North American Journal of Fisheries Management 37:1045–1053, 2017

ISSN: 0275-5947 print / 1548-8675 online
DOI: https://doi.org/10.1080/02755947.2017.1336136

ARTICLE

Factors Influencing Postrelease Predation for a Catch-And-Release Tropical Flats Fishery with a High Predator Burden

Robert J. Lennox*
Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, Ottawa, Ontario K1S 5B6, Canada; and Indifly Foundation, Post Office Box 4460, St Paul, Minnesota 55104, USA

Alexander Filous
Indifly Foundation, Post Office Box 4460, St Paul, Minnesota 55104, USA; and Fisheries Ecology Research Lab, Department of Biology, University of Hawaii at Mānoa, 1960 East-West Road, Honolulu, Hawaii 96822, USA

Sascha Clark Danylchuk
Indifly Foundation, Post Office Box 4460, St Paul, Minnesota 55104, USA; and Fish Mission, 11 Kingman Road, Amherst, Massachusetts 01002, USA

Steven J. Cooke and Jacob W. Brownscombe
Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, Ottawa, Ontario K1S 5B6, Canada

Alan M. Friedlander
Fisheries Ecology Research Lab, Department of Biology, University of Hawaii at Mānoa, 1960 East-West Road, Honolulu, Hawaii 96822, USA; and Pristine Seas, National Geographic Society, 1145 17th Street Northwest, Washington, D.C. 20036, USA

Andy J. Danylchuk
Indifly Foundation, Post Office Box 4460, St Paul, Minnesota 55104, USA; and Department of Environmental Conservation, University of Massachusetts Amherst, 160 Holdsworth Way, Amherst, Massachusetts 01002, USA

Abstract
Postrelease predation (PRP) of fishes released by anglers is a potentially significant contributor to overall mortality in recreational fisheries. We quantified PRP and examined the impacts of handling and release practices on Shortjaw Bonefish *Albula glossodonta*, a species of shallow-water Pacific bonefish that supports a recreational fishery throughout its range and is emerging as recreationally important to the economy in Anaa Atoll, French Polynesia. We caught, released, and monitored the postrelease movements of Shortjaw Bonefish on the shallow flats of Anaa Atoll via recreational angling gear and small floats attached to the bonefish. Using Cox proportional hazards regression of our observations of PRP we tested how handling practices (air exposure) and release strategies (retained for a short period versus immediate release) influenced the probability of PRP. There was some evidence that air exposure increased

*Corresponding author: robert.lennox@carleton.ca
Received August 17, 2016; accepted May 23, 2017

susceptibility to PRP. However, retention in a recovery bag for 30 min did not reduce PRP. Actually, retention in the recovery bag increased the number of sharks in the release area after 30 min suggesting that Shortjaw Bonefish should be released quickly to avoid aggregating sharks. In both the handling and release practices components of the study, the number of sharks encountered proximate to the release site was the strongest predictor of PRP. Anglers and guides fishing in areas of high predator density such as at Anaa Atoll should release bonefish quickly to minimize aggregation of sharks that depredate released bonefish. Avoiding fishing flats with high predator densities and frequently rotating fishing flats may be necessary to quell PRP. Acknowledging risks and accounting for PRP and its contribution to overall postrelease mortality is essential for maintaining sustainable recreational fisheries for this species.

Predation is a fundamental process that controls natural ecosystems and predators have an integral role in moderating their prey populations, ecological communities, and zoonotic outbreaks (Holt 1977; Sih et al. 1986; Packer et al. 2003; Ostfeld and Holt 2004; Knight et al. 2005). Consequently, predators are recognized to be important regulators of ecosystems and species (Lack 1954; Friedlander and DeMartini 2002; Creel and Christianson 2008). For the most part, natural selection operates via predators that preferentially target inferior components of the prey population (Genovart et al. 2010). Therefore, the individuals that are most vulnerable to predators are those that are injured, diseased, or impaired (Genovart et al. 2010). However, highly fit individuals can become prone to predation as a consequence of transient stress or exhaustion that weakens them in the short term.

Normal behavior, vigor, and refuge seeking can become impaired when fish are physiologically stressed or energetically exhausted (Danylchuk et al. 2007a; Cooke et al. 2014; Brownscombe et al. 2014). Exhaustion, stress, and cognitive impairment are common consequences experienced by fishes that are captured and released by fisheries. Captured fishes generally recruit anaerobic muscle fibres (i.e., white muscle) to power burst activity fuelled by the anaerobic metabolism of adenosine triphosphate (ATP), phosphocreatine, and glycogen (Milligan and Wood 1986; Dobson and Hochachka 1987; Wood 1991; Milligan 1996; Kieffer 2000). This can create significant physiological impairment via intracellular acidosis (Wood et al. 1983) and oxygen debt (Scarabello et al. 1991), contributing to cognitive impairment (Raby et al. 2012). Exhaustion of the white muscles also precludes further burst exercise in the short term, compromising an important pathway used in predator evasion (Domenici and Blake 1997). Physiological stress also causes cognitive impairment, which results in poor decision-making by fish confronted by predators, including reduced refuge use (Campbell et al. 2010; Cooke et al. 2014; Brownscombe et al. 2014). During this period of impairment, individuals recovering from the physiological effects of recreational angling become prone to post-release predation (i.e., PRP; Raby et al. 2014).

