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Depth-based barotrauma severity, reflex impairment and stress response in two species of ice-angled fish

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Abstract

Barotrauma is a frequent event in fish captured from depth, and anglers often attempt to remedy this problem by venting fish. Barotrauma has been frequently assessed in fish during the warm water season, but no work has been done during winter ice angling, and the need and/or effectiveness of venting for ice-angled fish has not been quantified. To answer these questions, bluegill *Lepomis macrochirus* Rafinesque and black crappie *Pomoxis nigromaculatus* (Lesueur) were angled through the ice, barotrauma assessed, and the effect of venting on reflex responsiveness and blood glucose levels after 1 or 2.5 h of holding were determined. Greater capture depths resulted in more severe barotrauma, with bluegill experiencing symptoms at shallower depths than black crappie. Bluegill reflex action mortality predictor (RAMP) scores improved more than black crappie scores following venting. These results suggest barotrauma impacts fish in winter fisheries in a similar fashion to fish in warmer conditions, with species-specific differences in their susceptibility to barotrauma and their response to venting.

KEYWORDS
black crappie, blood glucose, bluegill, catch-and-release, venting, winter

1 | INTRODUCTION

When fish are brought to the surface quickly during angling, barotrauma is a concern (Butcher et al., 2012). Barotrauma results from rapid decompression due to sudden decreases in the external pressure of the surrounding water (Carlson, 2012). Numerous studies in warmer, open waters found capture depth of fish is correlated with barotrauma onset and severity, as water pressure is greater at deeper depths and the decrease in external pressure upon retrieval is larger (Butcher et al., 2012; Drumhiller et al., 2014; Morrissey et al., 2005). Other studies looking at impacts of barotrauma severity on fish found that barotrauma onset and severity can have significant influence on post-release mortality and plasma stress markers (Drumhiller et al., 2014; Gravel & Cooke, 2008; Kerwath et al., 2013). In an effort to treat fish with barotrauma, anglers may "vent" the fish by inserting a needle into the swim bladder to release expanded gases, but the effectiveness of venting in facilitating recovery is unclear (Butcher et al., 2012; Wilde, 2009).

Compared with open water fishing, ice angling is often restricted in terms of the directionality of bait retrieval. In open waters, anglers may cast out and retrieve baits both horizontally and vertically, while ice anglers may only retrieve baits in a near-vertical fashion as the only open water is directly beneath holes they drill in the ice. This also means any fish hooked may also only be retrieved vertically and are often retrieved quickly (Louison et al., 2017b). There is therefore reason to believe the effect of capture depth on barotrauma onset and severity may be more pronounced in ice fisheries, but this has not been quantified in ice-angled fish. In addition, since it has been shown that the physiological response of fish to angling is altered in cold water (Logan et al., 2019; Louison et al., 2017a; Twardek et al., 2018), and barotrauma has been found to lead to the elevation of some plasma stress markers in fish caught from warmer waters (Gravel & Cooke, 2008), it is possible that the effects of barotrauma on the physiology of angled fish are different in the winter compared to the summer.

To determine the incidence of barotrauma in ice-angled fish, how barotrauma incidence and severity are influenced by capture depth of fish, the effectiveness of venting in treating affected fish, and how barotrauma severity affects post-release vitality and plasma stress markers, we angled two species of sportfish (black crappie *Pomoxis nigromaculatus* (Lesueur) and bluegill *Lepomis macrochirus* Rafinesque) through the ice at depths of 1–12 m. Captured fish were assessed for barotrauma signs, and a subset was assessed for reflex action mortality predictors (RAMP) (Davis, 2007) and blood glucose after 1 or 2.5 h of holding. A further subset of fish were vented to assess the effectiveness of that technique in improving outcomes for fish. Although exploitation and harvest are often high for bluegill and black crappie (Coble, 1988; Miranda & Dorr, 2000) with low release rates, post-release mortality may be critical in waters with harvest restrictions (including the site for the present study, which featured a bag limit of five for both bluegill and black crappie). The results from this study will contribute to our understanding of how colder water influences fishes' susceptibility to the physiological stressors from angling and will be useful in the development of best angling practices to avoid or minimise barotrauma effects for ice-angled fish.

2 | METHODS

2.1 | Study site

All angling took place at Shadow Lake in Waupaca, Wisconsin USA (N 44.3580, W 89.0859). Shadow Lake is a small water body (0.18 km^2) with a mean depth of 5.18 m and a maximum depth of 12.5 m. The lake bottom is composed of a mix of mud, sand and gravel. Popular game fish species that inhabit the lake in addition to bluegill and black crappie include largemouth bass *Micropterus salmoides* (Lacépède), yellow perch *Perca flavescens* (Mitchill) and northern pike *Esox lucius* L. Angling and data collection took place on the southwest end of the lake on 7, 8 and 10 January 2020, and at the northeast end on 9 January 2020.

2.2 | Angling gear and methods

Each day of the experiment began with the anglers drilling several holes in the ice at various water depths using a hand-held ice auger. Depths (in m) were measured at each site using Vexilar® ice-fishing sonar units. These units also allowed for the spotting of fish on the sonar readout, and anglers would therefore begin fishing when a fish appeared on the graph. All angling was done with traditional ice tackle consisting of short rods (<1 m in length) and reels spooled with 0.9 to 2.7-kg breaking strain monofilament line. Artificial plastic lures and live baits were used to attract and entice fish into striking. When an angler hooked a fish, they would bring the fish to the surface as quickly as possible, noting the depth (to the nearest 0.3 m) at which the fish was hooked, in an effort to minimise variation in fight time and potential impacts on barotrauma and the stress response, as studies have shown that physiological disturbances correlate positively with angling duration (Gustaveson et al., 1991; Meka & McCormick, 2005). Minimal fight times also are representative of ice anglers who bring fish to the surface quickly with little regard for barotrauma onset. Gut-hooked fish were excluded from testing to avoid any effects of deep hooking on the results.

