



Full length article

Effects of capture and handling on striped bass (*Morone saxatilis*) in the recreational fishery of coastal Massachusetts

Olivia T. Dinkelacker^a , Grace A. Casselberry^{a,*} , Lucas P. Griffin^{a,b},
 Sascha Clark Danylchuk^c, Steven J. Cooke^d, Andy J. Danylchuk^a

^a Department of Environmental Conservation, University of Massachusetts Amherst, Amherst, MA 01003, USA

^b Department of Integrative Biology, University of South Florida, Tampa, FL 33620, USA

^c Keep Fish Wet, Amherst, MA 01002, USA

^d Department of Biology, Carleton University, Ottawa, ON K1S 5B6, Canada

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ABSTRACT

Striped bass (*Morone saxatilis*) are a highly valued recreational fishery along the eastern coast of North America, with most hooked fish released voluntarily or due to regulations. Understanding how striped bass respond to capture and handling, particularly air exposure, is crucial for improving management and angler practices to maximize post-release survival. This study evaluated the physical and physiological condition of 521 striped bass subjected to catch-and-release angling across different gear and tackle types and five air exposure treatments using reflex action mortality predictors. A subset of striped bass ($n = 37$) caught on conventional gear and double treble hook lures were fitted with triaxial accelerometer biologgers to assess short-term post-release activity across three air exposure treatments. Reflex impairment increased with higher water temperatures, longer fight and handling times, increased air exposure, and hooking in locations other than the jaw. Physical injury from foul hooking was more frequent with conventional gear, while deep hooking occurred more often with fly gear. Post-release activity was influenced by time following release, with higher activity observed in striped bass not air exposed compared to those exposed for 30 s and 120 s. Within 20 min of release, all fish survived, demonstrating resilience to the tested conditions. Our findings suggest that anglers can minimize their impact by using single hooks, reducing fight and handling times, limiting air exposure, and avoiding high water temperatures, especially for striped bass larger than 65.4 cm. These findings can inform management decisions and hone best practices for catch-and-release of striped bass.

1. Introduction

Recreational fishing ranks among the most popular leisure activities globally and often represents the primary use of fish stocks (Arlinghaus et al., 2015; Coleman et al., 2004). Fish that are caught recreationally are sometimes harvested for food, although it is estimated that up to 60 % of fish caught worldwide are released back into the water (Cooke and Cowx, 2004b). Motivations behind releasing fish include compliance with slot or bag limits, seasonal closures, or as bycatch (Cooke and Schramm, 2007b). Increasingly, however, many anglers are motivated by a conservation ethic, leading to a large number of fish being voluntarily released (Policansky, 2002). While catch-and-release serves as a tool to minimize impacts on individual fish (Adams, 2017; Arlinghaus et al., 2007; Cooke and Philipp, 2004a), its broader success is largely

dependent upon the contribution of released fish to the maintenance of the population (Aas et al., 2002; Quinn, 1996).

Over the past few decades, a growing body of science has focused on the physical, physiological, and behavioral responses of fish to capture and handling (reviewed in Bartholomew and Bohnsack, 2005; Arlinghaus et al., 2007), with the outcome of these studies being used as the basis of ‘best practices’ to reduce negative impacts of angling on fish (Cooke and Suski, 2005; Brownscombe et al., 2017). For instance, fish subjected to catch-and-release experience varying levels of physical injury and physiological stress that can reduce post-release survival or have a range of sublethal impacts, including impaired swimming performance, reduced feeding ability, and diminished fitness (Cooke et al., 2002; Arlinghaus et al., 2007; Cooke and Cowx, 2004b; Cooke and Philipp, 2004a; Bartholomew and Bohnsack, 2005). The responses to

* Corresponding author.

E-mail address: gcasselberry@umass.edu (G.A. Casselberry).

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catch-and-release can be specific to gear type (Cooke et al., 2003a, 2003b), angling and handling practices (Brownscombe et al., 2017), target species, and environmental conditions (Cooke and Suski, 2005). To maximize the potential of catch-and-release as a conservation tool, it is imperative to quantify physical injury resulting from hooking (Muoneke and Childress, 1994), assess physiological and reflex impairment (Gagne et al., 2017; Brownscombe et al., 2015; McLean et al., 2020), evaluate post-release activity and behavior (Brownscombe et al., 2013; Holder et al., 2020; LaRochelle et al., 2021; Lennox et al., 2018; Griffin et al., 2022) and develop species-specific science-based best practices.

The integration of reflex action mortality predictors (RAMP) and triaxial accelerometer biologgers has become a reliable method for evaluating the cumulative effects of capture and handling on fish during release. Assessment of RAMP involves evaluating the presence or absence of multiple (usually between 2 and 5) reflexes identified to be consistently present in vigorous individuals (Davis, 2010; Raby et al., 2012). Previous studies provide evidence that these tests are often predictive of short-term post-release behavior and/or mortality (Raby et al., 2012; Brownscombe et al., 2013, 2015; Lennox et al., 2024). Triaxial accelerometer biologgers effectively quantify fine-scale activity, behavior, and short-term mortality of fish after release (Holder et al., 2020; LaRochelle et al., 2021; Griffin et al., 2022). These biologgers are attached to fish in a minimally invasive manner and measure acceleration (g) across three axes (x, y, z). When combined with RAMP assessments, they provide detailed insights into additional aspects of the angling event and environmental conditions, helping to bridge critical gaps in our understanding of how fish respond to capture, handling, and recovery (Brownscombe et al., 2013).

Striped bass (*Morone saxatilis*) are the target of one of the most popular and valuable recreational fisheries along the eastern seaboard of the North America. For example, in 2016, the striped bass recreational fishery generated approximately \$13 billion USD of economic activity and contributed nearly \$8 billion to the region's GDP annually (Southwick Associates, 2019). Striped bass undertake seasonal nearshore migrations typically from North Carolina in the fall and winter to Nova Scotia in the summer months (LeBlanc et al., 2020; Secor et al., 2020), providing anglers with a wide range of opportunities to target this species, resulting in an annual average catch rate of over 30 million (National Marine Fisheries Service, 2018). Although considerably more striped bass are harvested in the recreational fishery (over 80 %) than in the commercial fishery, even more of the striped bass caught by recreational anglers are released (National Marine Fisheries Service, 2018; Carr-Harris and Steinback, 2020). Despite high release rates in the recreational fishery, striped bass stocks along the Atlantic coast of North America are in decline (Atlantic States Marine Fisheries Commission, 2023). Intense overfishing, along with habitat degradation and poor recruitment, led to the collapse of the striped bass stock in the early 1980s (Richards and Rago, 1999; Uphoff, 2023), and although some rebuilding occurred because of subsequent management efforts, including a moratorium, reduced bag limits, quotas, and slot limits, the stock continues to be classified as overfished (Atlantic States Marine Fisheries Commission, 2023). In response to poor recruitment since 2019 (Durell and Weedon, 2023), the Atlantic States Marine Fisheries Commission (ASMFC) enacted an emergency regulation in 2023, decreasing the harvestable slot limit across US Atlantic states to fish between 28 and 31 in. (71.12–78.84 cm; Atlantic States Marine Fisheries Commission, 2022), resulting in an even higher number of striped bass mandatorily being released.

Understanding the fate of striped bass following release is imperative for informing management actions and changing social norms in the fishing community (Bruskotter and Fulton, 2007; Guckian et al., 2018). Current estimates of post-release mortality for striped bass in recreational fisheries range from 0 % to 67 % (Graves et al., 2009; Dean et al., 2024), reflecting the varied outcomes for fish depending on the range of angling factors that were tested and the duration monitored. Previous

research on striped bass identified a wide suite of factors that affect physical injury, physiological stress, and post-release mortality, including hooking location (Diodati and Richards, 1996; Millard et al., 2005; Dean et al., 2024), air temperature (Bettoli and Osborne, 1998), water temperature (Millard et al., 2005; Nelson, 1998; Wilde et al., 2000; Griffin et al., 2024), fight duration (Thompson et al., 2002; Griffin et al., 2024), handling time (Harrell, 1988; Nelson, 1998; Dean et al., 2024), and fish size (Lukacovic and Uphoff, 2002). However, many of these studies (Diodati and Richards, 1996; Nelson, 1998; Millard et al., 2005) held fish in confinement following release, which may have reduced exposure to predators and other natural environmental factors as well as introduced additional stress, potentially confounding results (Cooke et al., 2002). To overcome these methodical challenges, Graves et al. (2009) employed pop-up satellite archival tag technology to assess post-release survival of striped bass released, however the achieved sample size was small (n = 8). Dean et al. (2024) used acoustic transmitters to estimate a mortality rate of 10 % (n = 284) for striped bass caught on single and circle hooks; however, their study focused exclusively on fish captured with bait. Additionally, while fish responses to catch-and-release can vary by gear type (Brownscombe et al., 2017), only one study has investigated the responses of striped bass based on different gear types (i.e., conventional spin versus fly tackle; Griffin et al., 2024). Finally, none of the studies to date have specifically assessed the effects of air exposure, despite its significant impact on other recreationally targeted species (Cook et al., 2015; Griffin et al., 2022). As such, a substantial gap remains in our understanding of the scale and scope of how capture and handling affect the post-release survival of striped bass.

