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Effects of barotrauma and mitigation methods on released Australian bass *Macquaria novemaculeata*

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The effects of barotrauma on the short-term mortality and physical condition of Australian bass *Macquaria novemaculeata* were investigated after being: (1) conventionally angled and released during two tournaments in deep impoundments and (2) released untreated or subjected to venting or recompression during a manipulative experiment. All fish were released into two 20 m deep bathy-cages and monitored for 3 days. Of 238 *M. novemaculeata* angled during the tournaments, 43 (18·1%) had clinical signs of barotrauma or were vented and five of these later died (11·6% mortality). Catch histories varied significantly between both barotrauma and non-barotrauma fish and tournaments, but only hook ingestion significantly influenced mortality ($P < 0{\cdot}05$). During the manipulative experiment, venting significantly influenced mortality (13·3%) compared to no treatment or recompression (no deaths). Magnetic resonance images and dissections of barotrauma fish indicated large variation among clinical signs. On the basis of these results, wherever possible *M. novemaculeata* suffering barotrauma should be immediately released with no treatment. Fish that are unable to resubmerge should be recompressed, while those held in live wells and released in shallow water should be vented.

Key words: angling; freshwater fish; post-release mortality; recompression; swimbladder; venting.

INTRODUCTION

Barotrauma can occur in teleosts when they are rapidly retrieved from deep water (typically >10 m), and gases that are trapped in their blood, tissues or body cavities expand faster than they can be expelled (Parker *et al*., 2006). Although species specific, barotrauma is usually more severe in physoclistic than physostomous species, and can present as a hyperinflated or ruptured swimbladder, compressed, displaced or everted organs, internal or external haemorrhaging, gas embolisms and exophthalmia (Feathers & Knable, 1983; Rummer & Bennett, 2005; Hannah *et al*., 2008*a*; Jarvis & Lowe, 2008). In addition to these physiological changes, even mild decompression can render fishes positively buoyant and unable to return to pre-capture depths to feed and evade predation (Hannah *et al*., 2008*b*). Barotrauma is of obvious

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concern for angled-and-released fishes, as it can significantly contribute towards their cumulative stress and physical damage and, ultimately, post-release mortality (Arlinghaus *et al*., 2007).

Recognition of the adverse effects of barotrauma on angled fishes has resulted in numerous attempts to establish effective mitigation methods (Sumpton *et al*., 2010). The most popular approach involves venting the expanded gases by puncturing the swimbladder with a hypodermic needle (Wilde, 2009). The benefits of such a treatment, however, can vary often according to species-specific tolerances and the skill of the operator (Wilde, 2009). Alternative methods, such as immediate release or recompression by return to depth with a weighted device (*e.g.* a cage or barbless hook attached through the jaw), may be equally or more beneficial (Hannah & Matteson, 2007; Jarvis & Lowe, 2008; Brown *et al*., 2010; Sumpton *et al*., 2010). Intuitively, recompression might offer advantages over venting by facilitating gas homeostasis throughout the body, but few studies have tested this hypothesis (Hannah & Matteson, 2007).

Most studies that have assessed the effects of barotrauma in teleosts have used laboratory-based hyperbaric chambers (Shasteen & Sheehan, 1997; Parker *et al*., 2006), field-based tagging (mark–recapture or biotelemetry) (Bruesewitz *et al*., 1993; Nguyen *et al*., 2009) or confinement experiments (Render & Wilson, 1994; Diamond & Campbell, 2009). Of these methods, mark–recapture and biotelemetry tagging provide the most holistic assessment of the fate of released fishes. The former relies on accurate returns from anglers and both approaches are often very expensive, which can mean low replication and difficulty in differentiating mortality from barotrauma from other cumulative catch-and-release effects (Nguyen *et al*., 2009; Sumpton *et al*., 2010). In contrast, although hyperbaric chambers can isolate the effects of barotrauma and assess the utility of mitigation methods across adequate replication and under controlled conditions, such studies are logistically difficult and considerably removed from natural environments (Shasteen & Sheehan, 1997). By far, the most common approach involves field-based, confinement studies.

Most confinement studies to assess barotrauma follow the methods commonly applied to general catch-and-release research, except that fishes are often held in cages that are lowered to specific depths (St John & Syers, 2005). Concerns with this approach include the confounding effects of restricting individuals to a limited vertical distribution and inadvertently imposing recompression. Ideally, as in tagging studies, released fishes should be free to locate to their preferred depths. One method to facilitate such movements is to use large cages or enclosures (bathy-cages) that encompass the entire water column, or at least all capture depths (Brown *et al*., 2010). Bathy-cages have not been widely applied, but have the advantages of offering freedom of vertical movement (as in tagging studies) while still providing a controlled environment (like hyperbaric chambers) for manipulative experiments to isolate any specific effects of barotrauma and determine the utility of different handling methods. The latter experimental approach was used in this study to investigate the post-release fate of Australian bass *Macquaria novemaculeata* (Steindachner 1866) affected by barotrauma.

Macquaria novemaculeata is a popular freshwater species that is angled and released in large numbers throughout southern Australia (Hall *et al*., 2009*a*). The species has been widely introduced into impoundments for angling and to counter declines in their distribution and abundance as a result of river regulation (Growns

& James, 2005). Most impounded fish are prevented from undertaking their natural breeding migration, and therefore depend on artificial propagation and low mortality to maintain populations.