2.3 | Barotrauma assessment

Once a fish was caught, it was transported to one of sixteen 56 × 39 × 32 cm holding tanks filled with fresh lake water to be assessed for barotrauma. Water temperatures ranged from 0.5 to 2.9°C. On 8 January, the air temperature was colder than the water temperature (−7°C), so the water in the tanks was replaced with new lake water every 2 h. Barotrauma was assessed immediately after capture and included the recording of 6 barotrauma signs: gastric herniation into the buccal cavity, prolapsed anus, haemorrhaging in the mouth/gills/fins/anus, bloating, exophthalmia (eye bulge), and difficulty swimming down and maintaining orientation when placed into the holding tank (down swim). All of these metrics have been shown to be potential outcomes from barotrauma disturbances (Gravel & Cooke, 2008; Morrissey et al., 2005; Schreer et al., 2009). Fish were classified as having no barotrauma if they showed zero signs, light barotrauma if only down swimming was impaired, moderate barotrauma if visible bloating accompanied down swim impairment, and severe barotrauma if at least one additional sign listed above was observed alongside bloating and down swim impairment (usually haemorrhaging into the mouth or anus). Barotrauma was classified this way because this order followed the typical sequence of signs observed (i.e. there were zero fish that showed signs of haemorrhaging while also being able to swim down in their tank unimpaired) (Gravel & Cooke, 2008).

After barotrauma assessment, fish were selected at random to be released or kept for further assessment of venting practices. Kept fish were assigned to one of two treatment groups (vented or non-vented) prior to holding (see below). Venting was performed by inserting a 22-gauge, 2.5-cm hypodermic needle under the scales laterally just beneath the vertebrae (Alós, 2008) immediately following barotrauma assessment. Successful venting of fish with barotrauma was marked by the audible noise of gas escaping the swim bladder through the needle. Venting or non-venting was predetermined before each fish was caught to remove the potential bias that only venting fish with obvious barotrauma symptoms might incur on the subsequent RAMP/blood glucose data. Fish without barotrauma were vented by sticking them with the needle in the same body location as successfully vented fish with barotrauma. This was done to determine if the venting process itself would cause physiological disturbance to the fish, even if they did not suffer from barotrauma.

2.4 | Holding, RAMP and blood draw

Fish kept for venting assessment were either held for 1 or 2.5 h, whereas fish to be released were designated as controls (processed immediately without holding). Control fish were non-vented and were not held in the tanks prior to assessment. The holding time and vented status therefore separated both bluegill and black crappie into 5 blocks: controls (non-vented), 1-h × non-vented, 2.5-h × non-vented, 1-h × vented and 2.5-h × vented. Control fish were given RAMP assessment immediately following barotrauma assessment, while experimental fish were assessed for RAMP once their assigned holding time had expired. RAMP assessment in this study consisted of tests for four reflexes: burst swim, body flex, vestibular-ocular response and righting reflex (Louison et al., 2017b). The burst swim reflex was tested by grabbing the tail of the fish while in its holding tank to see if the fish burst-swam away in response. To test for body flex, the fish would be loosely held in hand for 10 s. If the fish did not flex its body or attempt to wriggle free within that time, it was labelled as impaired. The vestibular-ocular response was tested by holding the fish and rotating it to observe if the eye rolled in response, to maintain pitch with the handler. Lastly, the righting reflex was assessed by turning the fish upside down in the water and observing whether the fish could right itself. A score of 1 was given to a fish for each reflex that was impaired, while a score of 0 was given if the reflex was unimpaired (Davis, 2010). Fish with no impairments would therefore receive a score of 0, while a fish that had all reflexes impaired would be scored as a 4. Once RAMP assessment was finished, the mass and length of each fish were determined, and a representative subsample of fish across treatment blocks and capture depths were placed into a v-trough for the purpose of a blood draw to assess blood glucose levels. Fish that were not sampled for blood were released immediately after RAMP assessment.

To obtain a blood sample, a 22-gauge, 2.5-cm heparinised needle was inserted into the caudal vein on the ventral side of the fish between the anal and caudal fins. A single drop of blood was then dropped onto a Tyson Bio™ glucose test strip and placed into a Tyson Bio™ HT100 glucose metre to obtain blood glucose concentration; several studies have validated the use of point-of-care devices and as alternatives to laboratory analyses of physiological parameters such as blood glucose (Stoot et al., 2014). In the case of non-vented fish showing moderate or severe barotrauma symptoms, venting was conducted to allow the fish to swim successfully back down to depth.

2.5 | Data analysis

To define the effects of capture depth, species, fish size and all possible two-way interactions between those variables on barotrauma severity, a series of ordinal regressions featuring all possible combinations of those variables was run with barotrauma severity as the dependent variable (ordered from none to light to moderate to severe). Venting and holding time were not included in this model as venting and holding trials were conducted after barotrauma severity had been determined. All possible ordinal regression model combinations were compared, and top models were chosen using Akaike Information Criterion, adjusted for small sample sizes (AICc). Full multi-model comparisons also allowed for the determination of relative importance for each variable included in the model. Fixed factors were determined to be of importance if their sum of weights value exceeded 0.70, and two-way interactions were determined to be important if the sum of weights values were greater than 0.50 (Kittle et al., 2008; Wagenmakers & Farrell, 2004). Additionally, a two-sample Student *t*-test comparing capture depth between the two species was run. Following this, a series of binary logistic regressions was run to predict the depth at which each species had a 50% likelihood of suffering from a given level of barotrauma severity. These regressions were broken down by species and barotrauma severity, based on whether the captured fish (bluegill or black crappie) at a given depth had reached the given barotrauma severity level (light, moderate or severe). In each case, whether or not the fish had reached the barotrauma severity level in question (i.e. fish that suffered severe barotrauma also by definition suffered light barotrauma when logistic regression was used to determine the depth at which light barotrauma was likely to occur) was set as the dependent variable, with capture depth as the independent variable. After fitting the regression, the predicted depth at which a bluegill or black crappie experienced a 50% probability of having the given level of barotrauma was defined.

Subsequent analysis focused on predictors of RAMP score and blood glucose level. This analysis was performed only on fish that had been held for 1 or 2.5 h in the holding tanks, as a full factorial design that included controls was not possible (i.e. by definition, the control treatment did not involve venting, therefore, there were no vented controls). Spearman correlation was used to determine if RAMP score and blood glucose level were collinear (Zuur et al., 2010). After determining that they were not ($p = 0.21$), separate analyses were run for the two variables, with each as a respective dependent variable. First, a Poisson regression was used to assess the effects of species, barotrauma severity, fish size, whether the fish was vented and holding time on RAMP score. All two-way interactions between these variables were included in the model. Once again, AICc was used to determine top models from all possible combinations of those independent variables and interactions, and relative importance was determined for each individual independent variable and two-way interaction. An identical approach was used to determine the effects of these variables and interactions on blood glucose levels, except with a general linear model as opposed to Poisson regression, to account for the continuous nature of the blood glucose data. Additionally, a two-sample *t*-test was used to determine if a significant difference in blood glucose between control bluegill and control black crappie was evident.