The bonefishes, Albulidae, are a family of benthic marine fishes native to neritic habitat throughout the tropical seas (Colborn et al. 2001; Adams and Cooke 2015; Wallace 2015). These species are lauded by recreational anglers as hard-fighting fish (Cooke and Philipp 2008), but many species of bonefishes are threatened by habitat loss and pollution (Adams et al. 2013; Adams and Cooke 2015). Bonefish are particularly vulnerable to the impacts of catch and release because they can experience significant PRP, typically within 20 min of release (Cooke and Philipp 2004; Danylchuk et al. 2007a). This occurs because angling-related stressors often result in behavioral impairment (Brownscombe et al. 2013, 2015), and bonefish live in environments with high densities of opportunistic predators (Danylchuk et al. 2007a). Brownscombe et al. (2013) tested the use of recovery bags to hold bonefish prior to release. They found that holding bonefish in recovery bags prior to release resulted in significantly reduced behavioral impairment and higher survival postrelease. However, this experiment occurred in a tidal creek in The Bahamas with relatively low predator densities and little PRP occurred regardless of recovery treatment. The goal of our research was therefore to test the use of recovery bags to reduce PRP on bonefish in an environment with high predator densities. The coastal region of Anaa, a small atoll in French Polynesia, is one such environment, having high densities of sharks. The bonefish in Anaa are not the Bonefish *Albula vulpes*, the focal species of previous bonefish catch and release studies, but rather Shortjaw Bonefish *A. glossodonta*. This species is found in many regions the tropical Pacific Ocean, but is listed as vulnerable by the International Union for Conservation of Nature (Adams et al. 2013). There is a paucity of data available about the impacts of angling on Shortjaw Bonefish, but recreational fisheries for this species are common on South Pacific islands. Recently, recreational fishing tourism for Shortjaw Bonefish has emerged in Anaa, but there is concern that abundant sharks within the lagoon may represent significant predators of the released bonefish. Local management of this fishery and others for Shortjaw Bonefish would therefore benefit from research that documents the postrelease fate of this species in areas where predator burdens are high. To evaluate the recreational fishery in Anaa, we documented the extent of postrelease predation of captured Shortjaw Bonefish and conducted experiments to develop best practices for anglers and guides to implement in the fishery. We hypothesized that longer air exposure intervals would increase their vulnerability to postrelease predation by sharks (Danylchuk et al. 2007a) but that facilitated recovery from recreational angling stressors would be a viable tool to mitigate the risk (Brownscombe et al. 2013).

METHODS

Experiments on the impacts of angling handling and release practices on Shortjaw Bonefish were conducted at Anaa Atoll, French Polynesia (17.3419°S, 145.5087°W). Anaa is an ovular north-south oriented atoll comprised of a series of coral islands bordered by a reef. The atoll surrounds a relatively shallow lagoon measuring 90 km^2. The lagoon contains abundant fish populations that are exploited by locals in artisanal fisheries using stone weir-style traps, spear guns, harpoons, handlines, and gill nets. The lagoon also has Blackfin Reef Sharks *Carcharhinus melanopterus*, Sicklefin Lemon Sharks *Negaprion acutidens*, and Tawny Nurse Sharks *Nebrius ferrugineus* that are not directly exploited by fisheries. Shortjaw Bonefish inhabit the lagoon and are commonly found on sand flats extending from the shore where they are accessible to recreational anglers. Fluctuating water levels within the lagoon change the exposure of flats, which influences their availability to recreational angling. Flats are generally shallow, sandy, nearshore habitat. Shortjaw Bonefish search for food there and are also found off the flats in the deeper water at the center of the lagoon, where they are targeted by locals with handlines and bait. Throughout the study, we visually estimated the number of sharks sighted on each flat independent of fishing and maintained a count during each fishing session on a given flat.

For our study, 66 Shortjaw Bonefish (mean FL = 46 cm, 5 = SD) were angled from October 20 to December 16, 2015, by wading the shallow sand flats of Anaa. Anglers used 8-weight fly rods with 7.28–9.09-kg-test fluorocarbon tippet. Flies were tied on barbed hooks, sizes 4–6. Water temperature at fish capture averaged 28°C (SD, 1). For the first experiment, bonefish handling practices were examined by assigning fish to one of three handling treatment groups (0, 10, or 30 s air exposure) to simulate potential angler handling practices in the fishery. All fish were landed as quickly as possible, at which point they were transferred to an open-top, flow-through hypalon bag fixed with floats to ensure the fish was secure, submerged, and manual handling was minimized. Individuals were measured (cm, FL) and marked with external dart-style individually numbered anchor tags through the dorsal musculature and pterygiophores (Figure 1). Hook placement was noted prior to removal, but if the hook was lodged in the mouth cavity, the line was cut to reduce handling time. According to the treatment group assigned to the bonefish, it was then handled (no air exposure, 10 s air exposure, or 30 s air exposure). To monitor the fate of bonefish after release, we tethered each fish to a Styrofoam float by 5.4 kg test fluorocarbon by a small hook placed in the dorsal musculature at the posterior insertion of the dorsal fin (as in Cooke and Philipp 2004; Danylchuk et al. 2007b; Brownscombe et al. 2013). Fish that were not monitored for 10 min (e.g., because the line was cut by a coral) were excluded from the study. The float was attached to a separate spinning-style fishing rod with the bail open so that the fish could freely swim without resistance from the reel (Figure 2). The rod was used to confirm the fish's fate after trial releases revealed that the bonefish quickly travelled into the lagoon where they were difficult to track and the float line was often tangled on coral, which would have been interpreted as shark depredation without the close observation afforded by the fishing rod tether. Prior to release, each fish received a reflex impairment score (0–3; score of 0 indicative of no impaired reflexes), based on its response to three reflex action mortality predictors (RAMP): body flex, orientation, and tail grab (see Brownscombe et al. 2013). The body flex test was administered by holding the fish in air (<2 s), followed by an orientation test, in which it was placed supine in the water to determine whether it reoriented within 3 s. The tail grab–startle response was assessed last by startling the fish and evaluating whether it initiated a burst swimming response. We estimated the density of sharks in the vicinity of the angling event by visual count (as per Danylchuk et al. 2007a). Because we were fishing on shallow flats we could confidently assess the local density of sharks.