The assumption of minimal post-release mortality of *M. novemaculeata* has been validated for many angling scenarios, with total estimates <6% (Hall *et al*., 2009*a*; Dowling *et al*., 2010). This research has suggested that the species is quite robust, with most deaths attributed to fairly extreme treatments including the ingestion of hooks (Hall *et al*., 2009*a*, *b*). *Macquaria novemaculeata*, however, is physoclistic and barotrauma has been implicated as a potential mortality-causing factor for individuals angled from deep impoundments, but this has yet to be scientifically investigated (Hall *et al*., 2009*a*). This study attempted to address this shortfall by using field-based bathy-cages to quantify the short-term mortality and physical effects of barotrauma in *M. novemaculeata* after being: (1) conventionally angled and released during two tournaments in deep impoundments and (2) released untreated or subjected to venting or recompression during a manipulative experiment.

MATERIALS AND METHODS

The study was completed between April and June 2009 in Lake Glenbawn (32° 06′ S; 150° 59′ E) and Lake St Clair (32° 21′ S; 151° 17′ E) and Karangi Dam (30° 15′ S; 153° 01′ E) in New South Wales (NSW), Australia. Prior to starting work in each impoundment, a Lowrance LMS-525c DF echo sounder (Lowrance; www.lowrance.com) and a Greenspan ODO3000 probe (Tyco Environmental Systems; www.tycoflowcontrol.com.au) were used to locate an area >25 m depth with adequate dissolved oxygen (DO >4 mg l^{-1}) down to at least 15 m. Two floating cylindrical 69 000 l bathy-cages (each 2·5 m diameter × 20 m depth and made from 22 mm mesh) were then deployed and anchored at these locations. During each monitoring period, depth profiles of dissolved oxygen (DO) and temperature (° C) were recorded at 1 or 2 m intervals from the surface (near the cages) to the substratum with the Greenspan logger, and surface electrical conductivity (EC, mS cm^{-1}), pH and nephelometric turbidity units (NTU) were recorded with an Horiba U-10 meter (Horiba Ltd; www.horiba.com).

BAROTRAUMA FROM ANGLING

The first experiment involved up to 130 boat-based, tournament anglers targeting *M. novemaculeata* of fork length (L_F) >300 mm in Lake Glenbawn (in April) and Lake St Clair (in May). Both tournaments comprised two morning and one afternoon fishing sessions (each 5 h duration) followed by a shore-based, live weigh-in. The tournament rules stipulated two anglers per boat, each with one rod, rigged with artificial lures or flies. Adequate live wells were required with a minimum of 50% water exchange every 15 min while fish were held onboard, and a maximum stocking density of four fish.

At both tournaments, anglers were instructed to handle their fish as normal, measure L_F to the nearest 1 mm and record the following data: fishing depth, capture depth and time, fishing method, lure type, hook location and whether or not the hook was removed or the fish was vented. During weigh-in, researchers checked the datasheets and deemed fish to be suffering from barotrauma (barotrauma fish) if they were caught from >10 m depth or vented, or had compromised buoyancy in combination with at least one other clinical sign (*e.g.* a swollen coelomic cavity, exophthalmia or eversion of their stomach into their buccal cavity or intestines out of their anus). Any barotrauma fish were placed in 70 l polyvinyl chloride (PVC) tanks containing aerated, flow-through water for the remainder of the weigh-in and then transferred to the bathy-cages without further air exposure.

After each tournament, the caged barotrauma fish were monitored daily for mortality at the surface and fed school prawns *Metapenaeus macleayi* at *c*. 1% biomass per day. After

3 days, the bathy-cages were retrieved and any dead fish were counted and dissected and all survivors were released back into the wild.

INDUCED BAROTRAUMA AND MITIGATION METHODS

At Lake Glenbawn, all non-barotrauma fish were eventually released. In contrast, after being weighed-in at Lake St Clair, the non-barotrauma fish were immediately placed into six 1000 l and two 3000 l polyethylene land-based tanks at stocking densities of 15 and 40 fish per tank, respectively. Tanks were supplied with flow-through lake water at a rate of 5 l min^{-1} and diffuse aeration. Extra fish of L_F <300 mm that were angled, but not weighed-in nor suffered barotrauma during the tournament were also held. Fish were fed and monitored daily (as above). At the end of the tournament, all fish were transported to the Grafton Fisheries Centre (GFC) and held for 1 month following the methods described by Hall *et al.* (2009*a*).

On the first day of the manipulative experiment, 40 *M. novemaculeata* were transported from the GFC to Karangi Dam (Hall *et al.*, 2009*a*). Upon arrival, these fish were anaesthetized again, measured and randomly fin-clipped (top or bottom caudal, left pelvic and left pectoral) and then individually placed into 110 l cylindrical cages (0·5 m diameter × 0·7 m depth) constructed from PVC bins and lids, with two lateral windows (covered in 6 mm PVC mesh) for water exchange. A 3 kg weight and a length of 10 mm diameter rope were attached to each side to orientate the cages horizontally in the water column when stationary, but vertically during retrieval.