Finally, to define differences between the control blocks and each venting × holding time blocks in RAMP score and blood glucose for bluegill and black crappie, one-way ANOVAs and subsequent Tukey Honest Significant Difference post hoc tests (to compare

TABLE 1 Summary of relative importance derived from comparison of models containing a combination of fixed factors and two-way interactions, for each of the three dependent variables of interest

Factor	Barotrauma severity	RAMP score	Blood glucose
Species	**0.86**	**0.81**	**1.00**
Fish length	**0.85**	0.52	0.44
Capture depth	**1.00**	–	–
Vented (Y/N)	–	**1.00**	0.66
Holding time	–	0.45	**0.89**
Barotrauma severity	–	**0.99**	**0.72**
Species * Fish length	0.34	0.10	0.11
Species * Capture depth	0.45	–	–
Species * Vented	–	**0.52**	0.16
Species * Holding time	–	0.13	0.40
Species * Barotrauma severity	–	0.20	0.17
Fish length * Capture depth	0.36	–	–
Fish length * Vented	–	0.15	0.07
Fish length * Holding time	–	0.06	0.12
Fish length * Barotrauma severity	–	0.12	0.09
Capture depth * Vented	–	–	–
Capture depth * Holding time	–	–	–
Capture depth * Barotrauma severity	–	–	–
Vented * Holding time	–	0.10	0.14
Vented * Barotrauma severity	–	0.33	0.43
Holding time * Barotrauma severity	–	0.10	0.25

Note: Fixed factors with an importance value of over 0.7, and interactions with an importance value of over 0.5 are given in bold.

TABLE 2 List of top Ordinal Regression models along with the null model predicting the severity of barotrauma in black crappie and bluegill

Factors	AIC_c	ΔAIC_c	−2 log likelihood	Model weight (W_i)
Depth + Length + Species	206.652	0	193.89	0.199
Depth + Length + Species + Depth * Length	206.656	0.004	186.98	0.199
Depth + Length + Species * Depth * Species	207.717	1.065	192.69	0.117
Null model	288.316	81.664	282.10	3.7×10^{-19}

Note: The full model included the depth of capture, the length of the fish, the species of fish, and all two-way interactions among those variables. Ranking of models was done using the Akaike Information Criterion adjusted for small sample sizes (AIC_c).

between blocks and back to the control) were run. In these tests, the block (holding time × species) was the independent variable, and the respective variable (RAMP or glucose) was the dependent variable. A one-way ANOVA was also performed to compare fish sizes among the different treatment blocks. All analysis was carried out using R statistical software (R core team, Vienna, Austria) using the packages ggplot2 (Wickham 2016), ordinal (Christensen 2019), car (Fox and Weisberg 2019) and multcomp (Hothorn et al. 2008).

3 | RESULTS

A total of 118 fish (76 bluegill and 42 black crappie) were captured over the 4 days. Blood glucose readings were obtained from 46 bluegill and 35 black crappie (total 81 fish). With regards to the predictors of barotrauma severity, relative importance for all independent variables was determined (Table 1) and three top models were selected with ΔAICc values under 2, each of which was far more informative than the null model (Table 2). The best available model included capture depth of fish, species and fish length as predictor variables (Table 2), which were also the most important variables in full-model comparisons (Table 1). Fish caught from deeper depths exhibited more severe barotrauma (Figure 1). Larger fish were more prone to exhibit signs of severe barotrauma than shorter individuals, and bluegill were more susceptible to barotrauma than crappie, as crappie typically exhibited signs of each barotrauma stage at a deeper depth (Figures 1 and 2). Likelihood of occurrence for each barotrauma stage increased as depth increased for both species (Figure 2), with 50% likelihood of each successive stage generally occurring with each successive depth increase of ~2 m (although a model predicting the occurrence of light barotrauma could not be fitted for black crappie because only one specimen was captured that exhibited no barotrauma). Black crappie were also captured at deeper depths (mean = 7.95 m, range = 2.44–10.67 m) than bluegills (mean = 4.51 m, range = 1.83–9.75 m) (*t*-test, $p < 0.001$).

The top model for variables predicting RAMP score included venting, species, barotrauma severity, and the interaction between venting and species (Table 3). These variables were considered of importance due to high sum of weights values (Table 1). Fish that were vented showed improved reflexes in comparison to non-vented fish, and fish that exhibited more severe barotrauma had higher reflex impairment than fish with light or no barotrauma. The only important two-way interaction in predicting RAMP score was between venting and species (Table 1), as venting was more effective in reducing reflex impairment in bluegills than in black crappie (Figure 3). Fish size and holding time were not important variables in affecting RAMP scores (Table 1). The one-way ANOVAs and Tukey tests found that the non-vented × 1-h block in bluegill showed significantly higher reflex impairment than the controls and the non-vented blocks (Figure 4B). No difference between blocks was found for black crappie RAMP (Figure 4A). The lack of a significant difference between black crappie blocks suggests black crappie are resilient to increases in reflex impairment over time.

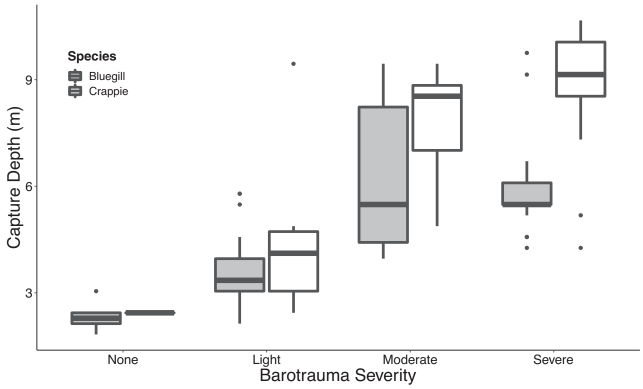

FIGURE 1 Increasing barotrauma severity related to the holding depth of bluegills and black crappies. The ends of the whiskers represent the maximum and minimum values within 1.5* the interquartile range. The lower and upper edges of the boxes indicate the 25th and 75th respective percentiles. Dots represent values that lie more than 1.5 times the IQR above the 75th percentile or below the 25th percentile. The midline indicates the median