After assessing fish-handling practices, we conducted a subsequent study on fish recovery and tested two potential release strategies to evaluate practical and accessible methods for

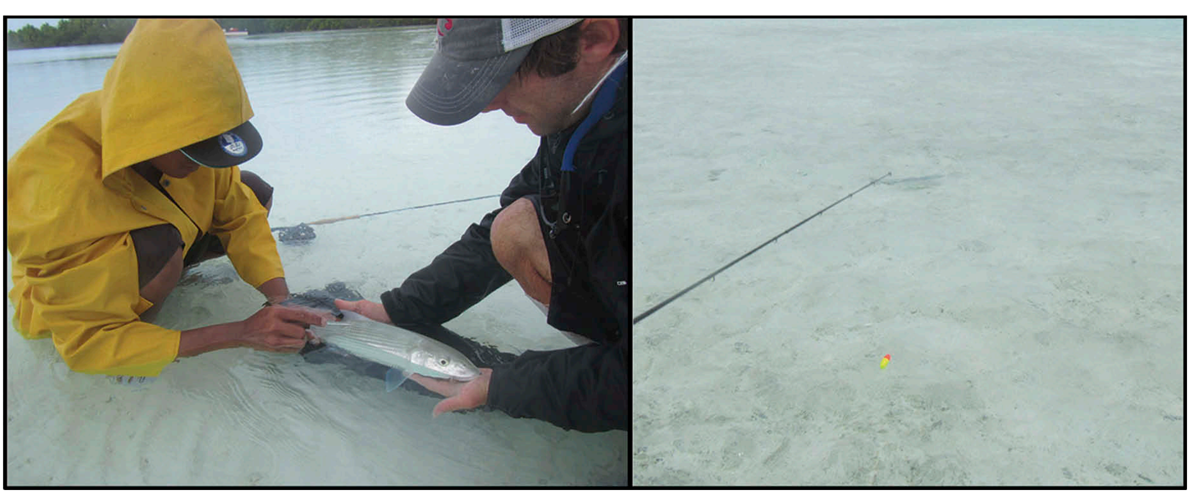

FIGURE 1. External dart tagging of Shortjaw Bonefish and postrelease monitoring with external float at Anaa Atoll.

FIGURE 2. A Shortjaw Bonefish head severed by a Blackfin Reef Shark after recreational angling catch and release.

postcapture care and their influence on PRP. For this experiment, fish were captured (as above) and either immediately released or held for 30 min for recovery. Immediately prior to release, length was quickly measured, fish were tagged with the bobber at the posterior dorsal fin insertion to assess postrelease behavior and survival, and the fish was released supine to assess orientation. Upon orientation, the tail grab reflex action was assessed (i.e., body flex was not assessed; RAMP score = 0–2). Fish in the holding treatment were initially placed in recovery bags and towed behind anglers for 30 min (see Brownscombe et al. 2013). However, we abandoned this practice in favor of stationary holding in a modified recovery bag (40 × 85 cm) for 30 min prior to release. The modified recovery bag held its structure better while providing ample water flushing and protection from predators.

Ethics statement.—Fish handling techniques, particularly air exposure intervals, were refined to simulate angler behavior in tropical Pacific bonefish fisheries, based on experience in French Polynesian bonefish fisheries, as well as global fisheries. The University of Massachusetts–Amherst Institutional Animal Care and Use Committee (protocol number 2013-0013) approved animal use and handling practices for this study.

Data analysis.—There were two outcomes of our PRP study: fish either survived or were depredated by sharks. Binary outcomes are effectively modeled by logistic regression; however, survival analysis (i.e., time-to-event analysis) increases statistical power by considering the monitoring period (Harrell 2015). Survival analysis was developed for medical studies in which patients experience different treatments; monitoring in such studies can extend for variable intervals, and therefore, survival analysis allows censorship when subjects drop out of studies or when studies end before an event occurs (i.e., right censorship). We modeled bonefish survival data using Cox proportional hazards regression, a semiparametric survival analysis (Harrell 2015). Cox proportional hazards was implemented using the coxph function in the R (R Core Team 2016) package survival (Therneau 2015). Models were fully prespecified, and no model selection was conducted to avoid biased parameter estimates (Harrell 2015). The proportionality of hazards assumption was assessed by regressing the Schoenfield residuals (extracted with the cox.zph function) against time at $\alpha = 0.05$ (Hosmer and Lemeshow 1999). Kaplan–Meier survival curves (Cox and Oakes 1984) were plotted for treatment predictors with the ggsurv function the survminer package (Kassambara and Kosinski 2016), which interfaces with ggplot2 (Wickham 2009). Two survival analyses were conducted, one each to determine the factors influencing bonefish PRP in the handling and release experiments. Treatment effects (air exposure interval and release practice), fish length, and number of visible sharks were considered as predictors in both models. Analyses of variance (function aov) and *t*-tests (function t.test) were used to examine relationships between predictor variables.

RESULTS

Accounts of Predation Events

While fishing, we encountered an average of 1.14 (SD, 1.26) sharks per angler-hour. Sharks were generally not overtly aggressive but were attracted to the presence of anglers, often approaching within 1 m of an angler. After landing a bonefish and before releasing it, we observed Blackfin Reef Sharks in the vicinity and noted two general behavioral states: (1) circling, or (2) moving across the flat. Sharks that were circling were clearly alert to the presence of a vulnerable fish and routinely swam within 1–2 m of anglers unhooking fish. Sharks that were moving across the flat often intercepted the scent trail of a fish recently captured or released, at which point there was an obvious change in the shark's behavioral state characterized by rapid swimming and a directional turn to follow the scent trail. Predation events were generally subtle without clouds of blood or large splashes but were often preempted by rapid swimming by the bonefish (Figure 2). Among bonefish that were depredated, the average survival was for 326 s (Figure 3).