Thirty and 10 of the caged fish were submerged to 20 and 5 m, respectively. After 24 h, each cage was retrieved to the surface at 1 m s^{-1} using a motorized line-hauler. The fish deployed to 5 m (controls) were also retrieved diagonally for 20 m. It was hypothesized that these fish would control for the effects of hauling, but without incurring barotrauma. The deployment depth of the controls was based on negligible barotrauma among >800 *M. novemaculeata* angled from <5 m during nine tournaments (Hall *et al.*, 2009*b*; Dowling *et al.*, 2010).

Immediately after reaching the surface, all fish were removed from their cages and assessed for barotrauma. Fish retrieved from 20 m (barotrauma fish) were handled in one of three ways: (1) 10 were recompressed by attaching a barbless hook (fixed to a weighted line) through their lower jaw membrane, relowering them to 15 m inside the bathy-cages (five fish per cage) and pulling on the line to release the hook, (2) 10 were vented by inserting a 16 gauge hypodermic needle into their swimbladder just posterior to the tip of the pectoral fin and (3) 10 were left untreated. The last two groups were released at the surface of each bathy-cage (five fish per cage) along with the 10 controls that were also left untreated (five fish per cage).

Caged fish were monitored daily for mortality at the surface and fed *M. macleayi* as above. After 3 days, the bathy-cages were retrieved and any dead fish were counted and dissected. The above methodology was repeated three times, providing totals of 30 fish for each of the four experimental groups.

Following the third experimental replicate, 10 and two fish were deployed in the 110 l cages to 20 and 5 m, respectively, and left for 16 h before being retrieved as above. All 12 fish were euthanased in a solution of benzocaine (>100 mg l^{-1}) and immediately transported to the Coffs Harbour Radiology for whole-body magnetic resonance imaging (MRI). The fish were individually positioned in a Philips Intera 1.5 tesla MRI machine (Philips Healthcare; www.healthcare.philips.com) with a small dual element coil, which produced 3·0 mm transaxial (cross section) and 2·5 mm coronal (dorsal) images in both T1-weighted and T2-weighted sequences from the head to caudal fin over 10 min. The MRI scans in each plane were then analysed along the medial section of each fish using an eFilm Lite digital imaging in communications and medicine (DICOM) reader (Merge Technologies Inc.; www.merge.com) to assess for any swimbladder expansion or rupture and associated organ movement. After scanning, fish were dissected and examined for internal clinical signs of barotrauma by incising longitudinally from the anus to the pelvic bone and removing the left medial coelomic cavity wall and pectoral fin. The macroscopic condition and position of all major organs were noted, and then the ventral surface of the swimbladder was also incised longitudinally to assess for any internal haemorrhaging or injuries.

DATA ANALYSES

The distributions of water quality variables were assessed for normality and equality of variance (by histograms, normal-quantile plots and goodness-of-fit tests), $\log_{10}(x + 1)$ transformed and analysed with robust ANOVA models (Welch's statistic) as they failed to meet the assumptions. To analyse the variation in depth profiles of DO and water temperature between impoundments, averages were taken for standardized depth intervals and group means were compared with Dunnett's C multiple comparison tests.

All data describing the capture and handling of each angled fish were collated as either categorical or continuous variables (mean ± S.D.). Size-frequency distributions (L_F intervals of 10 mm) of fish were compared between experiments using two-sample Kolmogorov–Smirnov tests. Collinearity between predictor variables was assessed by correlation matrices and contingency tables for continuous and categorical variables, respectively. When collinearity was detected, the variable that explained the greatest variation in mortality data was retained for further analyses. The variation in response variables between the two tournaments, and between barotrauma and non-barotrauma fish within each tournament, were assessed by fitting generalized linear models (GLM), with a normal error distribution and identity link function for continuous data and a binomial or multinomial error distribution and logit link function for categorical data.

The influences of each predictor variable on the mortality of *M. novemaculeata* at Lake Glenbawn and during the manipulative experiment at Karangi Dam were analysed by fitting generalized linear mixed models (GLMM) with a binary (dead or alive) response variable, logit link function and binomial error distribution using the lmer function in the R package lme4 (Bates, 2005). There were no deaths at Lake St Clair for further analyses. For the data from Lake Glenbawn, days and bathy-cages were included as random factors, and various combinations of capture and handling factors were included as fixed factors. The most parsimonious model was determined through a series of forward-selected models that were assessed according to Akaike's information criterion (AIC) (Quinn & Keough, 2002). For the manipulative experiment, replicate deployments and bathy-cages were included as random factors and treatment, retrieval time, L_F and each clinical sign were included as fixed factors in separate GLMMs. The few deaths in this experiment precluded further model fitting with combinations of fixed factors. All other sundry statistics were completed using JMP version 8 statistical software (SAS Institute Inc.; www.sas.com) at the $P < 0{\cdot}05$ significance level unless stated otherwise.

RESULTS

ENVIRONMENTAL CONDITIONS

The surface water (*i.e.* <0·5 m) was significantly warmer in Lake Glenbawn (22·1 ± 1·2° C) than in Lake St Clair (18·3 ± 0·5° C) and Karangi Dam (17·7 ± 0·5° C) (ANOVA, $F'_{2,241} = 757{\cdot}7$, $P < 0{\cdot}001$; Fig. 1). In addition, the temperature and DO depth profiles of the two lakes were stratified, with the greatest change between 15 and 20 m where DO decreased from >6 to <1 mg l^{-1} (Fig. 1). Thermal stratification was more pronounced in Lake Glenbawn (5° C difference between 0·5 and 17·0 m) than in Lake St Clair (1° C difference). By comparison, Karangi Dam had similar temperatures and DO across all depths (Fig. 1).