The best-fit model for blood glucose (Table 4) included species, fish length, barotrauma severity and holding time. Species, barotrauma severity and holding time were deemed important through full-model comparison, while fish length was not (Table 1). Black crappie had higher blood glucose levels for controls than bluegills (*t*-test, $p = 0.002$), and longer hold times coincided with increased blood glucose (Figure 4). One-way ANOVAs and Tukey tests found significant differences in glucose from the control in the vented × 2.5-h black crappie block as well as the non-vented × 2.5-h and vented × 1-h blocks in bluegill (Figure 4). Fish with severe barotrauma also had elevated blood glucose in comparison with fish with less barotrauma (mean = 2.17 mmol/L for light barotrauma, 3.01 mmol/L for severe barotrauma). Venting was not determined to be an important predictor of blood glucose (Table 1).

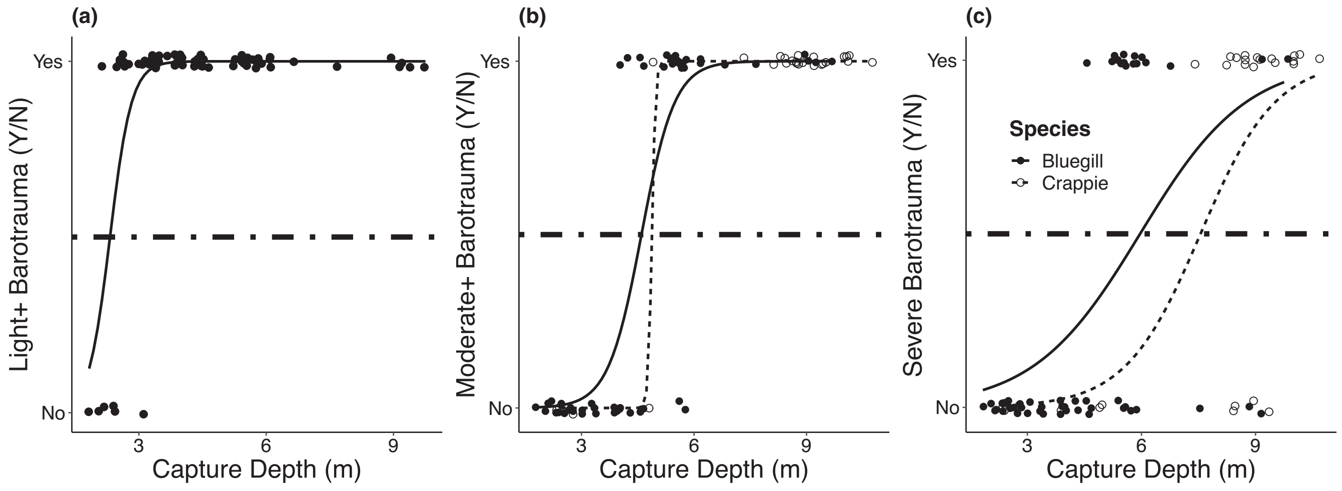

FIGURE 2 Curves derived from logistic regression models showing the relationship between holding depth and whether fish suffered from a) Light (or more severe), b) Moderate (or more severe) and c) Severe barotrauma. Results are separated by species (bluegill = solid line and closed circles, black crappie = dashed line and open circles). Black crappie are not shown in Panel A as only one individual crappie was caught with no barotrauma signs, preventing fitting of a logistic regression model. The point at which each curve intersect with the dot-dashed (-·-) line is the depth at which fish of that species are expected to have a 50% chance of suffering from the given level of barotrauma severity. Across barotrauma severities, bluegill were likely to experience higher barotrauma risks at a given depth compared to black crappie

TABLE 3 List of top Poisson Regression models predicting the RAMP score in black crappie and bluegill

Factors	AIC$_c$	ΔAIC$_c$	−2 log likelihood	Model weight (W$_i$)
Species + Vented+ Barotrauma Severity + Species * Vented	199.47	0	188.66	0.07
Vented + Barotrauma Severity	200.65	1.18	194.33	0.04
Species + Vented + Length + Barotrauma Severity + Species * Vented	200.91	1.44	187.76	0.03
Species + Vented + Barotrauma Severity	201.21	1.74	192.68	0.03
Species + Vented + Barotrauma Severity + Barotrauma Severity * Vented	201.30	1.83	188.15	0.02
Null model	215.48	16.00	213.42	2.44 × 10^{-10}

Note: The full model included the length of the fish, the species of fish, whether or not the fish was vented, the length of time it was held (1 or 2.5 h), the severity of barotrauma, and all two-way interactions among those variables. Ranking of models was done using the Akaike Information Criterion adjusted for small sample sizes (AIC$_c$).

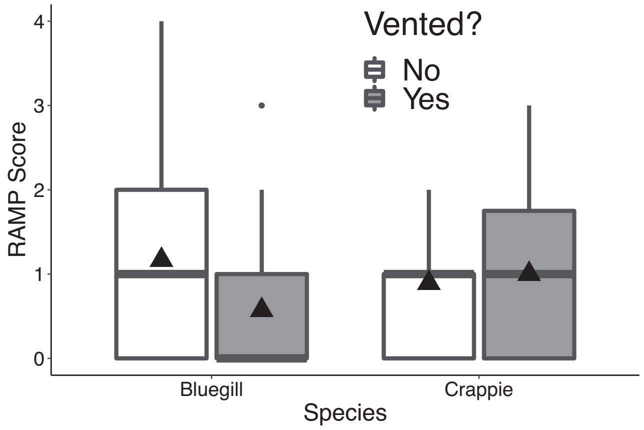

FIGURE 3 Reflex-action mortality predictor (RAMP) scores broken down by species and whether the fish was vented. Higher RAMP scores indicate greater impairment in ice-angled fish. For each box, the whiskers extend to the maximum and minimum values within 1.5* the interquartile range, the edges of the boxes represent the 25th and 75th percentiles, respectively, and the midline represents the median. Individual dots represent values that fell more than 1.5 times the IQR above the 75th percentile. Means for each treatment block are represented by the solid triangles