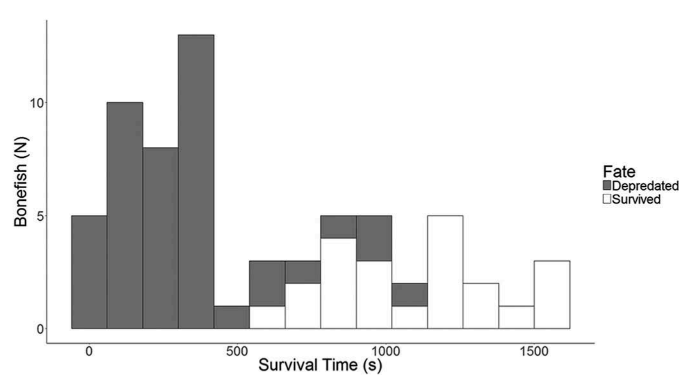

FIGURE 3. Histogram of postrelease monitoring of Shortjaw Bonefish released after experimental angling. Bonefish that were eaten by sharks are shaded in gray whereas survivors are represented in white bars. Results are combined for both handling and release experiments.

Analysis of PRP

Handling practices.—We captured, tagged, and released 40 Shortjaw Bonefish (mean = 45 cm FL, SD = 5) to study the effects of handling practices on PRP and mortality. One bonefish was depredated off the line by a shark prior to landing and was not included. Fifteen bonefish received no air exposure, 13 received a 10-s air exposure, and 12 received a 30-s air exposure (Table 1). Six bonefish were hooked in the interior mouth, but no fish bled or had visible tissue damage. Bonefish that received 30 s of air exposure had the highest mean RAMP scores upon release (mean = 0.25, SE = 0.13), but not significantly higher than those that received 10 s (mean = 0.15, SE = 0.13) or no air exposure (mean = 0.13, SE = 0.12; $F_{2,\ 37} = 0.24$, $P = 0.79$). There was no immediate mortality of captured fish prior to release; however, only 17 bonefish were categorized as survivors owing to postrelease predation by sharks. There was no significant difference in the estimated number of sharks present among the air exposure treatment groups ($F_{2,\ 37} = 0.23$, $P = 0.79$).

Bonefish briefly exposed to air (10 s) had significantly higher incidence of depredation than those not exposed to air ($z = 2.43$, $P = 0.02$); however, there was no difference for fish exposed 30 s to air ($z = 0.81$, $P = 0.42$; Figure 4). Length was not a significant factor ($z = 0.25$, $P = 0.80$); however, there was a significant effect of the number of sharks observed ($z = 4.26$, $P < 0.01$; test of proportionality of hazards: $\chi^2 = 3.24$, $P = 0.52$).

Release practices.—We compared PRP for 26 Shortjaw Bonefish (mean = 48 cm FL, SD = 5) separated into immediate release ($N = 13$) and 30-min-recovery treatment groups ($N = 13$). One additional bonefish was eaten by a shark prior to landing and was not included. For fish in the recovery treatment, the number of sharks present upon landing (1, SD = 1) increased significantly to a mean of 2 (SD, 2) after 30 min in the recovery bag ($t_{18} = 2.30$, $P = 0.03$). Consequently, there was a higher spread in estimated shark densities for fish held for 30 min (range = 0–8) than immediately released (range = 0–3), but no significant difference in estimated shark index between the two treatment groups ($t_{18} = 0.77$, $P = 0.45$). There

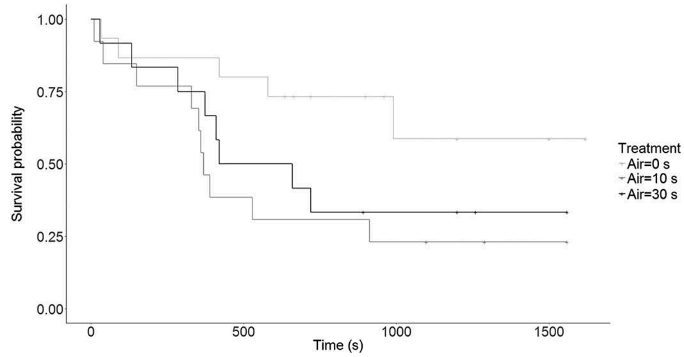

FIGURE 4. Kaplan–Meier survival curve of Shortjaw Bonefish survival in the three air-exposure treatments (0 s, 10 s, or 30 s).

was no immediate or holding mortality and all bonefish were released alive after 30 min in the recovery bag in good condition (mean RAMP score = 0.0). Bonefish that were immediately released had significantly higher reflex impairment than those held in the recovery treatment (RAMP score = 0.76; $t_{12} = -3.33$, $P = 0.01$). There was no difference in postrelease predation between the immediate release and 30-min-recovery treatments ($z = 0.20$, $P = 0.84$; Figure 5) nor was length a significant driver of depredation ($z = 1.26$, $P = 0.21$). Similar to the release practices, however, the number of sharks sighted was a significant factor ($z = 3.14$, $P < 0.01$; test of proportionality of hazards: $\chi^2 = 1.93$, $P = 0.59$).

DISCUSSION

Postrelease predation is an immediate conservation concern for Shortjaw Bonefish in Anaa and probably in other Pacific fisheries given that many such islands have particularly high predator densities (Stevenson et al. 2007). In this study, 66% of angled bonefish were depredated by Blackfin Reef Sharks on the flats and in the lagoon. Depredation of the Bonefish by Lemon Sharks *Negaprion brevirostris* or Great Barracuda *Sphyraena barracuda* in The Bahamas has been observed, albeit less frequently. Cooke and Philipp (2004)

TABLE 1. Summary of Shortjaw Bonefish catch-and-release treatments. In the first component, air exposure intervals (0, 10, 30 s) were compared, followed by a study in which release practices were compared (immediate release or 30 min recovery in a modified recovery bag).