BAROTRAUMA FROM ANGLING

Anglers weighed-in 117 and 121 *M. novemaculeata* during the two tournaments (Table I). Barotrauma occurred in 18·1% of all fish, but the percentage varied significantly between the two tournaments (29·9 *v.* 6·6%; Table I; GLM, $\chi^2_{1,1} = 23{\cdot}2$, $P < 0{\cdot}001$).

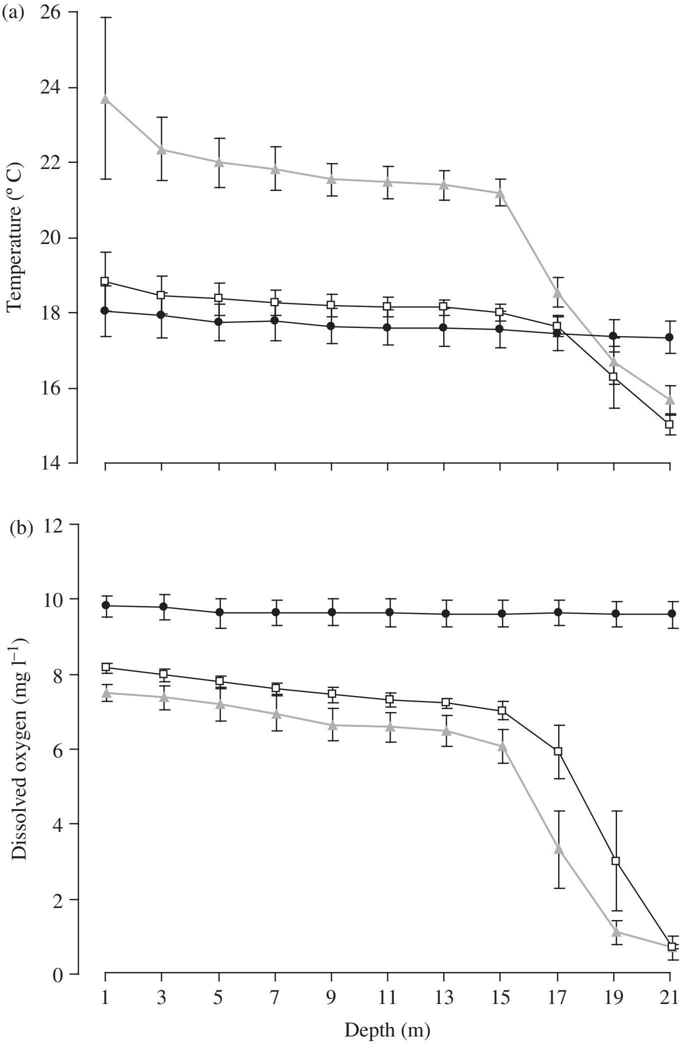

FIG. 1. (a) Temperature and (b) dissolved oxygen profiles during experiments with *Macquaria novemaculeata* in three deep impoundments: Lake Glenbawn (▲) in April, Lake St Clair (□) in May and Karangi Dam (●) in June (all 2009). Values are means ± S.D.

Although the total size distributions of angled *M. novemaculeata* were similar between the two lakes (Kolmogorov–Smirnov $Z = 0{\cdot}1$, $P > 0{\cdot}05$), barotrauma fish from Lake Glenbawn were significantly larger than those from Lake St Clair (Table I; GLM, $\chi^2_{1,1} = 6{\cdot}9$, $P < 0{\cdot}01$). In Lake Glenbawn, barotrauma fish were also significantly larger than non-barotrauma fish (GLM, $\chi^2_{1,1} = 21{\cdot}0$, $P < 0{\cdot}001$), whereas in Lake St Clair this trend was reversed, but not significant (GLM, $\chi^2_{1,1} = 0{\cdot}5$, $P > 0{\cdot}05$). The fishing and capture depths were also significantly deeper in Lake Glenbawn (1·0–31·6 m) than Lake St Clair (0·5–12·2 m) (Table I; GLM, $\chi^2_{1,1} = 40{\cdot}3$ and 41·8, $P < 0{\cdot}001$). Despite anglers fishing depths to 31·6 m in Lake Glenbawn, no fish were caught below 19·0 m. In both lakes, barotrauma fish were caught in

TABLE I. Mean ± S.D. and range (minimum–maximum) of continuous variables and the frequency of categorical variables for angled non-barotrauma and barotrauma *Macquaria novemaculeata* during the tournaments at Lake Glenbawn and Lake St Clair