The objective of our study was to quantify the physical injury and reflex impairment of striped bass across a range of gear types (i.e., conventional spin and fly tackle) and air exposure treatments using RAMP scores. Additionally, for a subset of fish, we assessed short-term (20-minute) post-release activity and behavior using triaxial accelerometer biologgers after different durations of air exposure. Our results can inform management decisions and species-specific science-based best practices that anglers can adopt to minimize their impact on striped bass intended for release.

2. Materials and methods

2.1. Capture and handling

Sampling occurred between May 6 and October 24, 2023 and May 5 and July 3, 2024 along the coast of Massachusetts, United States. Striped bass were caught by volunteer recreational anglers using conventional spin or fly fishing gear with a variety of artificial lures or flies. For each fish, we measured fight time as the duration (in seconds) from hooking to landing, and handling time as the duration (in seconds) from landing to release. To avoid confounding effects, several elements of fish handling were standardized across all treatments. Striped bass were landed by hand by grabbing the lower jaw, always held horizontally, and supported at the midbody. Dip nets were never used to assist with landing the fish due to the increased risk of external injury, which could be a confounding effect (Twardek et al., 2019). Similarly, lip gripping tools were not used to land fish to avoid the risk of injury and potential confounding effects (Danylchuk et al., 2008).

Once landed and before removing the hook, physiological condition was assessed using RAMP (Davis, 2010). Reflex action mortality predictor scoring consisted of assessing: 'body flex,' the presence of muscle contraction in the torso when a fish is lifted from the center of its body; 'tail grab,' the ability to exhibit rapid swimming behavior in an attempt to escape when the fish is grasped by the caudal peduncle; 'head complex,' the presence of consistent opercular movements; 'vestibular ocular response,' the ability of the eye to track and adjust with changes in the fish's orientation; and 'equilibrium,' the fish's ability to right itself within three seconds after being turned upside down in the water (Davis,

2010; Brownscombe et al., 2017; Lennox et al., 2024). Each reflex test was scored as 0 (impaired) or 1 (unimpaired), and the cumulative total was converted into a proportional value between 0 and 1. Following this first reflex assessment (from here on referenced as RAMP 1), hook type (single J or treble hook, and number of hooks per lure) and anatomical hooking location (e.g., jaw or mouth, gills, pharynx, stomach, foul) was noted. Striped bass were measured, hook(s) removed, and subjected to one of five randomly selected air exposure treatments, 0 s, 10 s, 30 s, 60 s, or 120 s. Observations of recreational anglers fishing from boat and from shore showed that air exposure durations predominantly ranged between 30 and 120 sec (O. Dinkelacker, personal observations). Just prior to release, a second RAMP assessment (from here on noted as RAMP 2) was completed to evaluate the cumulative impact of capture and handling. Water temperature ($^{\circ}\text{C}$) was recorded at the time of release.

2.2. Post-release activity

To further quantify the effects of capture and handling, the post-release behavior for a subset of striped bass was measured using a triaxial accelerometer biollogger (TechnoSmArt Axy-Depth, Guidonia Montecelio, Italy). Due to logistical considerations (e.g., interference with shallow water structures), this assessment was limited to fish caught from boats using conventional fishing tackle and with lures outfitted with double treble hooks. Biolloggers were temporarily affixed on the ventral side of the body with a Velcro strap (1 cm wide) wrapped between the first and second dorsal fins (LaRochelle et al., 2021) to measure post-release activity. Fish affixed with biolloggers were randomly assigned to one of three air exposure treatments, 0 s, 30 s, or 120 s. For the 30 s and 120 s air exposure treatments, loggers were secured while the fish was already out of the water to not increase handling time. For 0 s treatment, loggers were attached immediately after the striped bass was measured just prior to release, with logger attachment taking < 20 s.

The Velcro strap with the accelerometer biollogger affixed to the striped bass was tethered to a fishing rod with braided Dacron fishing line. Once the logger-attached fish was released, the reel was put in free-spool setting. To ensure minimal line tension and realistic swimming behavior during the post-release monitoring period, the line was also supported by a slip bobber. After a monitoring period of 20 min, the logger package was removed from the striped bass by tightening the drag of the fishing reel and pulling firmly on the line which undid the Velcro strap allowing the biollogging package to be retrieved (Lennox et al., 2018; LaRochelle et al., 2021; Griffin et al., 2022). All accelerometer biollogger trials were conducted at a current speed of less than 1.3 km/h.

2.3. Data processing and analysis

All data processing and analyses were conducted in R (R Core Team, 2024). Values are presented as mean \pm 1 standard deviation (SD). Statistical assumptions were evaluated according to Zuur et al. (2010), and if violated, non-parametric tests were implemented, or log transformations were applied prior to analyses. Model selection was informed by the Akaike Information Criterion (AIC), and all model assumptions were evaluated. For ANOVAs, generalized linear models, and linear mixed models, Tukey tests were implemented via the glht function from the multcomp package (Hothorn et al., 2024) to compare differences among significant predictors. Other R packages for data processing and visualizations included rstatix (Kassambara, 2023), lubridate (Spinu, 2024), ggplot2 (Wickham, 2020), data.table (Dowle et al., 2024), and sjplot (Lüdtke, 2024).

2.3.1. Angling metrics

Differences in total length, fight time, handling time, and water temperature of captured striped bass were tested across gear types and

air exposure treatments using a Wilcoxon-rank-sum test and a Kruskal-Wallis test, respectively. Spearman's correlation coefficients (ρ) were calculated separately for the relationship between fight time and fish length for striped bass captured via conventional and fly gear. To analyze the distribution of hooking locations across hook types (double hook versus single hook) and gear types, Chi-Squared tests of Independence were used.

2.3.2. RAMP assessment

To identify the best predictors of RAMP 1 and RAMP 2 scores, generalized linear models with a binomial distribution were developed using the glmmTMB function from the glmmTMB package (Magnusson et al., 2017). For RAMP 1 score, candidate models included water temperature, fight time, hooking location, total length, and gear type. Given that significant differences in total length were observed across gear types, models that incorporated gear type also included total length to account for this effect. A separate set of candidate models was developed for RAMP 2 score, incorporating water temperature, fight time, hooking location, total length, gear type, handling time, and air exposure. Due to the observed differences in body size across gear types and variations in handling time across air exposure groups, models including gear type accounted for body size, while those incorporating air exposure also included handling time.

Because RAMP 1 and RAMP 2 were paired assessments on a single fish, we then explored the factors that most influenced changes in RAMP score from landing (RAMP 1) to release (RAMP 2). For each fish where both RAMPs were assessed, a RAMP differential score was calculated by subtracting the proportional RAMP 2 score from the proportional RAMP 1 score. Therefore, larger RAMP differential scores indicated a lower RAMP 2 score compared to the fish's initial RAMP 1 score. A candidate linear model set was then generated to determine the factors that most influenced a change in RAMP score within individuals with explanatory variables including air exposure treatment, gear type, body size, water temperature, hook type, fight time, and handling time.

2.3.3. Decision tree analysis

Decision tree analysis was used to explore the complex, potentially interacting, and non-linear relationships between the physiological impairment of striped bass and a wide range of measured angling and environmental factors. Decision trees use binary recursive partitioning to construct a hierarchical structure of parent and child nodes, systematically splitting the data based on predictor variables to create an overall tree (Breiman et al., 1984; De'Ath and Fabricius., 2000; Olden et al., 2008). Given the observed correlation between the equilibrium test of RAMP 2 and post-release activity values, the decision tree analysis concentrated on this reflex test, employing a range of input variables, including fight time, air exposure, handling time, anatomical hook location (jaw versus elsewhere), water temperature, total length, gear type, and hook type (double versus single hook) to predict reflex outcomes. The dataset was randomly partitioned into a training set (75 % of the total data) for constructing the decision tree and a test set (25 % of the total data) for evaluating its predictive performance. The decision tree model was created using the C5.0 algorithm (Quinlan, 1992) from the R package C50 (Kuhn and Quinlan, 2021).

Evaluation of tree performance and tree tuning to enhance the predictive accuracy of the test data was done by creating cross tables and confusion matrices (Lantz, 2019) using the gmodels (Warnes et al., 2018) and caret (Kuhn, 2021) packages. We prioritized identifying factors driving the loss of equilibrium by assigning a penalty three times greater for misclassifications of reflex absence compared to misclassification of reflex presence when constructing the cost matrix (Lantz, 2019). Additionally, to address the imbalance in the data and prevent overfitting, we set a threshold that allowed tree splits on nodes with a minimum of eight observations (Lantz, 2019).