		Mean ± SD				
Treatment	Number treated	Length (cm)	Fight time (s)	Visible sharks	Total handling time (s)	Depredation (%)
Air: 0 s	15	45 ± 5	161 ± 33	1 ± 1	678 ± 209	33
Air: 10 s	13	43 ± 5	158 ± 31	1 ± 1	573 ± 76	77
Air: 30 s	12	47 ± 4	149 ± 18	1 ± 2	579 ± 100	67
Immediate release	13	48 ± 6	159 ± 47	1 ± 2	187 ± 132	69
30-min recovery	13	48 ± 4	138 ± 34	2 ± 2	1,829 ± 401	92
Total	66	46 ± 5	153 ± 34	2 ± 2	769 ± 594	67

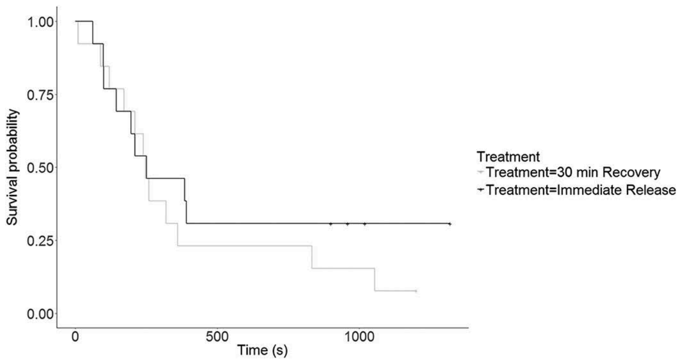

FIGURE 5. Kaplan–Meier survival curve of Shortjaw Bonefish survival in the two release practice treatments: immediate release or 30-min holding.

noted 0% and 39% depredation in low-predator (N = 23) and high-predator density areas (N = 18), respectively, Danylchuk et al. (2007a) observed only 1 mortality among 12 fish, Danylchuk et al. (2007b) observed 17% of 88 Bonefish depredated, and Brownscombe et al. (2013) noted 0% and 10% predation of Bonefish immediately released compared to held for 15 min recovery, respectively. The high frequency of Shortjaw Bonefish depredation at Anaa Atoll may raise concern about the viability of recreational catch-and-release angling in this location. However, fisheries have socioeconomic importance that extend beyond many biological considerations, and therefore, our efforts in this study focused on identifying best practices for anglers and guides targeting Shortjaw Bonefish in this fishery.

Shortjaw Bonefish appeared resilient to both 10-s and 30-s air exposure based on quantifications of reflex impairment and comparison with those individuals in the 0-s air exposure treatment group. Treatment with both 10-s and 30-s air exposures resulted in more frequent PRP than 0-s exposure, although only the 10-s exposure was significant. Danylchuk et al. (2007a), who considered the effects of longer air exposure on Bonefish, found infrequent depredation compared with individuals that were released more quickly. The response to angling and handling may have individual variation, and Danylchuk et al. (2007b) suggested that loss of equilibrium predicted PRP. Longer air exposure intervals in that study were predictive of loss of equilibrium, suggesting that restricting air exposure is relevant to improving survival of angled Bonefish. Bonefish in Danylchuk et al. (2007b) released without equilibrium had an average air exposure of 60 s, twice that of our longest air exposure interval, which might explain why we only observed loss of equilibrium in two individuals (one each at 10 s and 30 s air exposure). Brownscombe et al. (2013) advanced this paradigm by determining that it took 4 min for Bonefish to lose body flex, orientation, and tail-grab reflexes. In our study, we focused on brief air exposure (Cook et al. 2015; Lennox et al. 2016), which is probably why we did not observe extensive reflex impairment of bonefish being released.

There is an interest in mitigating the potential consequences of angling with tools (Farrell et al. 2001) and techniques (Brownscombe et al. 2013, 2017) for facilitating recovery of fish prior to release into the wild. Our initial approach to hold fish for 30 min in a recovery bag towed behind the angler (as in Brownscombe et al. 2013) was abandoned due to its negative effect on fish condition while wading through shallow water. For this reason, we modified the recovery bags to increase structural integrity and anchored them in the water where the fish would be able to rest and recover by active gill ventilation (i.e., there was minimal flow to provide assisted ventilation). The modified recovery bag performed well for protecting fish from sharks, and RAMP scores suggested that fish in the recovery treatment had improved condition compared with fish that were immediately released. The Bonefish that Brownscombe et al. (2013) allowed to recover for 15 min exited the release area sooner and with greater tailbeat frequency and amplitude after release than those immediately released. Correspondingly, we found that Shortjaw Bonefish had no reflex impairment after holding in the recovery bag. The bonefish in the recovery treatment underwent frequent PRP, probably because sharks were attracted to their scent while held in the bag (see Dallas et al. 2010); i.e., we observed more sharks after 30 min than when fish were first placed in the bag. Stress metabolites remain elevated in fish tissue for hours after induction (Friedlander et al. 2007; Suski et al. 2007). Murchie et al. (2009) found that Bonefish in The Bahamas were very stressed by transport and holding, and although recovery bags have now been extensively tested as a potential solution to postcapture physiological disturbances, few studies have attempted to establish whether such holding prolongs the stress response of fish. Even though probability of PRP was not higher for fish held 30 min than for those immediately released, we observed limited utility in the use of short durations for facilitated recovery.

According to a review of postrelease predation in fisheries, few studies have quantified the abundance of predators in postrelease mortality studies (Raby et al. 2014). The shallow, clear flats of Anaa were ideal for visually enumerating sharks to estimate their abundance after release. We encountered an abundance of Blackfin Reef Sharks while fishing at Anaa, and correspondingly, we measured a high probability of postrelease predation in the presence of sharks. Similar to studies conducted on congeneric Bonefish in The Bahamas (Cooke and Philipp 2004; Danylchuk et al. 2007a, 2007b; Brownscombe et al. 2013), we found that the most important factor contributing to Shortjaw Bonefish PRP was generally the number of visible sharks at the release location. Factors moderating shark density on the flats were not considered, and there were probably some spatial and temporal differences in the local shark density that would govern the probability of postrelease predation. Like other fish, sharks are capable of learning and can become habituated to interacting with commercial and recreational fisheries (Guttridge et al. 2009).