	Lake Glenbawn		Lake St Clair	
	Non-barotrauma	Barotrauma	Non-barotrauma	Barotrauma
Number of fish	82	35	113	8
L_F (mm)	320 ± 29 (270–400)	348 ± 27 (300–420)	330 ± 33 (270–430)	316 ± 24 (300–360)
Depth fished (m)	7·2 ± 4·9 (1·0–25·9)	17·7 ± 4·1 (10·0–31·6)	5·4 ± 2·7 (0·5–12·2)	9·2 ± 0·9 (7·9–10·6)
Depth caught (m)	3·4 ± 1·3 (1·0–7·6)	14·3 ± 3·4 (7·6–19·2)	3·0 ± 1·6 (0·5–8·0)	8·0 ± 2·1 (4·6–10·6)
Time in live well (min)	130 ± 69 (30–260)	161 ± 81 (15–290)	163 ± 68 (23–270)	77 ± 53 (16–150)
Time caught				
Morning	37	28	99	6
Afternoon	38	7	14	2
Fishing method				
Casting	35	3	99	5
Jigging	4	31	2	2
Trolling	25	1	8	0
Lure type				
Hard-bodied bibless	43	5	16	0
Hard-bodied bibbed	13	0	10	0
Soft plastic	2	30	60	3
Spinner bait	5	0	2	0
Surface lure	1	0	13	0
Fly	0	0	8	4
Hook location				
Mouth	63	31	100	7
Ingested	0	4	3	0
Body	0	0	2	0
Vented				
Yes	0	30	0	6
No	64	5	104	2

L_F, fork length.

significantly deeper water than non-barotrauma fish (Table I; GLM, $\chi^2_{1,1} = 176{\cdot}1$ and 20·5, $P < 0{\cdot}001$).

Although similar numbers of fish were caught during the afternoon and morning sessions at Lake Glenbawn, significantly more fish sustained barotrauma in the morning (80·0%, Table I; GLM, $\chi^2_{1,1} = 9{\cdot}8$, $P < 0{\cdot}01$). This trend was not repeated at Lake St Clair, with most fish caught during the morning, irrespective of whether or not they suffered barotrauma (Table I; GLM, $\chi^2_{1,1} = 0{\cdot}9$, $P > 0{\cdot}05$). Angling methods and lure types also differed significantly between the tournaments (Table I; GLM, $\chi^2_{2,2} = 68{\cdot}8$ and $\chi^2_{5,5} = 56{\cdot}3$, $P < 0{\cdot}001$) and between barotrauma and non-barotrauma fish within each tournament (Table I; GLM, $\chi^2_{2,2} = 74{\cdot}3$ and 7·2, $\chi^2_{4,4} = 81{\cdot}6$ and 13·5, $P < 0{\cdot}05$). Although casting was the most popular form of angling in both lakes, more barotrauma fish were caught by jigging than with other methods. Similarly, although more fish were caught with hard-bodied lures in Lake Glenbawn, most barotrauma fish were caught with soft plastics (85·7%); while in Lake St Clair a disproportionate number of barotrauma fish were caught with sinking flies, despite the greater usage of soft plastics (Table I). Both angling method and lure type were correlated with capture depth.

During both tournaments, 95·7% of fish were mouth hooked and only seven ingested hooks (Table I). All of the latter were caught with soft plastics that were jigged (Table I). Irrespective of anatomical location, all hooks were removed by anglers during both tournaments. At Lake Glenbawn, 85·7% of barotrauma fish were also vented, which represented 30·3% of the total catch, whereas at Lake St Clair, although 75·0% of barotrauma fish were vented, this equated to only 5·4% of the total catch (Table I).

No mortality was recorded among fish at Lake St Clair, whereas five of the 35 barotrauma fish held at Lake Glenbawn died, and two escaped, resulting in a total mortality 11·6%. The only factor that significantly influenced mortality in the final GLMM was hook location ($P < 0{\cdot}05$; Table II). Half of the barotrauma fish that ingested their hooks ($n = 4$) died compared with only 10·2% of those that were mouth hooked. Although mortality was also disproportionately greater among fish that were caught during the afternoon than the morning sessions, and time caught was retained in the final GLMM, this factor was not significant ($P > 0{\cdot}05$; Table II). Likewise, although all dead fish had been vented, this procedure was not a significant predictor of mortality, probably because there were few unvented barotrauma fish for comparison (Table II). Angling method and lure type showed significant collinearity with capture depth ($P < 0{\cdot}05$), so they were excluded from GLMMs.

INDUCED BAROTRAUMA AND MITIGATION METHODS

The prevalence of clinical signs of barotrauma among retrieved experimental fish did not differ significantly between replicates (GLM, $\chi^2_{2,2} = 2{\cdot}2$, $P > 0{\cdot}05$), but did

TABLE II. The influence of key variables on the mortality of angled *Macquaria novemaculeata* suffering from barotrauma and monitored in bathy-cages during an angling tournament at Lake Glenbawn. Results are from forward-selected generalized linear mixed models (GLMM) with days and bathy-cages included as random effects. P values for excluded factors were derived by adding each in turn to the final two-factor GLMM and assessing the change in deviance.

	β	χ^2	d.f.	P
Retained in final GLMM				
Hook location	3·1	5·1	2	<0·05
Time caught	2·4	3·4	1	>0·05
Excluded from final GLMM				
L_F		1·0	1	>0·05
Depth caught		0·8	1	>0·05
Time in live well		0·3	1	>0·05
Vented		0·5	1	>0·05

L_F, fork length.