4 | DISCUSSION

Bluegill and black crappie angled at deeper depths through the ice can be expected to exhibit more signs of barotrauma than fish at shallower depths. The probability of severe barotrauma was approximately 50% following capture at 6–7 m, whereas the probability of light barotrauma was approximately 50% following capture at 2–3 m. Barotrauma symptoms become more severe and prevalent following capture from deeper water. This relationship has been observed in numerous open water studies of species, including red snapper *Lutjanus campechanus* (Poey) (Butcher et al., 2012; Drumhiller et al., 2014; Rummer, 2007), Atlantic cod *Gadus morhua* L. (Ferter et al., 2015) and various groupers of the family *Epinephelinae* (Overton et al., 2008; Rudershausen et al., 2007). Barotrauma injury may result from overexpansion of the swim bladder, and the degree to which the swim bladder expands relies largely on the initial external pressure (Rummer & Bennett, 2005). External water pressure is greater at deeper depths and coincides with greater swim bladder expansion when angled to the surface. Barotrauma onset was effectively guaranteed at depths of >20 m and the severity of barotrauma at >20 m resulted in post-release mortality as high as 100% in some studies (Butcher et al., 2012; Rudershausen et al., 2007; Rummer, 2007). By contrast, occurrence of barotrauma was far less frequent and post-release mortality may be as low as 20% for red snapper angled from less than 20 m (Butcher et al., 2012; Rummer, 2007). In this study, the maximum capture depth of fish caught was ~11 m, and no fish were observed with drastic symptoms such as gastric herniation, which was prevalent in fish caught from 20 m or more in other studies (Butcher et al., 2012; Rudershausen et al., 2007). Even though extreme barotrauma symptoms were not observed in this study, difficulty in swimming down was typically the first sign observed in both bluegill and black crappie, and occurred after capture from 3 m (or even less). Fish that struggle to swim down in lakes that freeze over will be at increased risk of suffering mortality under ice at the surface (Kirillin et al., 2012). In addition, internal haemorrhaging in the gills and fins was often observed in fish captured from 6 to 10 m. This illustrates that even though the most severe barotrauma signs may not be observed following retrieval from less than 20 m, barotrauma increases in severity as the capture depth of fish increases, even at shallower depths.

The two species of fish investigated in this study appeared to differ in their susceptibility to barotrauma. Specifically, bluegill were projected to be at 50% risk for severe barotrauma at 0.46 m shallower depths compared with black crappie. Comparisons of barotrauma severity between different species have found that barotrauma injury differences may be related to the type of swim bladders present in the species, or differences in swim bladder wall thickness (Casper et al., 2013; Halvorsen et al., 2012; Rummer, 2007). For example, physoclistous hybrid striped bass *Morone chrysops* (Rafinesque) × *Morone saxatilis* (Walbaum) had more barotrauma-related injury than Nile tilapia *Oreochromis niloticus* (L.) and physostomous species Chinook salmon *Oncorhynchus tshawytscha* (Walbaum) and lake sturgeon *Acipenser fulvescens* (Rafinesque) when exposed to similar conditions (Casper et al., 2013; Halvorsen et al., 2012). Indeed, physostomous species can expel gas from the swim bladder via the pneumatic duct (Casper et al., 2013; Halvorsen et al., 2012) during retrieval through

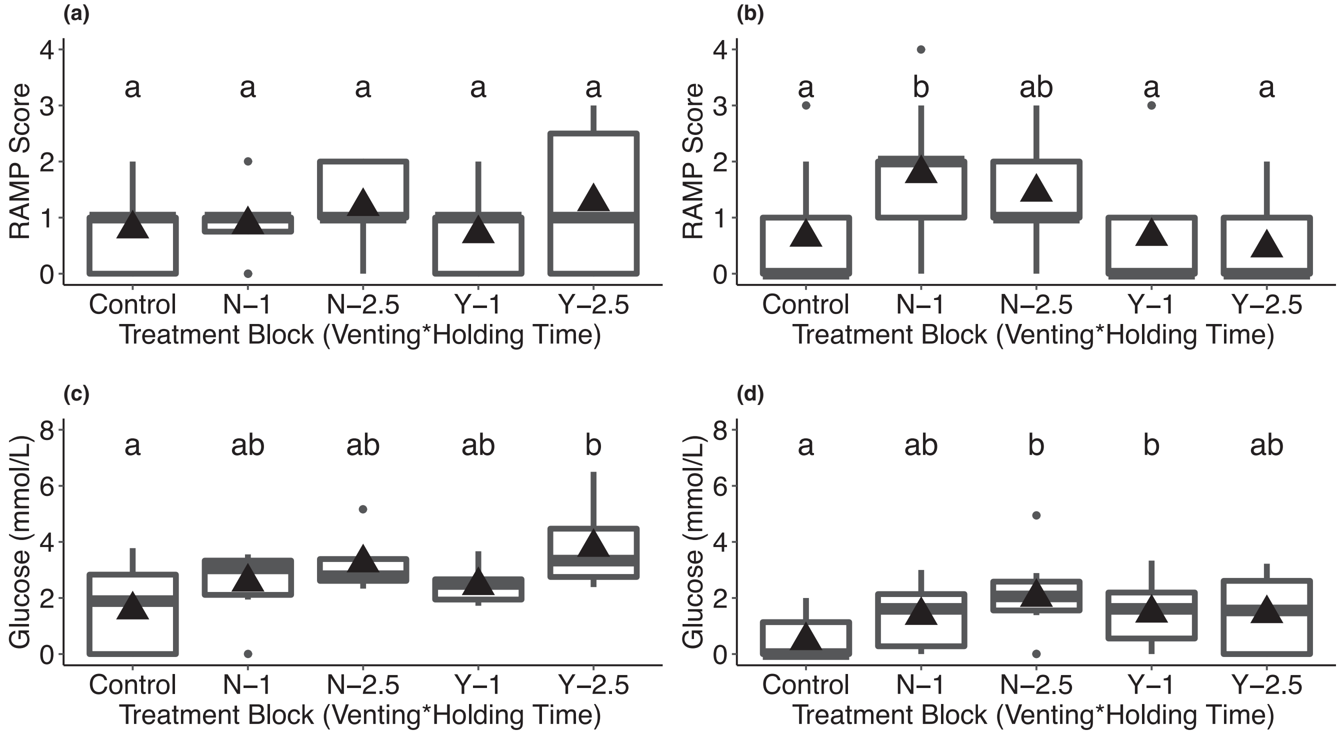

FIGURE 4 Boxplots showing RAMP and glucose concentrations for each vented × holding time treatment block. Panels A and C show data for black crappie, panels B and D show data for bluegill. Control = Fish processed immediately, N-1 = Unvented fish held for 1 h, N-2.5 = Unvented fish held for 2.5 h, Y-1 = Vented fish held for 1 h, Y-2.5 = Vented fish held for 2.5 h. Significant difference letters above each block derived from a one-way ANOVA and subsequent Tukey Honest Significant Difference post hoc test

