 of 22 (95%) using the combination of Mg^{2+} and lactate.

Extending these survival rates to the whole catch (172 blue sharks), the Mg^{2+}–lactate model predicts that 156 blue sharks would have survived (95% of the 163 healthy sharks) and 18 would have suffered postrelease mortality (5% of the healthy sharks and all 9 moribund sharks), yielding an overall 90% survival rate.

Discussion

The outcome of nontarget animals released in commercial longline fisheries is uncertain in large part due to the difficulty in acquiring survival data. With the advent of PSATs, it is now easier to derive long-term behavioral information from released animals. By incorporating blood analysis into a PSAT program, we sought a set of variables that could distinguish between healthy and unhealthy blue sharks, the most dominant species in bycatch of tropical marine longline fisheries (de Silva et al. 2001; Ward et al. 2004).

Physiological Indices of Stress

Fishing is an intervention that has the potential to cause wide-ranging disruption of normal physiology, although the nature of the physiological challenge depends on the fishing method. Another factor to consider is whether a change in a physiological variable necessarily has dire consequences for the animal. For example, severe blood loss is a stressor that would be expected to have profound effects on an active animal. In this study, blood loss (assessed as hematocrit) was common. One shark showed a hematocrit of only 14%, yet managed to survive at least 244 d until its tag jettisoned. Similarly, a shark that struggled violently might be expected to incur some degree of muscle damage. Again, the sharks that exhibited the greatest degree of muscle damage (as indicated by plasma CK and LDH) were also shown to survive long term. One survivor shark had blood CK and LDH levels sixfold greater than the highest levels seen in any moribund shark. Thus, many variables may change dramatically as a result of capture, but these perturbations are not necessarily lethal or irreversible.

Five variables distinguished the group of surviving sharks from the group of moribund sharks: Mg^{2+}, lactate, Hsp70 mRNA, K^+, and Ca^{2+}. Each of these variables is plausibly linked to strenuous muscular activity and the resulting physiological stress (acidosis) and tissue damage (myopathy). Intense muscle activity is fuelled by glycolysis, which causes depletion of muscle glycogen, production of lactate, and acidification of the muscle (Moyes and West 1995). The muscle changes rapidly impinge on the blood, increasing plasma lactate levels and causing an acidosis. Since plasma lactate levels should approximate the extent of muscle activity, these data suggest that moribund fish had exercised to exhaustion while on the fishing gear.

The threefold elevation in erythrocyte Hsp70 mRNA in moribund sharks reflects some degree of cellular stress. Fish erythrocytes, unlike mammalian erythrocytes, possess nuclei and remain transcriptionally active and retain the capacity to induce Hsp70 gene expression in response to thermal stress, as well as other types of cellular stress (Currie et al. 1999). In these sharks, it is unlikely that thermal stress was the trigger for Hsp70 induction but rather another form of cellular stress, such as oxidative stress. Furthermore, it is unclear if the stress signal arose directly within the erythrocyte or, alternatively, as a result of passage through stressed tissues (see Currie et al. 1999).

Increased plasma K^+ is normally attributed to cellular damage, but it can also be a response to acidosis, which causes a net efflux of K^+ from tissues, including muscle. Elevated plasma K^+ can alter the electrochemical gradients necessary for the function of excitable tissues, including cardiac and skeletal muscle. As a result, hyperkalemia can lead to cardiac ventricular arrhythmias and muscle weakness.

Plasma elevations in Mg^{2+} and Ca^{2+} may also be a reflection of a disturbance in muscle cell integrity or

TABLE 2.—Blood analysis of blue sharks.