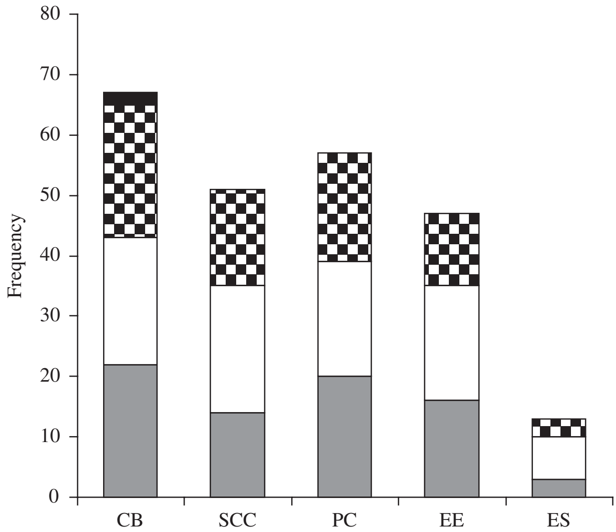

FIG. 2. Frequency of different clinical signs of barotrauma in *Macquaria novemaculeata* within each experimental group (before treatment) at Karangi Dam: controls (■), untreated barotrauma (⧆), vented (□) and recompressed (▩) ($n = 30$ fish per group). Clinical signs included compromised buoyancy (CB), swollen coelomic cavity (SCC), prolapsed cloaca (PC), expelled eggs (EE) and everted stomach into the buccal cavity (ES).

between deployment depths (GLM, $\chi^2_{1,1} = 2{\cdot}5$, $P < 0{\cdot}05$) and consequently treatment groups (GLM, $\chi^2_{3,3} = 47{\cdot}9$, $P < 0{\cdot}05$). Only two control fish had compromised buoyancy, whereas most treatment fish exhibited a range of clinical signs including compromised buoyancies, swollen coelomic cavities, prolapsed cloacas and expelled eggs (Fig. 2). Few fish everted their stomachs into their buccal cavities and no exophthalmia was recorded. Eight of the fish retrieved from 20 m had no external clinical signs of barotrauma, 11 had only one (usually compromised buoyancy), whereas the remainder ($n = 71$) had two or more signs.

The 47 fish that expelled eggs during retrieval were clearly females, but sex remained unknown for all others. Confirmed females had significantly more compromised buoyancies, swollen coelomic cavities and prolapsed cloacas than the unsexed fish (GLM, $\chi^2_{1,1} = 8{\cdot}3$, $P < 0{\cdot}05$). In contrast, more unsexed fish had their stomachs everted into their buccal cavities than confirmed females. Unsexed fish were significantly smaller than confirmed females, consequently L_F also had a significant effect on stomach eversions (GLM, $\chi^2_{1,1} = 7{\cdot}95$, $P < 0{\cdot}05$), and occurred in 17·1% of fish smaller than the median L_F of 331 mm, compared with only 3·5% of larger fish.

Four fish died; all during the last replicate and all were vented females, providing a mortality of 13·3% for this treatment group, and an overall rate of 3·3%. Thus, treatment (venting) and replicate deployments (third) significantly influenced mortality (GLMM, $\chi^2_{3,3} = 12{\cdot}6$, $P < 0{\cdot}01$ and variance = 11·1; Table III). Dissections revealed that in two of the four dead fish, vital organs had been punctured, including the gonad of a fully ripe female, which resulted in haemorrhaging and eggs protruding into the coelomic cavity. Excessive haemorrhaging inside the swimbladders of the other two fish was also evident, possibly caused by puncture wounds from the venting needles.

TABLE III. The influence of key variables on the mortality of *Macquaria novemaculeata* after being caged and retrieved to the surface from two depths in Karangi Dam. Results are from separate generalized linear mixed models for each variable with replicate deployments and bathy-cages included as random effects.

	χ^2	d.f.	P
Treatment	12·6	3	<0·01
L_F	1·8	1	>0·05
Retrieval time	0·2	1	>0·05
Compromised buoyancy	0·2	1	>0·05
Swollen coelomic cavity	4·4	1	<0·05
Expelled eggs	0·2	1	>0·05
Prolapsed cloaca	1·7	1	>0·05
Everted stomach	0·5	1	>0·05
Number of clinical signs	6·4	5	>0·05

L_F, fork length.

The different external clinical signs varied in their influence on the mortality of *M. novemaculeata*. There was greater mortality among those with swollen coelomic cavities ($P < 0·05$; Table III) compared with other fish, whereas compromised buoyancies, stomach eversions, prolapsed cloacas and expelled eggs had no discernable effect ($P > 0·05$; Table III). Similarly, the number of clinical signs in each fish did not affect mortality ($P > 0·05$; Table III).

Post-mortem MRI and dissections of fish showed the swimbladders of the two controls were more inflated than those of the 10 fish retrieved from 20 m [Fig. 3(a), (b)]. Most of these latter fish had ruptured swimbladders and severe haemorrhaging [Fig. 3(c), (d)]. The internal injuries also differed between sexes. Males typically had relatively smaller gonads, and as a result more room for gases to expand [Fig. 3(c), (d)] than females [Fig. 3(e), (f)]. Males also tended to be smaller, so their overall coelomic cavity spaces were smaller. These factors may have contributed towards their observed greater stomach eversions, organ movements and swimbladder ruptures (and associated haemorrhaging). Conversely, most females had less coelomic cavity available for swimbladder expansion owing to their large ripe gonads [Fig. 3(e), (f)]; thus organ compressions and egg expulsions were more likely to occur, with liver haemorrhages obvious in many.