TABLE 4 List of top General Linear Models predicting Blood Glucose concentration (in mmol/L) in black crappie and bluegill

Factors	AIC_c	ΔAIC_c	−2 Log Likelihood	Model Weight (W_i)
Species + Length + Barotrauma Severity + Holding Time	195.55	0	182.41	0.05
Species + Length + Holding Time	196.07	0.52	185.26	0.04
Species + Length + Barotrauma Severity + Holding Time + Holding Time * Length	196.14	0.59	180.60	0.04
Species + Length + Holding Time + Holding Time * Length	196.66	1.11	183.52	0.03
Null Model	232.79	37.26	228.63	4.42×10^{-10}

Note: The full model included the length of the fish, the species of fish, whether or not the fish was vented, the length of time it was held (1 or 2.5 h), the severity of barotrauma, and all two-way interactions among those variables. Ranking of models was done using the Akaike Information Criterion adjusted for small sample sizes (AIC_c).

the water column, while physoclistous species cannot. While physoclistous swim bladders are found in both bluegill and black crappie, differences in the swim bladders of the two species have not been described. The swim bladders of Nile tilapia appear to have thicker walls than those of hybrid striped bass, possibly resulting in less expansion of the swim bladder due to increased stiffness and causing the observed differences in barotrauma injury (Casper et al., 2013; Halvorsen et al., 2012). Differences in the volume, thickness or shape of the swim bladders between bluegills and black crappie could possibly explain the difference in barotrauma susceptibility, as swim bladder expansion is partially dependent on the volume and shape of the organ (Rummer & Bennett, 2005). Relatively, large swim bladders with thin walls would be more elastic and thus make fish more prone to barotrauma injury through increased swim bladder expansion. However, in the absence of specific data regarding the morphology of the swim bladders in these two species, these proposed mechanisms remain speculative. Regardless, bluegill appear to be most at risk for barotrauma injury during ice angling, although the specific mechanism for why has yet to be determined.

Venting was found to be the most important factor in affecting RAMP scores, although venting only reduced RAMP scores in bluegill and not black crappie. These results echo earlier work, as multiple studies have suggested that the success of venting in reducing the long-term effects of barotrauma is species-specific. In one study, venting benefitted saddletail snapper *Lutjanus malabaricus* (Bloch & Schneider) but did not affect any of the other species tested (Sumpton et al., 2010). Another study found venting slightly benefitted fish with barotrauma caught from shallower waters but harmed fish caught in deeper waters (Wilde, 2009). Black crappie were captured from deeper depths than bluegills on average in this study and were less susceptible to barotrauma at similar depths. As in previous studies, the effects of venting were split among species and capture depths, as shallower-dwelling bluegill seemed to benefit more from venting while black crappie that tended to be captured at deeper depths were unaffected. Black crappie not benefitting from venting echoes earlier results in this species, which found minimal benefits for venting (Childress et al. 1988). Despite this result, it appears that bluegill, irrespective of their similar morphology, do benefit from venting to a greater degree than black crappie. The RAMP scores of black crappie never differed significantly from the controls, while the RAMP scores of non-vented × 1-h bluegills were significantly higher from the controls. It should also be noted that differences in physiological responses to ice angling between species have been found previously. For instance, Louison et al. (2017b) found bluegills exhibited a more acute stress response than yellow perch to the same angling stressor, so this result adds to the body of work showing species-specific responses to ice angling. It is possible that bluegill may simply be more vulnerable to reflex impairment because of barotrauma than black crappie due to physiological and anatomical differences between the two species. Independent of species, however, the finding that more severe barotrauma led to greater reflex impairment in both species of fish adds to the body of evidence showing the adverse effects of barotrauma on the health of angled fish.

In addition to RAMP score, treatment blocks showed differences in blood glucose concentrations as a result of the combined effects of capture, air exposure and barotrauma, and the effects of venting appeared to differ between species. Louison et al. (2017b) also observed a significant difference between species in cortisol response to the same stressor, as bluegill showed higher cortisol levels following ice-angling capture than yellow perch. Another study found species-specific differences in magnitude and duration for both cortisol and glucose in seven Mediterranean fish species (Fanouraki et al., 2011). This suggests the observed difference in blood glucose between bluegill and black crappie could result from a difference in species-specific stress responses. Holding time was also an important factor in blood glucose levels, as fish held for 2.5 h had significantly higher blood glucose levels than controls for both species, independent of venting treatment (Figure 4). Previous studies have suggested stress marker elevation in response to angling is delayed and prolonged in ice-angled fish compared to fish in warm waters, which accounts for the higher concentrations seen in fish held for longer (Logan et al., 2019; Louison et al., 2017a). The holding time in this study was less than in those studies (2.5 h max. for this study compared to 4 h max), and in concurrence with those studies blood glucose levels may indeed still be on the rise at the 2.5 h time point. In addition, glucose levels were moderately impacted by barotrauma severity, although not to the same degree as RAMP scores. This coincides with a study of smallmouth bass in 2008 that found barotrauma severity to impact the elevation of chemical stress indicators (Gravel & Cooke, 2008). Owing to the delayed nature of glucose elevation in winter, it appears that the impacts of capture, and possibly subsequent venting, on the stress response in angled fish is complicated.