However, Papastamatiou et al. (2009) observed that Blackfin Reef Sharks in the lagoon of Palmyra Atoll had high fidelity to well-defined home ranges and therefore may not be likely to travel long distances to anglers. Subsequently, Papastamatiou et al. (2011) provided limited evidence for informed or oriented movement patterns among Blackfin Reef Sharks; rather, sharks patrolled within defined home ranges. Together, this suggests that Blackfin Reef Sharks in the Anaa lagoon were patrolling relatively small home ranges but in high abundance on flats. Ultimately, PRP of bonefish was likely a function of chance encounters with sharks. Given the high shark densities, the chance of encounter probability with sharks was high. Further research or local knowledge may reveal areas of the lagoon where shark densities are consistently low, where fishing activities would have a lower impact. Areas with abundant sharks should be avoided whenever possible given the high probability of PRP.

Recovery of fish from exercise takes hours because fish must clear metabolites from the blood, restore substrates for anaerobic exercise (ATP, phosphocreatine, glycogen), buffer the blood, and repay oxygen debt (Wood et al. 1983; Scarabello et al. 1991; Wood 1991; Kieffer 2000). Friedlander et al. (2007) captured Bonefish at Palmyra Atoll and found that cortisol, the glucocorticoid stress hormone in fish, remained elevated for 3 d after angling. Even after 5 d holding for recovery, acoustically tagged bonefish had short intervals of signal transmission in the acoustic array, and it was hypothesized that most fish had been eaten by sharks soon after release (Friedlander et al. 2007). The period of vulnerability to predators could be longer than we were able to monitor (but see Cooke and Philipp 2004); however, most of the depredation was observed soon after release, and we monitored fish surviving up to 27 min while attached to the spinning rod. Nonetheless, electronic tagging with transmitters may assist in refining mortality estimates for longer periods after release. Another benefit to using telemetry would be to eliminate any confounding effects of tethering fish because the bobber and line create drag that can impede fish swimming. Cooke and Philipp (2004), who used intragastric acoustic transmitters to confirm the fate and survival of Bonefish, observed that mortality of the electronically tagged fish after 24 h was similar to those bobber-tagged after 30 min. Therefore, telemetry may not improve estimates of fate, particularly given complications in determining whether moving tags represent the tagged fish or a predator that depredated the tagged fish.

Recreational angling-based tourism that focuses on catching species of conservation concern such as Shortjaw Bonefish can be an important contributor to conservation (Cooke et al. 2016) and can yield economic benefits that uplift communities (Barnett et al. 2016). However, the sustainability of recreational Shortjaw Bonefish fisheries is affected by postrelease mortality in Anaa. Across fishery sectors, postrelease mortality is sometimes pervasive but fisheries can persist as long as it is recognized and the fishery is managed in such a way that postrelease mortality does not exceed the harvestable surplus of the population (i.e., compensatory not additive mortality). Demographic information and catch records will therefore be important to this fishery for proper management. The responsibility of managers, guides, and anglers is to mitigate postrelease mortality by instituting and adhering to best practices and to use available information to generate appropriate management strategies that account for mortality such that fishing effort and catch are moderated in a sustainable way. Our efforts to identify effective mitigation measures yielded some useful recommendations for anglers participating in these fisheries. Even brief exposure to air may increase susceptibility of Shortjaw Bonefish to PRP, and we deduced that fish held for 30 min attracted sharks. Therefore, anglers should strive to minimize handling time and release fish as quickly as possible to avoid aggregating sharks. Landing nets may be a useful tool for landing fish rapidly, barbless hooks should be used to reduce unhooking time, specialized hook removal tools, and strong fishing gear (e.g., line, tippet, rod) should be used so as not to prolong fighting time. In this study we also cut the line instead of removing hooks lodged in the mouth to reduce handling time. Photographs can be taken underwater to avoid air exposure (Cook et al. 2015). Avoiding fishing in areas where sharks are highly visible and frequently rotating fishing flats to avoid priming sharks on bonefish can contribute to reduce PRP in this fishery. Anglers should avoid fishing for bonefish when predation risk is elevated, such as when sharks are circling or when multiple sharks are sighted while fighting or unhooking a fish. Shortjaw Bonefish recreational fisheries have the potential to be an important economic sector for Anaa Atoll and continued efforts to refine best practices in these fisheries will be necessary to increase the long-term sustainability.

ACKNOWLEDGMENTS

This study was funded by Indifly, Hinano Bagnis, and an anonymous donor. We thank Costa del Mar, Patagonia, Inc., Nautilus Fly Reels, G. Loomis, RIO Products, and Umpqua Feather Merchants for their support. R.J.L. was supported by a travel grant from Carleton University and A.F. was supported by the University of Hawaii's Fisheries Ecology Research Laboratory. Cooke is supported by NSERC and the Canada Research Chairs Program. Brownscombe was supported by NSERC and the Steven Berkeley Marine Conservation Fellowship from the American Fisheries Society. A. J. Danylchuk was supported by the National Institute of Food and Agriculture, U.S. Department of Agriculture, and the Massachusetts Agricultural Experiment Station and Department of Environmental Conservation. Cooke and A. J. Danylchuk were both Bonefish and Tarpon Trust Research Fellows. Assistance and knowledge from Raphael, Ganaanui and Louise Raveino were indispensable for the success of this project, and we gratefully acknowledge their contributions and expertise.

REFERENCES

Adams, A. J., and S. J. Cooke. 2015. Advancing the science and management of flats fisheries for bonefish, tarpon, and permit. Environmental Biology of Fishes 98:2123–2131.

Adams, A. J., A. Z. Horodysky, R. S. McBride, T. C. MacDonald, J. Shenker, K. Guindon, H. D. Harwell, R. Ward, and K. Carpenter. 2013. Conservation status and research needs for tarpons (Megalopidae), ladyfishes (Elopidae), and bonefishes (Albulidae). Fish and Fisheries 15:280–311.