2.3.4. Post-release activity

To prepare the raw acceleration data for analysis, static acceleration values for each axis were calculated by multiplying raw acceleration values by 9.81 m s^{-2} (gravitational acceleration, g) and averaged using a 2 s box smoother (Shepard et al., 2008; Brownscombe et al., 2018) with the *rollmean* function in the R package zoo (Zeileis et al., 2023). Subsequently, dynamic acceleration (fish movement) values were derived by subtracting the static acceleration values from the raw detection data. Overall dynamic body acceleration (ODBA, in units of g), an index of locomotor activity (Gleiss et al., 2011; Brownscombe et al., 2013), was then calculated using the absolute sum of the dynamic acceleration from all three axes (x, y, and z; Gleiss et al., 2011), and the mean was calculated at each minute post-release. Spearman correlation tests were employed to explore the relationship of RAMP 2 and individual reflexes that were most frequently failed in the study with ODBA. Additionally, T-tests were conducted to evaluate differences in ODBA values between striped bass with present and absent equilibrium. A linear model via the *lm* function in base R was used to assess the effects of water temperature, fight time, handling time, air exposure, and total length on post-release activity. We also fitted linear mixed models using the *lmer* function from the *lme4* package (Bates et al., 2015) to explore the effect of these angling factors as well as time following release on averaged ODBA values, which were aggregated at two-minute intervals to account for short-term fluctuations. Trial ID was always included as a random effect. Given that significant differences in handling time were observed across air exposure groups, handling time was incorporated in all candidate models including air exposure. To further explore the relationship of air exposure and ODBA across the monitoring period, including assessing potential differences in recovery timing among air exposure groups, we fitted separate linear mixed models for each air exposure group with minutes post-release (two-minute intervals) as the only covariate and trial ID as a random effect. Lastly, ANOVAs were used to identify differences in ODBA across air exposure groups at two-minute intervals.

3. Results

3.1. Angling metrics

A total of 521 striped bass were captured for this study; 332 on conventional gear and 189 on fly gear. Striped bass ranged in size from 25.4 cm to 102.8 cm total length. Mean total length was significantly higher for striped bass caught on conventional gear ($70.5\text{ cm} \pm 9.6\text{ cm}$) than those caught on fly gear ($62.8\text{ cm} \pm 11.3\text{ cm}$; $W = 29739$, $p < 0.001$). Gear type and body size were incorporated into future models and analyses to account for these effects. Striped bass were caught in water temperatures between $10\text{ }^{\circ}\text{C}$ and $24.4\text{ }^{\circ}\text{C}$ ($15.5\text{ }^{\circ}\text{C} \pm 2.1\text{ }^{\circ}\text{C}$) with no significant differences in temperature across gear types ($W = 21009$, $p > 0.05$) or air exposure groups ($H(4) = 2.01$, $p > 0.5$). Fight time ranged from 5 s to 558 s ($137\text{ s} \pm 82\text{ s}$) and there was no significant difference in fight time across gear types ($W = 21009$, $p > 0.05$) or air exposure groups ($H(4) = 2.01$, $p > 0.5$). Fight time was significantly, positively correlated with body size for striped bass caught on conventional gear and fly gear ($p < 0.001$; Fig. 1). Handling time ranged from 4 s to 434 s ($176\text{ s} \pm 76\text{ s}$), and there was no significant difference across gear types ($W = 22182$, $p > 0.05$). Handling time for striped bass in the 120 s air exposure treatment was significantly higher ($241\text{ s} \pm 66\text{ s}$; $H(4) = 70.53$, $p < 0.001$) than for striped bass in other air exposure groups (0 s: $175\text{ s} \pm 80\text{ s}$, $p < 0.001$; 10 s: $153\text{ s} \pm 67\text{ s}$, $p < 0.001$; 30 s: $157\text{ s} \pm 69\text{ s}$, $p < 0.001$; 60 s: $166\text{ s} \pm 60\text{ s}$, $p < 0.001$), driven by the duration of air exposure. Handling time and air exposure were included together in future models to account for these effects.

Data on RAMP 1 score was collected for 402 (conventional: $n = 263$, fly: $n = 139$) striped bass, all of which were retained for analysis of RAMP 1. The RAMP 2 assessment was done for 447 striped bass (conventional: $n = 274$, fly: $n = 173$), all of which were retained for analysis of RAMP 2. Some fish ($n = 45$) were not able to be sampled for RAMP 1

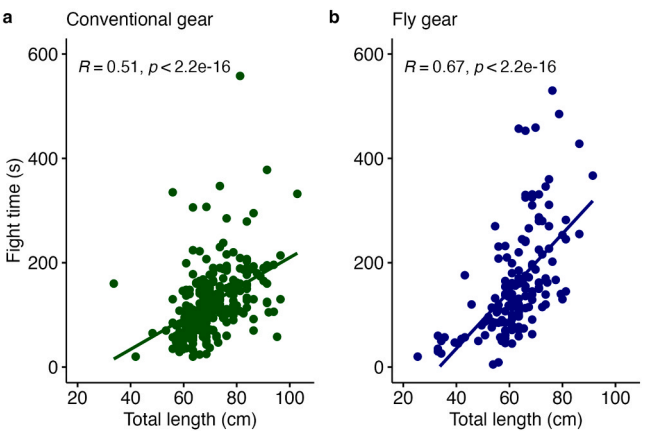


Fig. 1. The relationship between fight time and total length for striped bass captured via a) conventional gear or b) fly fishing. Spearman’s ρ correlation coefficients (R) and corresponding p-values are displayed along with the linear regression line of best fit for each gear type.

scores due to hook placement and/or configuration. For instance, a poor hook set on a single, barbless hook would result in the fish easily spitting the hook during the righting reflex assessment on RAMP 1, prohibiting further evaluation. Because of this, we opted to omit RAMP 1 assessments for fish we thought were at risk of escape, instead choosing to complete all other aspects of the assessment.

Data on anatomical hook location was recorded on 500 fish sampled for this study (conventional: $n = 318$, fly: $n = 182$; Table 1). Of these, striped bass caught on conventional gear were primarily hooked in the jaw or corner of the mouth, followed by foul hooking (e.g., head, eye), in the gills, and deep hooking in the pharynx or stomach. Striped bass caught on fly gear were predominately hooked in the jaw or corner of the mouth, but saw more frequent instances of deep hooking when compared to conventional gear (Table 1). Striped bass captured with conventional gear were more often caught with double hooks, while fish captured on fly gear were more often caught on single hooks. For double hooked tackle, the second hook (trailing hook) was lodged 53 % of the time on conventional gear and 0 % of the time on fly gear. With conventional gear, the first hook was lodged in the jaw significantly more

Table 1
Details on hook location and count for striped bass caught on conventional or fly fishing gear for both single and double hook trials.

	Conventional		Fly	
	n	%	n	%
Overall Hooking Location				
Foul hooked (head, eye, etc.)	22	6.9	1	0.5
Gills	12	3.8	8	4.4
Jaw or corner mouth	275	86.5	146	80.2
Pharynx or stomach	9	2.8	27	14.8
Hook Count				
Double hooks	193	60.7	5	2.7
Single hooks	125	39.3	177	97.3
First Hook Location				
Foul hooked (head, eye, etc.)	19	9.8	0	0.0
Gills	7	3.6	1	20.0
Jaw or corner mouth	161	83.4	2	40.0
Pharynx or stomach	6	3.1	2	40.0
Second Hook Location				
Foul hooked (head, eye, etc.)	65	64.4	0	0.0
Gills	6	5.9	0	0.0
Jaw or corner mouth	24	23.8	0	0.0
Pharynx or stomach	6	5.9	0	0.0
Single Hook Location				
Foul hooked (head, eye, etc.)	3	2.4	1	0.6
Gills	5	4.0	7	4.0
Jaw or corner mouth	114	91.2	144	81.4
Pharynx or stomach	3	2.4	25	14.1

often than in other locations ($X = 353.47$, $df = 3$, $p < 0.001$), and the second hook was significantly more often fouled hooked than hooked in other locations ($X = 87.55$, $df = 3$, $p < 0.001$). Though sample size was limited, the first hook on double hook fly tackle was most often hooked in the jaw or in the throat. With single hook conventional gear, striped bass were mostly hooked in the jaw, followed by the gills, foul hooked, or deep in the mouth. Fly angled striped bass caught on single hooks were mostly hooked in the jaw, followed by deep in the throat, the gills, and foul hooked.