5 | CONCLUSIONS

In this study, deeper capture depths led to more severe barotrauma for ice-angled fish. While many studies have focused on barotrauma following capture from 20 m or more (Butcher et al., 2012; Drumhiller et al., 2014), this study suggests severe barotrauma, including haemorrhaging (43% of fish), may occur in 10 m or less. Mild symptoms such as brief swim impairment (92% of fish) may even result from ~3 m capture depths, possibly increasing mortality risk as a result (Drumhiller et al., 2014; Gravel & Cooke, 2008; Kerwath et al., 2013; Rudershausen et al., 2014; Schreer et al., 2009). Mortality was not quantified directly, but fish caught from deeper depths exhibited higher RAMP scores, and impairment in swimming down (likely fatal if fish are unable to escape the surface ice) was readily observed. Even independent of the ability to swim and escape surface ice, reflex impairment and RAMP scores have been positively linked to delayed mortality probability in previous studies (Barkley & Cadrin, 2012; Davis, 2007, 2010). Considering this relationship, the reflex impairment observed in this study suggests that post-release mortality from barotrauma may be high in cold lakes where fish are angled from depth. Blood glucose was also more elevated in fish suffering from more severe barotrauma, demonstrating further the sub-lethal effects of capture from depth. As previous studies have shown, stress marker elevations are delayed and prolonged in ice-angled fish (Louison et al., 2017a; Twardek et al., 2018), these effects of barotrauma may not be quantified until hours following release. Due to the potentially lethal impacts of ice-angling barotrauma, it is essential that ice-anglers strive to avoid barotrauma onset in the fish they catch. With regards to mitigation, it appears that venting may be an effective tool, but its effectiveness varies by species. However, prevention of barotrauma is preferable to necessary treatment. Because depth is a primary factor influencing barotrauma, ice anglers engaging in productive catch-and-release should strive to capture fish in shallower waters where possible.

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REFERENCES

Alós, J. (2008) Influence of anatomical hooking depth, capture depth, and venting on mortality of painted comber (Serranus scriba) released by recreational anglers. *ICES Journal of Marine Science*, *65*(9), 1620–1625. https://doi.org/10.1093/icesjms/fsn151

Barkley, A.S. & Cadrin, S.X. (2012) Discard mortality estimation of yellowtail flounder using reflex action mortality predictors. *Transactions of the American Fisheries Society*, *141*(3), 638–644. https://doi.org/10.1080/00028487.2012.683477

Butcher, P.A., Broadhurst, M.K., Hall, K.C., Cullis, B.R. & Raidal, S.R. (2012) Assessing barotrauma among angled snapper (Pagrus auratus) and the utility of release methods. *Fisheries Research*, *127-128*, 49–55. https://doi.org/10.1016/j.fishres.2012.04.013

Carlson, T.J. (2012) Barotrauma in fish and barotrauma metrics. *Advances in Experimental Medicine and Biology*, *730*, 229–233. https://doi.org/10.1007/978-1-4419-7311-5_51

Casper, B.M., Halvorsen, M.B., Matthews, F., Carlson, T.J. & Popper, A.N. (2013) Recovery of barotrauma injuries resulting from exposure to pile driving sound in two sizes of hybrid striped bass. *PLoS One*, *8*(9), e73844. https://doi.org/10.1371/journal.pone.0073844

Childress, W.M. (1988). Catch-and-release mortality of white and black crappie. In: Barnhart, R.A. & Roelofs, T.D. (Eds.), *Catch-and-release fishing: A decade of experience*. Symp Proceed. Nat. Conf. Arcata, Ca: Humbolt State University, pp. 175–186. 30 Sept. – 1 Oct. 1987.

Christensen, RHB (2019). *"ordinal—Regression Models for Ordinal Data"*. R package version 2019.12-10. Available from https://CRAN.Rproject.org/package=ordinal

Coble, D.W. (1988) Effects of angling on bluegill populations: Management implications. *North American Journal of Fisheries Management*, *8*(3), 277–283. https://doi.org/10.1577/1548-8675(1988)008<0277:eoaobp>2.3.co;2

Davis, M.W. (2007) Simulated fishing experiments for predicting delayed mortality rates using reflex impairment in restrained fish. *ICES Journal of Marine Science*, *64*(8), 1535–1542. https://doi.org/10.1093/icesjms/fsm087

Davis, M.W. (2010) Fish stress and mortality can be predicted using reflex impairment. *Fish and Fisheries*, *11*(1), 1–11. https://doi.org/10.1111/j.1467-2979.2009.00331.x

Drumhiller, K.L., Johnson, M.W., Diamond, S.L., Reese Robillard, M.M. & Stunz, G.W. (2014) Venting or rapid recompression increase survival and improve recovery of red snapper with barotrauma. *Marine and Coastal Fisheries*, *6*(1), 190–199. https://doi.org/10.1080/19425120.2014.920746

Fanouraki, E., Mylonas, C.C., Papandroulakis, N. & Pavlidis, M. (2011) Species specificity in the magnitude and duration of the acute stress response in Mediterranean marine fish in culture. *General and Comparative Endocrinology*, *173*(2), 313–322. https://doi.org/10.1016/j.ygcen.2011.06.004

Ferter, K., Weltersbach, M.S., Humborstad, O.B., Fjelldal, P.G., Sambraus, F., Strehlow, H.V. et al. (2015) Dive to survive: Effects of capture depth on barotraumas and post-release survival of Atlantic cod (Gadus morhua) in recreational fisheries. *ICES Journal of Marine Science*, *72*(8), 2467–2481. https://doi.org/10.1093/icesjms/fsv102

Fox, J. & Weisberg, S. (2019). *An R companion to applied regression*, 3rd edition. Thousand Oaks, CA: Sage. Available from https://socialsciences.mcmaster.ca/jfox/Books/Companion/

Gravel, M.-A. & Cooke, S.J. (2008) Severity of barotrauma influences the physiological status, postrelease behavior, and fate of tournament-caught smallmouth bass. *North American Journal of Fisheries Management*, *28*(2), 607–617. https://doi.org/10.1577/M07-013.1

Gustaveson, A.W., Wydoski, R.S. & Wedemeyer, G.A. (1991) Physiological response of largemouth bass to angling stress. *Transactions of the American Fisheries Society*. *12*, 629–636. https://doi.org/10.1577/1548-8659(1991)120<0629:prolbt>2.3.co;2

Halvorsen, M.B., Casper, B.M., Matthews, F., Carlson, T.J. & Popper, A.N. (2012) Effects of exposure to pile-driving sounds on the lake sturgeon, Nile tilapia and hogchoker. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1748), 4705–4714. https://doi.org/10.1098/rspb.2012.1544

Hothorn, T., Bretz, F. & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal*, *50*(3), 346–363.