Barnett, A., K. G. Abrantes, R. Baker, A. S. Diedrich, M. Farr, A. Kuilboer, T. Mahony, I. McLeod, G. Moscardo, M. Prideaux, N. Stoecki, A. van Luyn, and M. Sheaves. 2016. Sportfisheries, conservation and sustainable livelihoods: a multidisciplinary guide to developing best practice. Fish and Fisheries 17:696–713.

Brownscombe, J. W., L. P. Griffin, T. Gagne, C. R. Haak, S. J. Cooke, and A. J. Danylchuk. 2015. Physiological stress and reflex impairment of recreationally angled bonefish in Puerto Rico. Environmental Biology of Fishes 98:2287–2295.

Brownscombe, J. W., L. Nowell, E. Samson, A. J. Danylchuk, and S. J. Cooke. 2014. Fishing-related stressors inhibit refuge-seeking behavior in released subadult Great Barracuda. Transactions of the American Fisheries Society 143:613–617.

Brownscombe, J. W., T. P. Parmar, J. Almeida, E. Giesbrecht, J. Batson, X. Chen, S. Wesch, T. D. Ward, C. M. O'Connor, and S. J. Cooke. 2017. The efficacy of assisted ventilation techniques for facilitating the recovery of fish that are exhausted from simulated angling stress. Fisheries Research 186:619–624.

Brownscombe, J. W., J. D. Thiem, C. Hatry, F. Cull, C. R. Haak, A. J. Danylchuk, and S. J. Cooke. 2013. Recovery bags reduce post-release impairments in locomotory activity and behavior of bonefish (*Albula* spp.) following exposure to angling-related stressors. Journal of Experimental Marine Biology and Ecology 440:207–215.

Campbell, M. D., R. Patine, J. Tolan, R. Strauss, and S. L. Diamond. 2010. Sublethal effects of catch-and-release fishing: measuring capture stress, fish impairment, and predation risk using a condition index. ICES Journal of Marine Science 63:513–521.

Colborn, J., R. E. Crabtree, J. B. Shaklee, E. Pfeiler, and B. W. Bowen. 2001. The evolutionary enigma of bonefishes (*Albula* spp.): cryptic species and ancient separations in a globally distributed shorefish. Evolution 55:807–820.

Cook, K., R. J. Lennox, S. J. Cooke, and S. G. Hinch. 2015. Fish out of water: how much air is too much air for released fish? Fisheries 40:452–461.

Cooke, S. J., Z. S. Hogan, P. A. Butcher, M. J. W. Stokesbury, R. Raghavan, A. J. Gallagher, N. Hammerschlag, and A. J. Danylchuk. 2016. Angling for endangered fish: conservation problem or conservation action? Fish and Fisheries 17:249–265.

Cooke, S. J., V. Messmer, A. J. Tobin, M. S. Pratchett, and T. D. Clark. 2014. Refuge-seeking impairments mirror metabolic recovery following fisheries-related stressors in the Spanish flag snapper (*Lutjanus carponotatus*) on the Great Barrier Reef. Physiological and Biochemical Zoology 87:136–147.

Cooke, S. J., and D. P. Philipp. 2004. Behavior and mortality of caught-and-released bonefish (*Albula* spp.) in Bahamian waters with implications for a sustainable recreational fishery. Biological Conservation 118:599–607.

Cooke, S. J., and D. P. Philipp. 2008. Improving the sustainability of catch-and-release bonefish (Albula spp.) fisheries: insights for anglers, guides and fisheries managers. Pages 359–381 *in* J. S. Ault, editor. Biology and management of the world's tarpon and bonefish fisheries. CRC Press, Boca Raton, Florida.

Cox, D. R., and D. Oakes. 1984. Analysis of survival data. Chapman and Hall, London.

Creel, S., and D. Christianson. 2008. Relationships between direct predation and risk effects. Trends in Ecology and Evolution 23:194–201.

Dallas, L. J., A. D. Shultz, A. J. Moody, K. A. Sloman, and A. J. Danylchuk. 2010. Chemical excretions of angled bonefish *Albula vulpes* and their potential use as predation cues by juvenile lemon sharks *Negaprion brevirostris*. Journal of Fish Biology 77:947–962.

Danylchuk, A. J., S. E. Danylchuk, S. J. Cooke, T. L. Goldberg, J. B. Koppelman, and D. P. Philipp. 2007a. Post-release mortality of bonefish, *Albula vulpes*, exposed to different handling practices during catch and release angling in Eleuthera, The Bahamas. Fisheries Management and Ecology 14:149–154.

Danylchuk, S. E., A. J. Danylchuk, S. J. Cooke, T. L. Goldberg, J. Koppelman, and D. P. Philipp. 2007b. Effects of recreational angling on the post-release behavior and predation of bonefish (*Albula vulpes*): the role of equilibrium status at the time of release. Journal of Experimental Marine Biology and Ecology 346:127–133.

Dobson, G. P., and P. W. Hochachka. 1987. Role of glycolysis in adenylate depletion and repletion during work and recovery in teleost white muscle. Journal of Experimental Biology 129:125–140.

Domenici, P., and R. Blake. 1997. The kinematics and performance of fish fast-start swimming. Journal of Experimental Biology 200:1165–1178.

Farrell, A. P., P. E. Gallaugher, J. Fraser, D. Pike, P. Bowering, A. K. Hadwin, W. Parkhouse, and R. Routledge. 2001. Successful recovery of the physiological status of Coho Salmon on board a commercial gillnet vessel by means of a newly designed revival box. Canadian Journal of Fisheries and Aquatic Sciences 58:1932–1946.

Friedlander, A., J. Caselle, J. Beets, C. Lowe, B. Bowen, T. Ogawa, K. M. Kelley, T. Calitri, M. Lange, and B. Anderson. 2007. Aspects of the biology, ecology, and recreational fishery for bonefish at Palmyra Atoll National Wildlife Refuge, with comparisons to other Pacific Islands. Pages 28–56 *in* J. S. Ault, editor. Biology and management of the world's tarpon and bonefish fisheries. CRC Press, Boca Raton, Florida.