3.2. Reflex indices

Proportional RAMP 1 scores (0: fully impaired, 1: fully unimpaired) ranged from 0.4 to 1.00 (0.82 ± 0.19), and RAMP 2 scores from 0.2 to 1.00 (0.75 ± 0.21) across all treatments and gear types. During RAMP 1, striped bass most commonly failed the equilibrium test (conventional: 36.9 %, fly: 15.8 %), the tail grab (conventional: 36.9 %, fly: 11.5 %), and the body flex (conventional: 33.8 %, fly: 27.3 %). No striped bass failed vestibular ocular response or ventilation during RAMP 1. Similarly, in RAMP 2 striped bass most commonly failed body flex (conventional: 55.8 %, fly: 45.7 %), tail grab (conventional: 53.7 %, fly: 31.8 %) and equilibrium (conventional: 31.4 %, fly: 23.7 %). During RAMP 2, one striped bass caught on conventional spin gear lost vestibular ocular response, one lost head complex and one lost both of these reflexes. One striped bass caught on fly gear lost vestibular ocular response during RAMP 2. Striped bass that lost either vestibular ocular response or head complex experienced air exposure durations of 60 s or 120 s and were either foul or gill hooked. The striped bass that lost both vestibular ocular response and head complex was 86.4 cm, was air exposed for 120 s, foul hooked, had a fight time of 295 s, and handling time of 315 s. Both fight and handling times were longer than the average.

Variation in the proportional RAMP 1 score was best modeled by an additive binomial generalized linear model including gear type, fight time, water temperature, total length, and anatomical hook location. Independent of body size, gear type had a significant effect on RAMP 1 score, with striped bass caught on conventional gear exhibiting lower scores compared to those caught on fly gear ($z = 5.39$, $p < 0.001$; Fig. 2a). Further, fight time had a significant inverse correlation with RAMP 1 ($z = -4.34$, $p < 0.001$; Fig. 2b). Water temperature, total length and anatomical hook location had no significant effect ($p > 0.05$). Variation in RAMP 2 was best modeled by an additive binomial

generalized linear model, including water temperature, fight time, handling time, air exposure, gear type, total length, and anatomical hook location. RAMP 2 decreased significantly with increasing water temperature ($z = -2.42$, $p = 0.02$; Fig. 3a), fight time ($z = -3.76$, $p < 0.001$; Fig. 3b), and handling time ($z = -5.2$, $p < 0.001$; Fig. 3c). Striped bass air exposed for 120 s had significantly lower RAMP 2 scores than those in the 0 s air group ($z = -3.07$, $p = 0.02$), and the 30 s air group ($z = -3.01$, $p = 0.02$; Fig. 3d). Striped bass captured via fly gear had significantly higher RAMP 2 scores than those caught on conventional gear ($z = 3.05$, $p < 0.01$; Fig. 3e). The effects of total length and anatomical hook location were not significant ($p > 0.05$).

RAMP differential scores ranged from -0.4 – 0.6 with a mean differential of 0.08 ± 0.02 , meaning that RAMP 2 scores were on average slightly lower than initial RAMP 1 scores. The best performing linear model for the drivers of RAMP differential included only air exposure (Fig. 4; F-statistic: 11.81, $p < 0.001$). Striped bass that were not exposed to air while being handled had significantly lower RAMP differential than those that were air exposed for 60 or 120 s (t value range: 3.1–5.7, $p < 0.01$ for both pairwise comparisons). Similarly, striped bass that were air exposed for only 30 s had significantly lower RAMP differential scores than those that were air exposed for 120 s (t value = 4.3, $p < 0.001$).

3.3. Decision tree analysis

The decision tree predicting the outcome of the equilibrium test identified air exposure, and total length as the most important factors for predicting reflex outcome with an attribute usage of 100 % and 76.75 % respectively. Hook type contributed 49.02 %, gear type 39.78 %, handling time 34.17 %, water temperature 23.53 %, anatomical hook location 21.29 %, and fight time 19.05 %. The decision tree model achieved a prediction accuracy of 62 %, correctly identifying the absence of equilibrium 22 of 33 times in the test dataset. The first data split used air exposure duration, grouping 0 s, 10 s, 30 s, or 60 s versus 120 s. The shorter air exposure duration group was then split by total length branching at greater than and less than or equal to 65.4 cm (Fig. 5). Most failed equilibrium tests were predicted for fish in the 0–60 s air exposure group, with a total length over 65.4 cm, caught on single hooks and fly gear, with fight time exceeding 232 s. The second highest number of failed equilibrium tests was predicted for striped bass that were air exposed for 120 s.

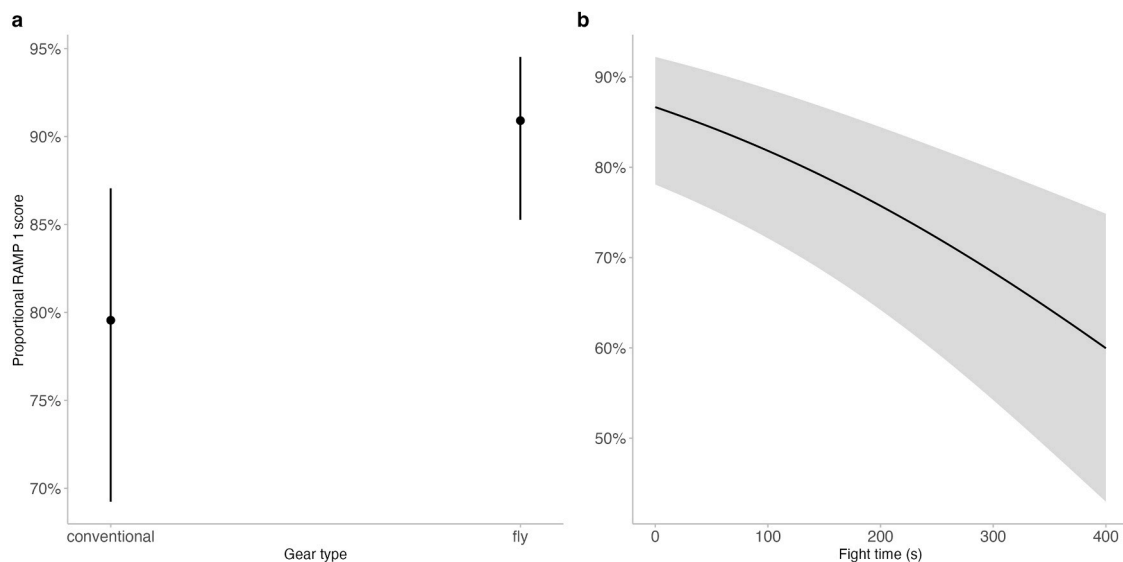


Fig. 2. The influence of a) gear type (with predicted means bounded by 95 % confidence intervals) and b) fight time (95 % confidence interval shaded around the line of best fit) on proportional RAMP 1 score.