Kerwath, S., Wilke, C. & Götz, A. (2013) The effects of barotrauma on five species of South African line-caught fish. *African Journal of Marine Science*, *35*(2), 243–252. https://doi.org/10.2989/1814232X.2013.805594

Kirillin, G., Leppäranta, M., Terzhevik, A., Granin, N., Bernhardt, J., Engelhardt, C. et al. (2012) Physics of seasonally ice-covered lakes: a review. *Aquatic Sciences*, *74*(4), 659–682. https://doi.org/10.1007/s00027-012-0279-y

Kittle, A.M., Fryxell, J.M., Desy, G.E. & Hamr, J. (2008) The scale-dependent impact of wolf predation risk on resource selection by three sympatric ungulates. *Oecologia*, *157*, 163–175. https://doi.org/10.1007/s00442-008-1051-9

Logan, J.M., Lawrence, M.J., Morgan, G.E., Twardek, W.M., Lennox, R.J. & Cooke, S.J. (2019) Consequences of winter air exposure on walleye (Sander vitreus) physiology and impairment following a simulated ice-angling event. *Fisheries Research*, *215*, 106–113. https://doi.org/10.1016/j.fishres.2019.03.014

Louison, M.J., Hasler, C.T., Fenske, M.M., Suski, C.D. & Stein, J.A. (2017a) Physiological effects of ice-angling capture and handling on northern pike, Esox Lucius. *Fisheries Management and Ecology*, *24*, 10–18. https://doi.org/10.1111/fme.12196

Louison, M.J., Hasler, C.T., Raby, G.D., Suski, C.D. & Stein, J.A. (2017b) Chill out: physiological responses to winter ice-angling in two temperate freshwater fishes. *Conservation Physiology*, *5*(1), cox027. https://doi.org/10.1093/conphys/cox027

Meka, J.M. & McCormick, S.D. (2005) Physiological response of wild rainbow trout to angling: impact of angling duration, fish size, body condition, and temperature. *Fisheries Research*, *72*(2-3), 311–322. https://doi.org/10.1016/j.fishres.2004.10.006

Miranda, L.E. & Dorr, B.S. (2000) Size selectivity of crappie angling. *North American Journal of Fisheries Management*, *20*(3), 706–710. https://doi.org/10.1577/1548-8675(2000)020<0706:ssoca>2.3.co;2

Morrissey, M.B., Suski, C.D., Esseltine, K.R. & Tufts, B.L. (2005) Incidence and physiological consequences of decompression in smallmouth bass after live-release angling tournaments. *Transactions of the American Fisheries Society*, *134*(4), 1038–1047. https://doi.org/10.1577/t05-010.1

Overton, A.S., Zabawski, J. & Riley, K.L. (2008) Release mortality of undersized fish from the snapper–grouper complex off the North Carolina Coast. *North American Journal of Fisheries Management*, *28*(3), 733–739. https://doi.org/10.1577/m07-025.1

Rudershausen, P.J., Buckel, J.A. & Hightower, J.E. (2014) Estimating reef fish discard mortality using surface and bottom tagging: Effects of hook injury and barotrauma. *Canadian Journal of Fisheries and Aquatic Sciences*, *71*(4), 514–520. https://doi.org/10.1139/cjfas-2013-0337

Rudershausen, P.J., Buckel, J.A. & Williams, E.H. (2007) Discard composition and release fate in the snapper and grouper commercial hook-and-line fishery in North Carolina, USA. *Fisheries Management and Ecology*, *14*(2), 103–113. https://doi.org/10.1111/j.1365-2400.2007.00530.x

Rummer, J.L. (2007) Factors affecting catch and release (CAR) mortality in fish: Insight into CAR mortality in red snapper and the influence of catastrophic decompression. In W.F. Patterson III, J.H. Cowan Jr, G.R. Fitzhugh & D.L. Nieland (Eds.), *Red snapper ecology and fisheries in the U.S. Gulf of Mexico*, pp. 113–132. Bethesda, MD: American Fisheries Society.

Rummer, J.L. & Bennett, W.A. (2005) Physiological effects of swim bladder overexpansion and catastrophic decompression on red snapper. *Transactions of the American Fisheries Society*, *134*(6), 1457–1470. https://doi.org/10.1577/t04-235.1

Schreer, J.F., Gokey, J. & DeGhett, V.J. (2009) The incidence and consequences of barotrauma in fish in the St. Lawrence River. *North American Journal of Fisheries Management*, *29*(6), 1707–1713. https://doi.org/10.1577/m09-013.1

Stoot, L.J., Cairns, N.A., Cull, F., Taylor, J.J., Jeffrey, J.D., Morin, F. et al. (2014) Use of portable blood physiology point-of-care devices for basic and applied research on vertebrates: a review. *Conservation Physiology*, *2*(1), cou011. https://doi.org/10.1093/conphys/cou011

Sumpton, W.D., Brown, I.W., Mayer, D.G., Mclennan, M.F., Mapleston, A., Butcher, A.R. et al. (2010) Assessing the effects of line capture and barotrauma relief procedures on post-release survival of key tropical reef fish species in Australia using recreational tagging clubs. *Fisheries Management and Ecology*, *17*(1), 77–88. https://doi.org/10.1111/j.1365-2400.2009.00722.x

Twardek, W.M., Lennox, R.J., Lawrence, M.J., Logan, J.M., Szekeres, P., Cooke, S.J. et al. (2018) The postrelease survival of walleyes following ice-angling on Lake Nipissing, Ontario. *North American Journal of Fisheries Management*, *38*(1), 159–169. https://doi.org/10.1002/nafm.10009

Wagenmakers, E.J. & Farrell, S. (2004) AIC model selection using Akaike weights. *Psychonomic Bulletin & Review*, *11*(1), 192–196. https://doi.org/10.3758/BF03206482

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. New York, NY: Springer-Verlag. Available from https://ggplot2.tidyverse.org. ISBN 978-3-319-24277-4.

Wilde, G.R. (2009) Does venting promote survival of released fish? *Fisheries*, *34*(1), 20–28. https://doi.org/10.1577/1548-8446-34.1.20

Zuur, A.F., Ieno, E.N. & Elphick, C.S. (2010) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, *1*(1), 3–14. https://doi.org/10.1111/j.2041-210x.2009.00001.x

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