Shark category	Hsp70 mRNA	Plasma ions and metabolites (mM)								Osmolarity (mosmols)	Plasma enzymes (U/L)[a]				
		Lactate	Glucose	Mg^{2+}	K^+	Ca^{2+}	Cl^-	Na^+	Urea		ALT	AST	CK	ALP	LDH
Moribund															
Mean	1.33	27.72	4.16	1.57	7.01	3.70	236	264	352	1,089	5.22	26.9	537	3.14	118
SE	0.24	4.07	0.69	0.08	0.66	0.14	5	4	11	18	0.22	11.2	490	0.40	107
n	7	9	9	9	9	9	7	7	8	8	9	9	9	7	9
Survivor															
Mean	0.45	5.80	4.75	0.98	5.12	3.13	240	263	357	1,039	6.82	38.3	3,468	4.40	679
SE	0.13	2.96	0.40	0.05	0.44	0.11	4	1	4	10	0.85	22.3	2,282	0.51	462
n	9	11	11	11	11	11	11	11	11	5	11	11	11	5	11
P-value[b]	<0.004	<0.0009	nsd	<0.00001	<0.04	<0.003	nsd	nsd	nsd	nsd	nsd	nsd	nsd	nsd	nsd
Unknown															
Mean	0.62	8.35	4.94	1.05	4.59	3.21	245	263	348	1,068	10.12	16.2	1,134	3.56	264
SE	0.05	2.05	0.23	0.04	0.17	0.05	3	3	5	10	3.78	4.3	409	0.15	87
n	15	25	25	25	25	25	23	23	25	20	25	25	25	18	25

[a] Abbreviations are as follows: ALT = alanine aminotransferase (enzyme number 2.6.1.2; IUBMB 1992), AST = aspartate aminotransferase (2.6.1.1), CK = creatine kinase (2.7.3.2), ALP = alkaline phosphatase (3.1.3.1), and LDH = lactate dehydrogenase (1.1.1.27).
[b] Derived from two-tailed *t*-tests comparing variables in moribund and surviving sharks. The data are compared in relative terms in Figure 2, with the mean of the data for survivors set at a value of 1; nsd = not significantly different.

pH regulation. Muscle has high levels of Mg^{2+} and Ca^{2+}, so muscle damage may also account for the increase in these divalent cations. As with K^+, the acidosis could lead to a change in Mg^{2+} and Ca^{2+} distribution, acting through proton-dependent transporters. Although sharks are osmoconformers, they maintain plasma divalent cations well below those found in the seawater using combinations of transporters driven by electrochemical gradients. Thus, an increase in these ions could arise from a greater influx or reduced excretion.

Many of these changes seen in sharks are reminiscent of the early stages of a condition known as capture myopathy or exertional myopathy, best studied in mammals and birds (Spraker 1993). Captured wildlife experience elevated epinephrine in combination with intensive muscle activity. The effects culminate in muscle damage, which leads to release of myoblobin and muscle enzymes, as well as a disruption in electrolyte balance. The muscle damage can be transient or lead to permanent lesions. The high levels of myoglobin arising in the blood can cause kidney damage in mammals and birds. In blue sharks, most of the muscle mass is composed of myoglobin-poor white muscle and it is not clear that damage of this muscle would lead to myoglobinuria, though we did not measure it. Also, capture myopathy progresses from an acute phase (hours) to days and weeks. In a study of captured dusky sharks *Carcharhinus obscurus*, about 24 h of recovery were needed to see a return of electrolytes to precapture levels (Cliff and Thurman 1984). In our study, we have no way of knowing if released sharks experienced prolonged effects, such as those seen with capture myopathy, but if so, they did not appear to affect their survival.

Caveats in Estimating Survival and Mortality

The main goal of most tagging studies is to estimate population dynamics and as such, it is appropriate to tag only those animals that are captured in excellent condition. When such an approach is used to assess postrelease survival, there is the potential to overestimate survival because the animals in the poorest condition are not tagged. In our study, 95% of the sharks (163 of 172) were landed in apparently healthy condition and would have been tagged, resources permitting. Of this group, the sampled and tagged sharks showed 100% survival. In fact, only one tagged shark exhibited postrelease mortality; it was the first animal tagged and it is likely that this shark succumbed to our efforts to sample (unsuccessfully) and tag (successfully) the animal. After its release, a blood film was seen around the shark, suggesting it was harmed during handling. Collectively, these results suggest that overtly healthy sharks have a high probability of survival if released, whether this was assessed by PSAT data alone (100% survival; 11 of 11 sharks) or biochemical profiling (95%, or 22 of 23 sharks were indistinguishable from survivors).