DISCUSSION

It is well established that the fate of angled-and-released fishes depends on the cumulative and often interacting effects of a range of biological, technical and environmental variables (Arlinghaus *et al.*, 2007). Partitioning the relative importance of individual factors within these three groups is often difficult, but their isolation and comprehension of their mechanisms are essential for focusing strategies to improve post-release welfare. The results from this study contribute towards such a protocol for *M. novemaculeata*. By quantifying the physical damage and mortality of this species after incurring barotrauma during conventional angling and then partitioning the effects of this factor under controlled conditions in the manipulative experiment,

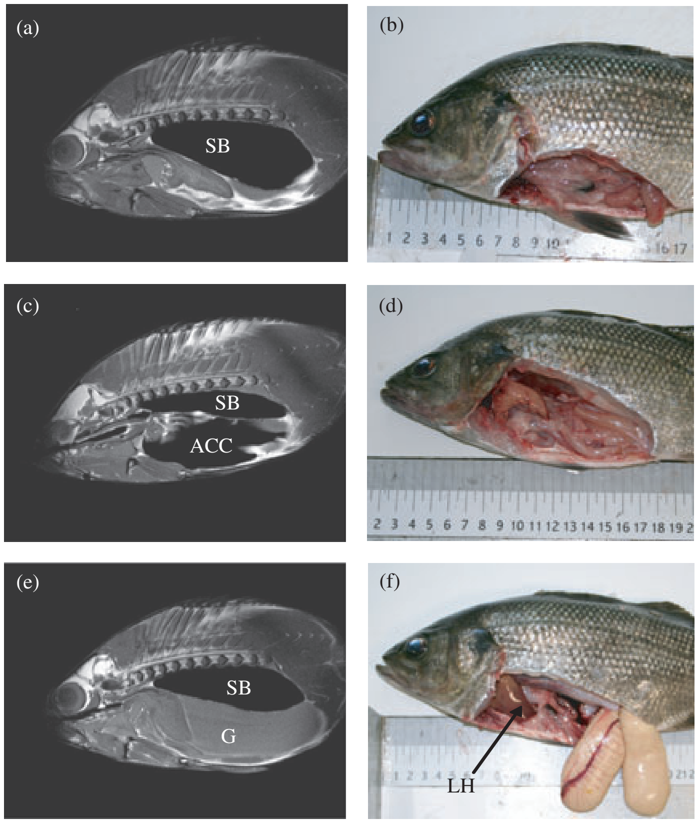

FIG. 3. (a), (c), (e) Magnetic resonance images and (b), (d), (f) dissections of *Macquaria novemaculeata* after being caged and retrieved to the surface from two depths in Karangi Dam: (a), (b) a male retrieved from 5 m with an expanded swimbladder (SB) and small coelomic cavity; (c), (d) a male retrieved from 20 m with anterior movement of the organs and swimbladder rupture resulting in air expansion in the coelomic cavity (ACC) and (e), (f) a female retrieved from 20 m with an expanded swimbladder (SB), large mass of gonads (G) and compression of other organs resulting in liver haemorrhage (LH). Graduations on the rulers are in cm.

its importance in the overall mortality model has been assessed. By doing so, it facilitates coherent recommendations for future management; the specifics of which can be considered by first discussing the probable range of sublethal and lethal effects directly and indirectly attributable to barotrauma, and why these occurred.

As for previously assessed *M. novemaculeata* that were angled and released from shallow water (*i.e.* without barotrauma; Hall *et al*., 2009*a*; Dowling *et al*., 2010), there was considerable variability in the measurable effects among barotrauma fish monitored during the two tournaments. While these effects clearly resulted in proportionally greater fatalities among the barotrauma fish (*e.g.* up to 12 *v*. 6%), there were still some common, dominant deleterious factors, especially anatomical hook location. More specifically, as in the non-barotrauma *M. novemaculeata* monitored by Hall *et al*. (2009*a*) and most teleosts in general irrespective of capture depth (Arlinghaus *et al*., 2007), the ingestion of hooks was identified as a significant predictor of the fatalities among barotrauma fish at Lake Glenbawn. Further, all of the dead fish had their ingested hooks removed by anglers; a practice previously demonstrated to typically cause increased mortalities in most teleosts (Hall *et al*., 2009*b*).

Although anatomical hook location explains some of the deaths of tournament-caught barotrauma fish, other factors were also clearly important, because three of the five fatalities were mouth hooked. The cumulative influence of barotrauma and other collinear variables (*e.g.* the time of day and temperature or DO changes during retrieval) could account for these deaths, but based on the results from the manipulative experiment, venting probably had a stronger overall effect. For example, there was no mortality among any of the *M. novemaculeata* that had induced barotrauma at Karangi Dam and were either released at the surface of the bathy-cages or after recompression. Similarly, no controls died. The only deaths were four vented females that had injured vital organs. While tournament anglers might be expected to be reasonably proficient at minimizing harm to released fishes (Dowling *et al*., 2010), some may have inadvertently caused damage during venting, and so contributed towards the mortality of mouth-hooked individuals at Lake Glenbawn.