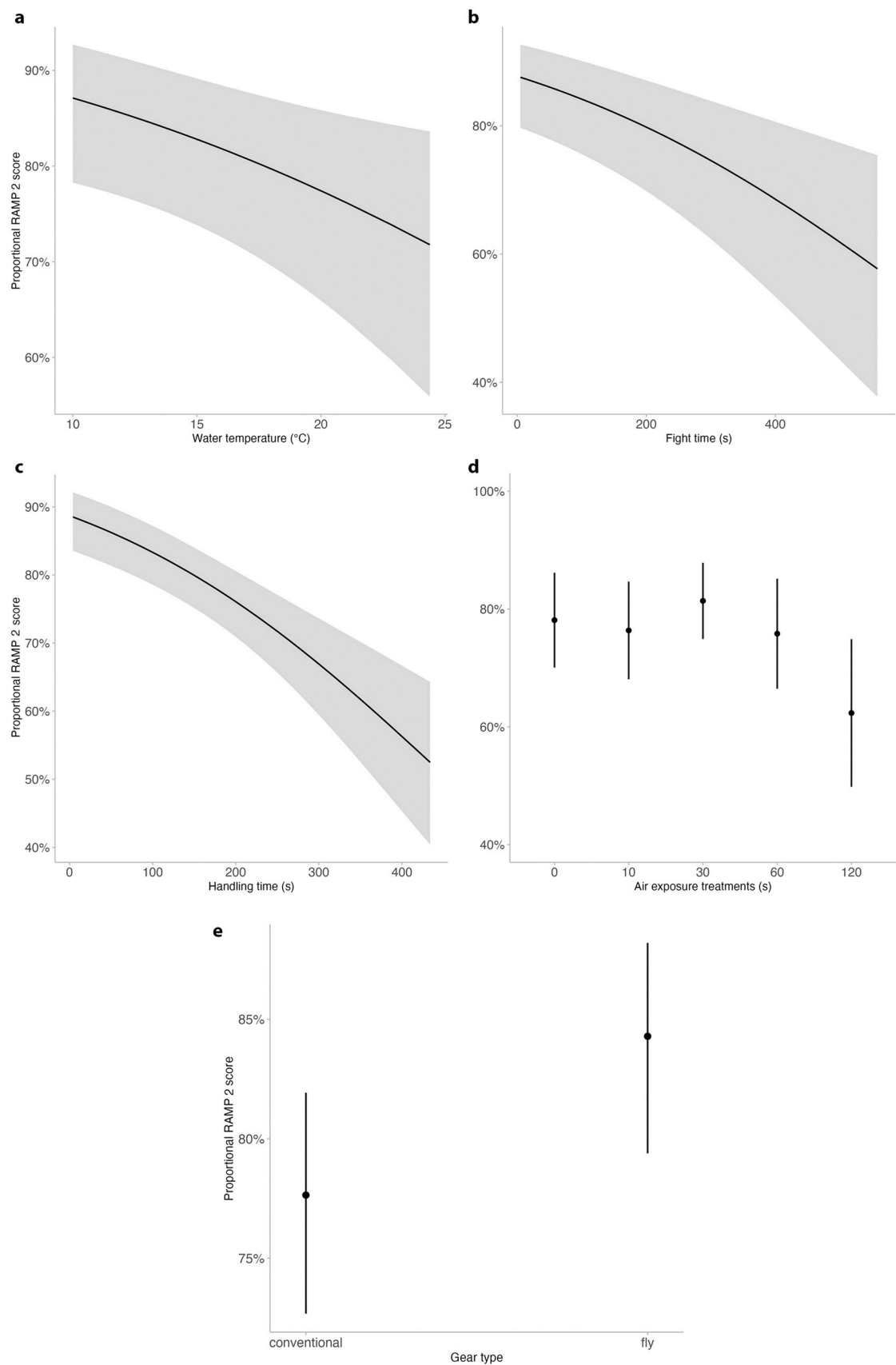


Fig. 3. The relationship between proportional RAMP 2 score and a) water temperature, b) fight time, c) handling time, d) air exposure, and e) gear type. For water temperature, fight time, and handling time, predicted means are represented by the linear trend line bounded by the 95 % confidence interval, which is shaded. For air exposure and gear type, predicted means are points bounded by 95 % confidence intervals.

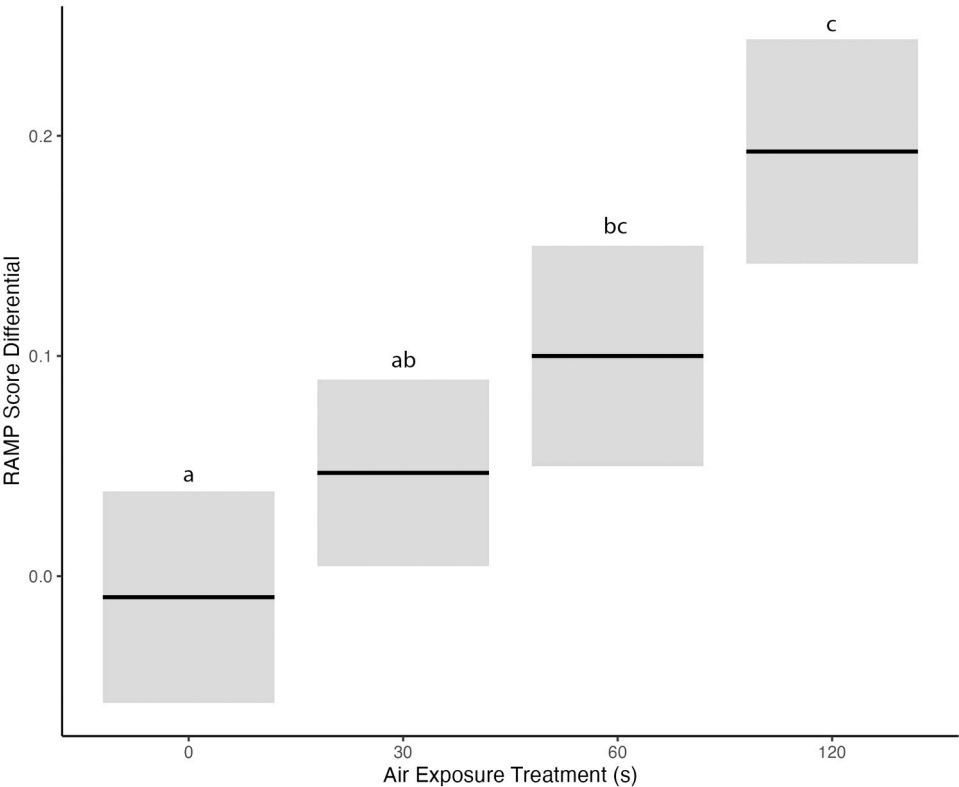


Fig. 4. Predictive plot for the relationship between RAMP score differential and air exposure treatment group. Means are presented as lines bounded by shaded 95 % confidence intervals. Differing letters denote significant differences across air exposure treatment groups.

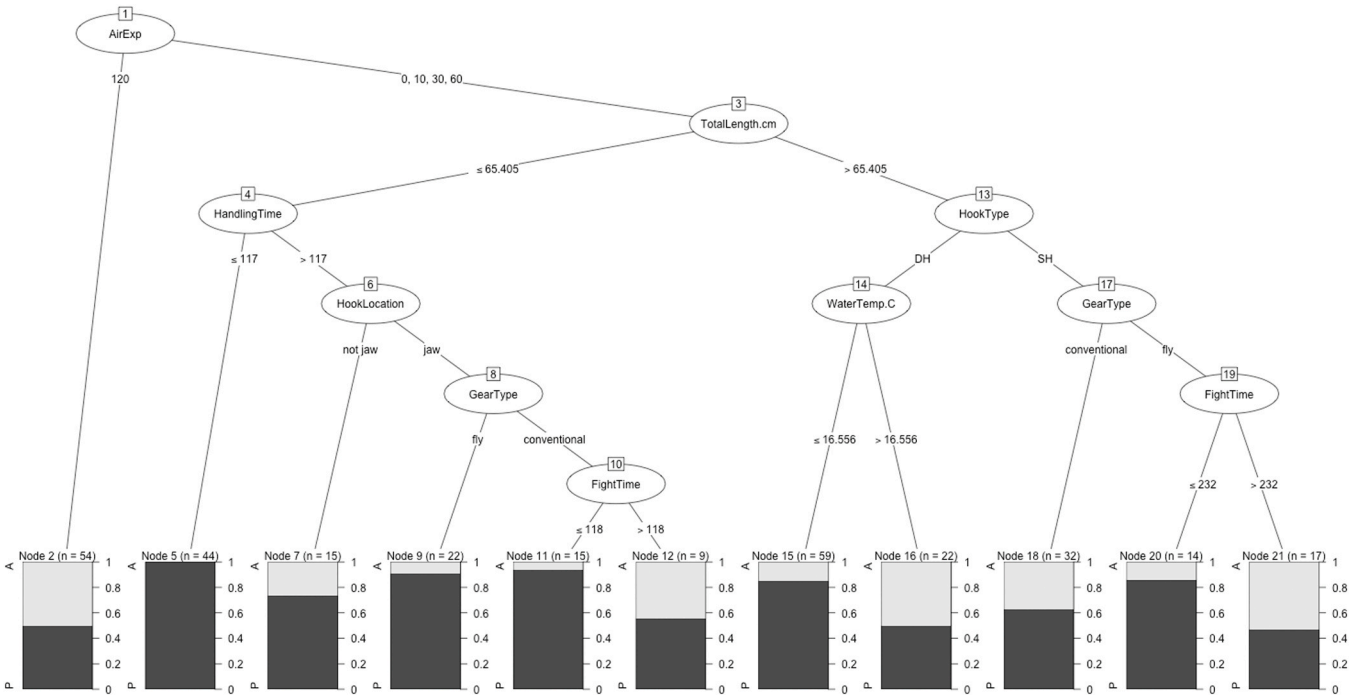


Fig. 5. Decision tree showing the importance of air exposure, total length (cm), hook type (DH = double hook, SH = single hook), gear type, handling time (s), water temperature (°C), hook location, and fight time (s) in determining the presence or absence of equilibrium in striped bass. The number of trials included in the resulting node are indicated at the top of each node's stacked bar graph (e.g., Node 2 (n = 54)). The proportion of observed fish that passed the equilibrium test (i.e., the righting reflex was present) is shaded in dark grey. The proportion of observed fish that failed the equilibrium test (i.e., the righting reflex was absent) is shaded in light grey.