Friedlander, A. M., and E. E. DeMartini. 2002. Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: the effects of fishing down apex predators. Marine Ecology Progress Series 230:e264.

Genovart, M., N. Negre, G. Tavecchia, A. Bistuer, L. Parpal, and D. Oro. 2010. The young, the weak and the sick: evidence of natural selection by predation. PLOS (Public Library of Science) ONE [online serial] 5(3):e9774.

Guttridge, T. L., A. A. Myrberg, I. F. Porcher, D. W. Sims, and J. Krause. 2009. The role of learning in shark behaviour. Fish and Fisheries 10:450–469.

Harrell, F. 2015. Regression modeling strategies: with applications to linear models, logistic and ordinal regression, and survival analysis. Springer, Berlin.

Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology 12:197–229.

Hosmer, D. W., and S. Lemeshow. 1999. Applied survival analysis: regression modelling of time to event data. Wiley, New York.

Kassambara, A., and M. Kosinski. 2016. survminer: drawing survival curves using 'ggplot2'. R package version 0.2.4. Available: https://CRAN.R-project.org/package=survminer. (July 2017).

Kieffer, J. D. 2000. Limits to exhaustive exercise in fish. Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology 126:161–179.

Knight, T. M., M. W. McCoy, J. M. Chase, K. A. McCoy, and R. D. Holt. 2005. Trophic cascades across ecosystems. Nature 437:880–883.

Lack, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford, UK.

Lennox, R. J., I. Mayer, T. B. Havn, M. R. Johansen, K. Whoriskey, S. J. Cooke, E. B. Thorstad, and I. Uglem. 2016. Effects of recreational angling and air exposure on the physiological status and reflex impairment of European Grayling (*Thymallus thymallus*). Boreal Environment Research 21:461–470.

Milligan, C. L. 1996. Metabolic recovery from exhaustive exercise in Rainbow Trout. Comparative Biochemistry and Physiology Part A: Physiology 113:51–60.

Milligan, C. L., and C. M. Wood. 1986. Intracellular and extracellular acid-base status and H^+ exchange with the environment after exhaustive exercise in the rainbow trout. Journal of Experimental Biology 123:93–121.

Murchie, K. J., S. E. Danylchuk, C. E. Pullen, E. Brooks, A. D. Shultz, C. D. Suski, A. J. Danylchuk, and S. J. Cooke. 2009. Strategies for the capture and transport of bonefish, *Albula vulpes*, from tidal creeks to a marine research laboratory for long-term holding. Aquaculture Research 40:1538–1550.

Ostfeld, R. S., and R. D. Holt. 2004. Are predators good for your health? Evaluating evidence for top-down regulation of zoonotic disease reservoirs. Frontiers in Ecology and Environment 2:13–20.

Packer, C., R. D. Holt, P. J. Hudson, K. D. Lafferty, and A. P. Dobson. 2003. Keeping the herds healthy and alert: implications of predator control for infectious disease. Ecology Letters 6:797–802.

Papastamatiou, Y. P., D. P. Cartamil, C. G. Lowe, C. G. Meyer, B. M. Wetherbee, and K. N. Holland. 2011. Scales of orientation, directed walks and movement path structure in sharks. Journal of Animal Ecology 80:864–874.

Papastamatiou, Y. P., C. G. Lowe, J. E. Caselle, and A. M. Friedlander. 2009. Scale-dependent effects of habitat on movements and path structure of reef sharks at a predator-dominated atoll. Ecology 90:996–1008.

R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available: https://www.R-project.org/. (August 2017).

Raby, G. D., M. R. Donaldson, S. G. Hinch, D. A. Patterson, A. G. Lotto, D. Robichaud, K. K. English, W. G. Willmore, A. P. Farrell, M. W. Davis, and S. J. Cooke. 2012. Validation of reflex indicators for measuring vitality and predicting the delayed mortality of wild Coho Salmon bycatch released from fishing gears. Journal of Applied Ecology 49:90–98.

Raby, G. D., J. R. Packer, A. J. Danylchuk, and S. J. Cooke. 2014. The understudied and underappreciated role of predation in the mortality of fish released from fishing gears. Fish and Fisheries 15:489–505.

Scarabello, M., G. J. F. Heigenhauser, and C. M. Wood. 1991. The oxygen debt hypothesis in juvenile Rainbow Trout after exhaustive exercise. Respiratory Physiology 84:245–259.

Sih, A., P. Crowley, M. McPeck, J. Petraaka, and K. Strohmeier. 1986. Predation, competition, and prey communities: a review of field experiments. Annual Review of Ecology, Evolution, and Systematics 16:269–311.

Stevenson, C., L. S. Katz, F. Micheli, B. Block, K. W. Heiman, C. Perle, K. Weng, R. Dunbar, and J. Witting. 2007. High apex predator biomass on remote Pacific islands. Coral Reefs 26:47–51.

Suski, C. D., S. J. Cooke, A. J. Danylchuk, C. M. O'Connor, M. A. Gravel, T. Redpath, K. C. Hanson, A. J. Gingerich, K. J. Murchie, S. E. Danylchuk, and J. B. Koppelman. 2007. Physiological disturbance and recovery dynamics of bonefish (*Albula vulpes)*, a tropical marine fish, in response to variable exercise and exposure to air. Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology 148:664–673.

Therneau, T. 2015. A package for survival analysis in S, version 2.38. Available: https://CRAN.R-project.org/package=survival. (August 2017).

Wallace, E. M. 2015. High intraspecific genetic connectivity in the Indo-Pacific bonefishes: implications for conservation and management. Environmental Biology of Fishes 98:2173–2186.

Wickham, H. 2009. ggplot2: elegant graphics for data analysis. Springer-Verlag, New York.

Wood, C. M. 1991. Acid-base and ion balance, metabolism, and their interactions, after exhaustive exercise in fish. Journal of Experimental Biology 160:285–308.

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