Estimating mortality is also contingent upon assumptions. In some models, one moribund shark was categorized as a survivor. While it is possible that this shark might have survived if released, it is also possible that the shark was damaged in ways that were unrelated to capture myopathy, such as hook trauma. The pleiotropic effects of capture may explain the variation in condition not explained by our model; about 76% of the outcome can be predicted from Mg^{2+} and lactate levels. In selecting individuals to tag, we avoided only 5% of the sharks: those landed in a moribund state.

TABLE 2.—Extended.

Shark category	Protein (g/L)	Albumin (g/L)	Hematocrit (%)
Moribund			
Mean	11.4	3.00	16.1
SE	0.9	0.22	1.5
n	7	7	6
Survivor			
Mean	14.6	2.60	19.4
SE	0.6	0.24	2.4
n	5	5	5
P-value[a]	nsd	nsd	nsd
Unknown			
Mean	13.9	3.22	19.9
SE	0.7	0.27	0.8
n	18	18	18

While we think it is likely these moribund sharks would have died within a day, they were not tagged and it is possible they might have survived if released. This constituted a risk of overestimating mortality in our study, however the moribund sharks represented only 5% of the total catch (9 of 172) and the blood analyses suggested that only 6% of "healthy" sharks (2 of 33) had a profile resembling a moribund shark. Collectively, the combination of PSATs and biochemical analyses greatly reduced the likelihood that we overestimated either survival or mortality.

Implications for Fisheries

No other study has combined these two techniques to develop predictors of postrelease survival. Our central conclusion is that most blue sharks captured under the fishing conditions we employed would likely survive upon release. Considering only the sharks that produced valid tagging data, we conclude there is a very high probability that sharks readily survive the capture and release process. Using the known survivors to establish biochemical predictors of survival, we predict that 95–100% of apparently healthy animals would have survived, and 90–95% of all sharks would have survived upon release.

The veracity and utility of this conclusion depends on many factors. In terms of fishing strategy, our technique paralleled that used in the Hawaiian commercial longline fishery for large pelagic fishes (Ito et al. 1998). If exhaustive exercise was indeed the cause of demise of moribund blue sharks, then it would seem reasonable to suggest that the chances of survival would be better with short sets (i.e., a shorter interval of time between capture and release). Many species die shortly after being hooked, leading to a loss from the longline gear. Sharks, as well as billfish, survive on hooks for longer periods, leading to an increase in catch success with longer soak times (Ward et al. 2004). However, it is not clear if the longer soak times lead to greater postrelease mortality. Another factor that might influence postrelease survival is water temperature. Blue sharks are also captured in temperate water fisheries, and it is likely that the lower water temperature would reduce locomotor activities and perhaps increase the likelihood of survival.

Although this study focused on blue sharks, a similar approach—tagging combined with biochemical analysis—could be applied to other species of concern, including other nontarget species (e.g., sea turtles, marine mammals) or game fish captured in catch-and-release tournaments (e.g., marlins). Transferring this approach to other species demands careful attention to the physiology of the animal. Other marine predatory fish can experience much greater disruptions in blood chemistry. For example, we analyzed blood from three mako sharks *Isurus oxyrinchus* (data not shown), which possessed plasma lactate concentrations of 35–60 mM, which was greater than the highest levels seen in blue sharks. Furthermore, exhaustive exercise can elevate tuna lactate levels up to 100 mM (Arthur et al. 1992). Thus, our approach may translate well to other fisheries, but the magnitude of change in any of these variables may be species specific. It is also critical to be aware of the influence of timing. In our study, long sets were used and we could not estimate the time spent on the hook, which would have been useful in our analyses. In our study, blood samples were readily collected, but this is more challenging in many of the larger animals found in a bycatch (e.g., leatherback sea turtles *Dermochelys coriacea*) or game fish (e.g., blue marlin). The use of a large research vessel also enabled us to process and flash-freeze samples immediately upon collection, conveniences that might not be feasible in all fishing settings. Despite the challenges in collecting blood samples in parallel with PSATs, we believe the approach can yield important predictive information about postrelease survival, which should help guide fisheries management.

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