3.4. Post-release activity

Thirty-seven striped bass were subjected to accelerometer biollogger trials and assigned to air exposure groups of either 0 s ($n = 13$), 30 s ($n = 12$), or 120 s ($n = 12$). The monitoring period was prematurely concluded after 15 min on two occasions due to the risk of line entanglement. Striped bass affixed with an accelerometer had total lengths ranging from 68.6 cm to 94 cm ($76.7 \text{ cm} \pm 7.1 \text{ cm}$), fight times ranging from 70 s to 216 s ($132 \text{ s} \pm 29 \text{ s}$), handling times ranging from 180 s to 374 s ($248 \text{ s} \pm 51 \text{ s}$), and were captured in water temperatures between 12.2°C and 19.4°C ($14.4^\circ\text{C} \pm 1.7^\circ\text{C}$). There was no significant difference in total length ($H(2) = 1.03$, $p > 0.05$), fight time ($H(2) = 2.71$, $p > 0.05$), and water temperature ($H(2) = 0.87$, $p > 0.05$) across air exposure treatments. Similar to striped bass subjected solely to the RAMP assessment, those in the 120 s air exposure group ($279 \text{ s} \pm 41 \text{ s}$) had significantly longer handling times ($H(2) = 8.99$, $p < 0.01$) driven by air exposure duration compared to striped bass in the 30 s air exposure group ($222 \text{ s} \pm 43 \text{ s}$, $p = 0.01$) and approached significance compared to those in the 0 s group ($242 \text{ s} \pm 52 \text{ s}$, $p = 0.08$). Handling time was incorporated in the model that included air exposure as a covariate to account for this effect.

Across trials, ODBA values (averaged across each minute post-release) ranged from 0.03 g to 1.55 g ($0.24 \text{ g} \pm 0.18 \text{ g}$), with individuals demonstrating variable responses in ODBA after release (Fig. S1). Despite a trend showing increasing ODBA values with increasing RAMP 2 score, there was no significant correlation between RAMP 2 and ODBA ($\rho(35) = 0.17$, $p > 0.05$). Of the three reflexes most commonly lost by striped bass, only equilibrium was significantly correlated with ODBA (equilibrium: $\rho(35) = 0.33$, $p = 0.05$, body flex: $\rho(35) = -0.12$, $p > 0.05$, tail grab: $\rho(35) = 0.1$, $p > 0.05$). Striped bass that passed the equilibrium test (i.e., righted themselves in three seconds or less) during the second RAMP assessment had significantly higher ODBA values ($0.26 \text{ g} \pm 0.15 \text{ g}$) compared to striped bass that lost equilibrium ($0.18 \text{ g} \pm 0.04 \text{ g}$; $t = -2.81$, $p < 0.01$). Specifically, striped bass that passed the equilibrium test demonstrated significantly higher ODBA between 4:00 and 15:59 min post-release (t range: -5.38 to -2.03 , $p \leq 0.05$ for all pairwise comparisons) compared to those that

failed the test (Fig. 6).

The linear model showed no effect of fight time ($F(1,30) = 0.4$, $p > 0.05$), water temperature ($F(1,30) = 0.01$, $p > 0.05$); total length ($F(1,30) = 0.66$, $p > 0.05$), handling time ($F(1,30) = 0.08$, $p > 0.05$), or air exposure ($F(2,30) = 0.37$, $p > 0.05$) on ODBA. Across all trials averaged, time-binned ODBA values were best modeled by a linear mixed model containing minutes post-release (aggregated by two-minute intervals) as the only covariate and individual trial ID as the random effect. It revealed a significant positive correlation between time following release and post-release activity ($F(9, 319.07) = 12.31$, $p < 0.001$; Fig. 7). Specifically, following a significant drop in ODBA from the first two-minute interval (0:00–1:59 min) to the second (2:00–3:59 min, $z = -3.64$, $p = 0.01$), ODBA levels increased over time, reaching significantly higher values at 8:00 min post release and beyond (z range: $4.94 - 7.96$, $p < 0.01$ for all pairwise comparisons) compared to the lowest levels during 2:00–3:59 min bin. Activity was significantly higher from 10 min onward compared to the 4:00–5:59 min interval (z range: $4.1 - 6.0$, $p < 0.01$ for all pairwise comparisons). At the 6:00–7:59 min interval, activity was significantly lower than that observed at the 10:00–11:59 min interval ($z = 3.5$, $p = 0.02$) and from 16:00 min through the end of the trial (z range: $3.4 - 4.9$, $p < 0.02$). Activity levels were also significantly higher at the 18:00–20:00 min interval than at 0:00–1:59 min ($z = 0.07$, $p < 0.01$).

When examining ODBA for each air exposure group individually, linear mixed models with individual as a random effect showed that ODBA values significantly increased with minutes post-release (0 s; $F(9, 106.01) = 3.64$, $p < 0.001$, Fig. 8a), 30 s ($F(9, 99) = 6.78$, $p < 0.001$, Fig. 8b), 120 s ($F(9, 96.1) = 2.79$, $p < 0.01$, Fig. 8c). Specifically, striped bass that were not air exposed (0 s) exhibited significantly lower activity levels during 2:00–3:59 min compared to minutes 10:00–11:59 min ($z = 3.45$, $p = 0.01$), 16:00–17:59 min ($z = 3.38$, $p = 0.03$), and 18:00–20:00 min ($z = 4.7$, $p < 0.001$). Additionally, their ODBA values during 4:00–5:59 min were significantly lower than those observed during 18:00–20:00 min ($z = 3.5$, $p = 0.02$). Striped bass subjected to 30 s air exposure demonstrated significantly reduced activity levels during 2:00–3:59 min compared to all subsequent time points starting from minutes 8:00–9:59 (z range: $3.4 - 5.31$, $p < 0.05$ for all pairwise

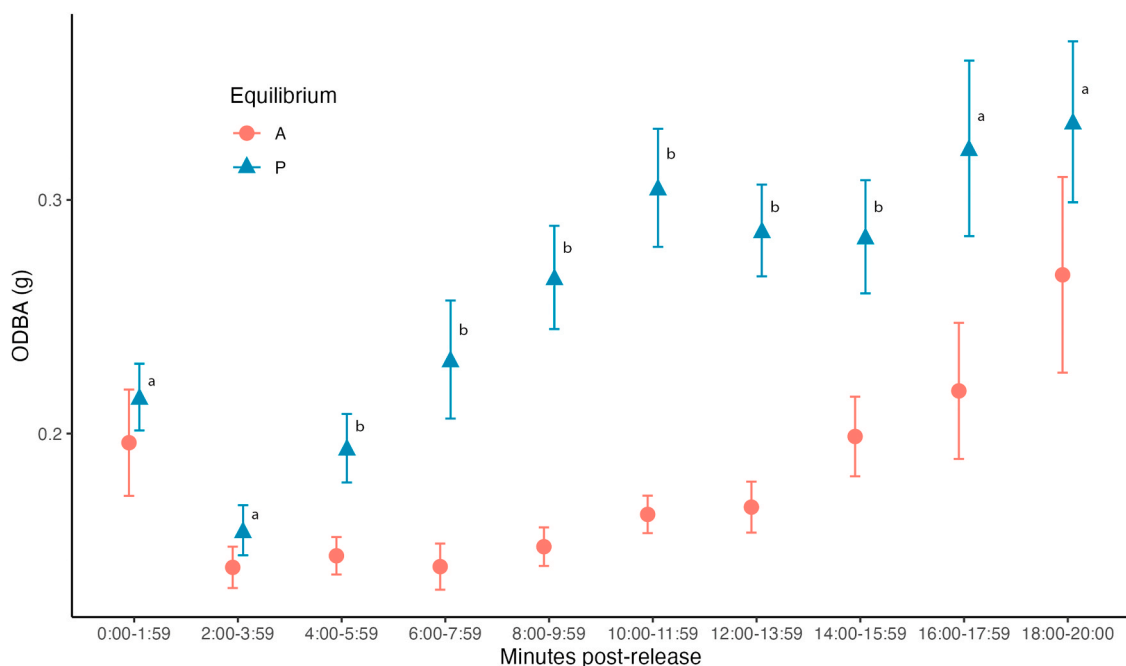


Fig. 6. Overall dynamic body acceleration (ODBA) aggregated into two-minute bins post-release for striped bass with absent (A) and present (P) equilibrium prior to release (during the RAMP 2 assessment). Means are bounded by 95 % confidence intervals. Letters represent the significant results of Tukey post-hoc tests, with the differing letters denoting significant differences in ODBA at the respective intervals within each air exposure treatment group across equilibrium test results.

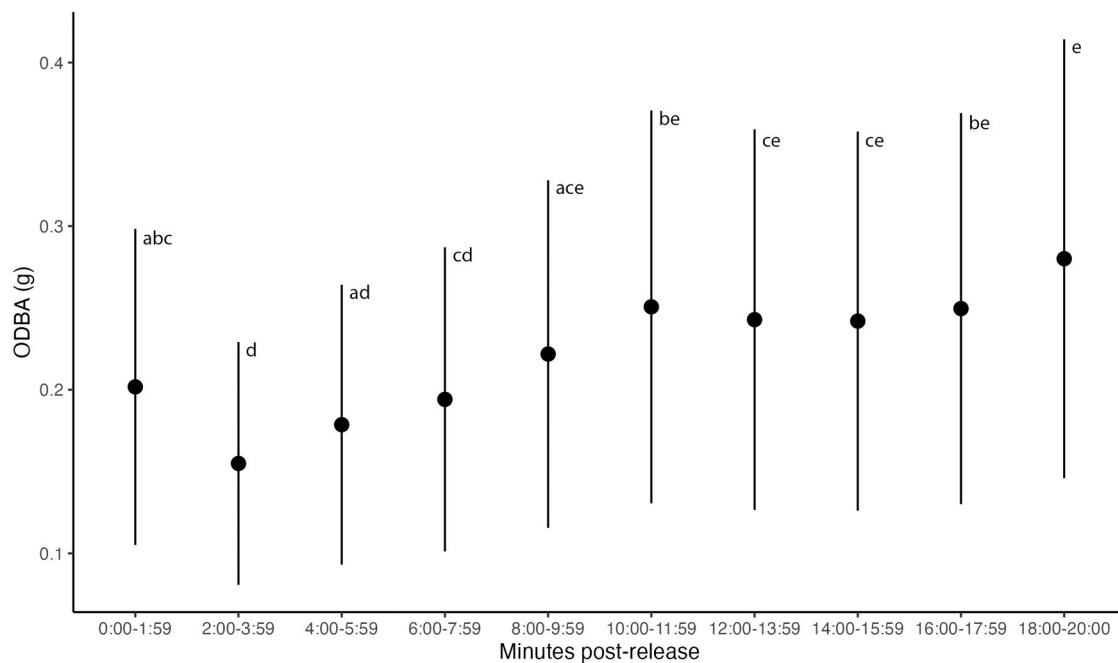


Fig. 7. The relationship between overall dynamic body acceleration (ODBA) and minutes post-release aggregated across two-minute intervals, based on the best fitting linear model. Predicted means are bounded by 95 % confidence intervals and significant differences among time intervals are indicated by lettering. Letters represent the significant results of Tukey post-hoc tests, with the differing letters denoting significant differences in ODBA at the respective intervals.

comparisons). Furthermore, ODBA values during minutes 4:00–5:59 min were significantly lower than those recorded during minute 10:00 and extending through the end of the trial (z range: 3.25 – 4.53, $p < 0.05$ for all pairwise comparisons). Striped bass subjected to air exposure for 120 s demonstrated significantly lower ODBA levels during 2:00–3:59 min when compared to 12:00–13:59 min ($z = 3.4$, $p = 0.02$), 14:00–15:59 min ($z = 3.3$, $p = 0.03$), and 19:00–20:00 ($z = 3.73$, $p < 0.01$).

Striped bass swimming behavior differed significantly across air exposure treatment groups, particularly early in the observation period. Averaged ODBA values in the 2:00–3:59 min interval ($F(2, 71) = 5.81$, $p < 0.01$) and 4:00–5:59 min interval ($F(2, 71) = 4.74$, $p = 0.02$) differed significantly among air exposure groups. Striped bass that were not air exposed (0 s) exhibited significantly higher activity levels during 2:00–3:59 min than those air exposed for 30 s ($t = -3.07$, $p < 0.01$) or 120 s ($t = -2.78$, $p = 0.02$). Additionally, striped bass in the 0 s air exposure group also had significantly higher ODBA levels at minutes 4:00–5:59 compared to those subjected to 30 s of air exposure ($t = -3.02$, $p < 0.01$).

4. Discussion

Overall, our assessment of striped bass following capture and handling revealed an immediate post-release survival rate of 100 % across all gear types and air exposure treatments, based on RAMP 2 assessments immediately prior to release as well as fish monitored for 20 min post-release with accelerometer data loggers. Despite the lack of observed mortality, this study identified factors that most influenced striped bass post-release behavior and increased physiological stress. Physical injuries were observed more frequently with conventional gear and lures with double hooks, resulting in a higher incidence of foul hooking compared to both conventional and fly gear using single hooks, regardless of hook type (e.g., treble, circle, J). Conversely, deep hooking was more common with fly gear and single hooks than with conventional gear, regardless of whether single or double hooks were used. Reflex assessments indicated an increase in reflex impairment associated with prolonged fight times for both RAMP 1 and RAMP 2, while higher

water temperatures, extended handling durations, and increased air exposure emerged as significant factors during the RAMP 2 assessment. Additionally, striped bass caught using conventional gear exhibited greater impairment compared to those caught with fly gear, for both RAMP 1 and RAMP 2 scores. Short-term post-release activity was significantly influenced by time following release, with quicker recovery observed in striped bass that were not exposed to air compared to those subjected to air exposure for 30 s and 120 s. To minimize the effects of catch-and-release angling on striped bass, anglers should limit fight time to under 118 s, handling time to under 117 s, and air exposure to under 60 s. They should also opt for single hooks and avoid fishing at water temperatures above 16.6 °C. These measures are especially important for striped bass larger than 65.4 cm, as these fish were more susceptible to angling stress.

The negative impact of hooking injuries is well-documented and recognized as a primary cause of angling-related mortality for fish (Muoneke and Childress, 1994; Bartholomew and Bohnsack, 2005; Cooke and Suski, 2005; Cooke and Wilde, 2007c; Pelletier et al., 2007). The greater incidence of deep hooking for striped bass caught on single hook fly fishing gear may be attributed to the smaller size of flies, which can be easily ingested deep within the fish's buccal cavity, in contrast to the larger lures typically used in conventional fishing. Similar to deep hooking, the higher rates of foul hooking and external tissue damage from double hook lures on conventional gear could have both immediate and long-term detrimental effects. The decision tree's ability to assess the influence of relatively infrequent events, like foul hooking, revealed that hooking location influenced equilibrium loss for striped bass. Fish hooked in locations other than the jaw more often lost equilibrium compared to those hooked in the jaw. The greater levels of physical injury in striped bass caught with double hook lures likely contributes to the lower RAMP scores observed in those caught on conventional gear compared to those caught on fly gear. Although our study did not assess subsequent sub-lethal impacts, foul hooking and associated tissue damage may heighten the risk of parasites, disease, and fungal infections (Meka, 2004; Schramm and Davis, 2006; Teffer et al., 2017).

Anaerobic metabolism during intense exercise elevates lactate levels and disrupts blood chemistry, resulting in metabolic acidosis and

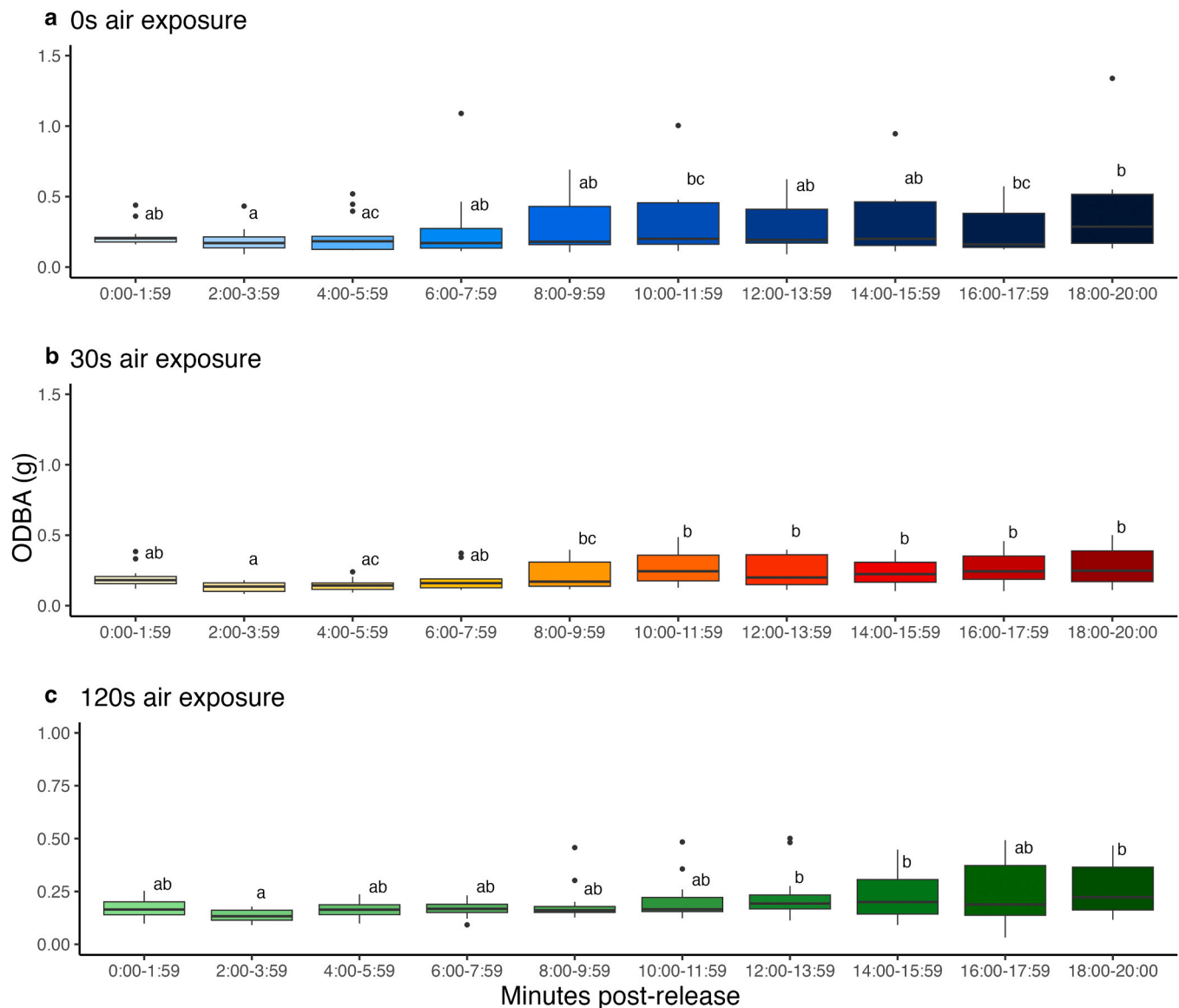


Fig. 8. Overall dynamic body acceleration (ODBA) across two-minute intervals post-release for striped bass air exposed for a) 0 s, b) 30 s, and c) 120 s. Boxes represent 25th and 75th percentiles with the horizontal line representing the median. Whiskers show upper and lower extremes with outliers presented as points. Letters represent the significant results of Tukey post-hoc tests, with the differing letters denoting significant differences in ODBA at the respective intervals within each air exposure treatment group.

impaired physiological functions. These changes hinder muscle and nerve activity, compromising fish condition and recovery following release (Kieffer, 2000). Consistent with this, RAMP 1 score results indicate that fight time significantly affects striped bass, with more reflexes lost as fight duration increases. Moreover, our results demonstrate a significant positive correlation between fight time and body size in striped bass. The decision tree analysis identified total length as the second most important factor in predicting the loss of equilibrium, indicating that striped bass larger than 65.4 cm tend to have poorer outcomes. In other recreationally caught species, loss of equilibrium has been attributed to higher rates of post-release predation and fishing-induced mortality (Danylchuk et al., 2007; Gingerich et al., 2007; Raby et al., 2012; Griffin et al., 2022) as well as delayed ability to locate refuge habitats, which could be fatal in high predator burden areas (Brownscombe et al., 2014). Research on other recreationally targeted species indicates that larger fish experience greater lactic acid buildup (Meka and McCormick, 2005; Martin et al., 2023) and have slower lactate clearance rates compared to smaller fish (Martin et al.,

2023), suggesting that larger fish are more adversely affected by the effects of exhaustive exercise and more prone to equilibrium loss as a result.

The normal physiological response of exhaustively exercised fish involves enhancing oxygen supply to their muscles to meet elevated demands following exertion (Wood, 1991; Wang et al., 1994). However, when exposed to air, fish struggle to repay oxygen debt due to gill collapse and adhesion, which disrupts physiological homeostasis and can lead to extracellular acidosis (Ferguson and Tufts, 1992; Cook et al., 2015). In our study, air exposure significantly affected the physiological condition of striped bass, with 120 s of exposure resulting in significantly lower RAMP 2 scores compared to fish that were not air exposed or those exposed for only 30 s. Air exposure was also the only significant predictor for striped bass exhibiting a decline in RAMP score between the RAMP 1 and RAMP 2 assessments, with fish air exposed for 120 s substantially more likely to have a larger decline in RAMP 2 score than those air exposed of 0 or 30 s. Moreover, the decision tree identified air exposure as the most important predictor of equilibrium outcomes,

revealing that 50 % of striped bass lost equilibrium after 120 s of air exposure, regardless of other angling factors. These results suggest that prolonged periods of air exposure impose considerable stress on striped bass during catch-and-release angling, identifying 120 s as a threshold for increased stress response. Air exposure is a common element of catch-and-release angling, with anglers often removing fish from the water to take photographs with their catch and to remove hooks prior to release. Prior to this study, the effects of air exposure had not been assessed for striped bass making this finding especially crucial for enhancing best practice guidelines for the catch-and-release of striped bass. Modeling of RAMP 2 assessments revealed that extended handling times, which are often inflated by prolonged air exposure, contribute further to angling stress in striped bass. This is consistent with findings from Harrel (Harrell, 1988), who demonstrated that handling time is a critical factor influencing cumulative stress and post-release survival in striped bass.

Physiological processes in fish are closely tied to water temperature, and elevated temperatures can contribute to stress and post-release mortality (Gale et al., 2013). High water temperatures reduce the availability of dissolved oxygen (Coutant, 1985). Consequently, when fish are already experiencing oxygen depletion due to anaerobic metabolism during the fight, elevated temperatures can exacerbate this limitation and intensify physiological stress (Muoneke and Childress, 1994; Davie and Kopf, 2006). Our findings support previous research on the catch-and-release of striped bass, demonstrating that water temperature significantly influences their physiological response (Thompson et al., 2002; Griffin et al., 2024). While not significant for the first RAMP assessment, the second RAMP assessment demonstrated a significant decline with increasing water temperatures, suggesting there may be some level of interaction between the added stress of handling time, which can include air exposure, and water temperature for striped bass. The decision tree analysis identified 16.6 °C as a temperature threshold for striped bass. Detrimental impacts were observed in warmer water temperatures for fish larger than 65.4 cm. Under these conditions, 50 % of the fish experienced a loss of equilibrium.

Reflex action mortality predictors are well-established indicators of reflex impairment (Davis, 2010; Raby et al., 2012) and are often predictive of post-release physiological and behavioral impairment, as well as mortality (Raby et al., 2012; Brownscombe et al., 2013, 2015). The significant relationship observed between the equilibrium test and ODBA supports the notion that reflex tests can effectively capture universal stress responses in fish (Davis et al., 2010). The lack of a significant relationship between overall RAMP score and ODBA in our study could be a product of a small sample size or species-specific differences in morphology, physiology, and behavior that influence the effectiveness of various reflex indicators in assessing physiological impairment.

Physiological disturbances caused by various angling factors can alter routine swimming behavior (Kieffer, 2000; Cooke et al., 2002; Cooke and Philipp, 2004a), and short-term post-release activity patterns often serve as indicators of the long-term fate of fish (Beitinger, 1990; Brownscombe et al., 2014). In our study, no significant influence of water temperature, fight time, handling time, air exposure, or total length on post-release activity was detected when using the raw ODBA values. However, when ODBA values were binned to examine the influence of time post-release on striped bass behavior, time after release and air exposure duration significantly influenced activity levels. Two to four minutes after release, striped bass that were not air exposed were already exhibiting higher activity levels than the 30 and 120 s air exposed fish. Throughout the 20 min observation period, striped bass that were not air exposed continued to display faster recovery than air exposed fish. Fish exposed for 120 s never achieved the same breadth of ODBA values as fish that were not air exposed. Suppressed activity after release demonstrates the vulnerability of striped bass to post-release mortality, particularly if greater physical injury and sub-lethal impacts occur (Bartholomew and Bohnsack, 2005; Raby et al., 2014). Fish with impaired swimming performance are susceptible to post-release

predation, particularly in regions with high predator burdens. For instance, Danylchuk et al. (2007) found that bonefish (*Albula vulpes*) that lost equilibrium, which often corresponding to the duration of air exposure, were six times more likely to be preyed upon than those that maintained equilibrium. The northeastern United States, and coastal Massachusetts in particular, is experiencing rebounding predator populations, including white sharks (*Carcharodon carcharias*) and grey seals (*Halichoerus grypus*) (Skomal et al., 2012). Although depredation and post-release predation (within 20 min) were not observed during this study, anglers targeting striped bass in the northeastern United States have reported shark and seal depredation events in the fishery via social science surveys (Casselberry et al., 2022, O. Dinkelacker, unpublished data).

Overall, the immediate and short-term survival rate of striped bass following release was high (100 %), and only 0.9 % of fish lost four or more of the assessed reflexes, indicating their resilience to the factors evaluated in this study. However, it is important to note that this study only assessed short-term (20 min) post-release activity and survival, and delayed sub-lethal effects that could lead to post-release mortality days or weeks later (Kneebone et al., 2021). Further research is warranted to explore striped bass post-release activity, behavior, and survival, with extended monitoring periods beyond 20 min, and including a broader variety of gear types, particularly the use of live bait, to reflect the diverse nature of the striped bass recreational fishery.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Dr. Andy Danylchuk reports financial support was provided by Woods Hole Sea Grant. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2025.107459.

Data availability

Data will be made available on request.

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