The potential for a dominant effect of incorrect venting among the barotrauma fish is also supported by no correlation between the severity of their external clinical signs and short-term mortality; a relationship previously identified for several species (Gravel & Cooke, 2008; Diamond & Campbell, 2009). It is possible, however, that such a correlation could eventually manifest due to delayed mortality beyond 3 days, with more severely traumatized *M. novemaculeata* (that were correctly vented) eventually succumbing to their injuries.

Any such longer-term mortality (or sublethal injuries) could also be sexually or seasonally biased. For example, during the manipulative experiment females were reproductively active and had less space in their coelomic cavities than males, which meant that the latter had greater organ movements, leading to ruptured swimbladders and stomach eversions. Because ruptures can rapidly heal in many species (Shasteen & Sheehan, 1997; Parker *et al*., 2006), it is unclear whether such damage could eventually cause more deaths or alternatively promote survival by releasing the pressure in the coelomic cavity and halting organ compression (Diamond & Campbell, 2009). Further research is required to assess this issue for *M. novemaculeata* at different times throughout their reproductive cycle, and also to investigate whether any reduced reproductive output results from the compression or expulsion of ripe female eggs.

The possibility for longer-term mortality or sublethal effects of *M. novemaculeata* suffering barotruama, combined with the clear short-term physiological and physical effects, support the development of appropriate handling and mitigation methods wherever possible. Of the three *a posteriori* options that were assessed, the immediate release of untreated barotrauma fish was perhaps the least invasive and most effective. Other studies also support this conclusion, particularly if surface intervals are short (Parker *et al*., 2006; Jarvis & Lowe, 2008). For example, research with largemouth bass *Micropterus salmoides* (Lacepède 1802) decompressed in hyperbaric chambers showed that the full effects of barotrauma may not occur until *c*. 5 min after reaching the surface (Feathers & Knable, 1983). Thus, if fishes are immediately released they may have a greater chance of resubmerging.

Alternatively, if buoyancy is compromised and fish are unable to submerge, then the results from the manipulative experiment suggest that they should be recompressed by lowering to capture depth with a weighted line. Few other studies have assessed the relative merits of recompression and the other two treatments examined here, but the available results suggest that it is at least as equally as effective as venting (Brown *et al.*, 2010; Sumpton *et al.*, 2010).

While the immediate release of unwanted *M. novemaculeata* with either no treatment or assistance from a weighted line is desirable, both methods are logistically difficult during live weigh-in tournaments where individuals are confined onboard for extended intervals (*e.g.* up to 6 h; Dowling *et al.*, 2010). Under such conditions, the severity of barotrauma may increase and render fish positively buoyant, with the potential of sustaining further physical damage through contact with conspecifics and the top of the live well. Equally important, tournament fishes are almost always eventually released in shallow water at the lakes' edge where compromised buoyancy would expose them to increased predation, exposure or boat traffic (Keniry *et al.*, 1996; Nguyen *et al.*, 2009). For such individuals, the only viable option may be venting immediately after capture, although clearly anglers need to be educated about the correct techniques and the size of venting needles needs to be appropriate for the species to minimize injuries. Alternatively, tournament organizers might adopt a measure-and-dated photograph system of documenting fishes, so that all can be immediately released untreated or, if necessary, recompressed to their capture depth with a weighted device. This may be particularly relevant for tournaments held when females are spawning to reduce the risk of puncturing swollen gonads.

Notwithstanding the potential benefits of the handling methods above for releasing *M. novemaculeata* with barotrauma, perhaps a more proactive approach is to develop *a priori* measures that minimize its occurrence (Feathers & Knable, 1983). Predictably, like most studies (Schreer *et al.*, 2009), the main factor responsible for the severity and incidence of barotrauma in *M. novemaculeata* was their capture depth. But this factor varied significantly between the two tournaments, along with several other technical and environmental factors that also varied between barotrauma and non-barotrauma fish. The potential influences of these other factors on capture depth also provide insight into some possible *a priori* measures to prevent barotrauma in *M. novemaculeata*.

In particular, water DO and temperature differed significantly between the two tournaments, and probably exerted a strong influence on the vertical distribution of fish (Jones *et al.*, 2008). During the Lake Glenbawn tournament (in early autumn), there was a pronounced thermal stratification and high surface water temperatures may have forced fish to remain deep (Coutant, 1985). But there was also a distinct DO stratification that resulted in anoxic water >15–20 m, which would have limited *M. novemaculeata* to a narrow vertical distribution. In contrast, the Lake St Clair tournament was held in late autumn, when the surface was significantly cooler and there was a less pronounced thermocline and slightly deeper anoxic layer, allowing fish to utilize more of the water column. Dowling *et al.* (2010) recorded a greater incidence of barotrauma in *M. novemaculeata* during winter, when presumably the impoundments were less stratified. So although fish may not need to remain deeper to avoid hot surface waters, increased DO concentrations during winter would allow them access to deeper waters. Pronounced stratification is a common feature of many deep impoundments in Australia during summer and autumn, and so pre-emptive analyses of DO and temperature profiles may provide some indication of periods during which fish are most at risk from barotrauma and tournaments could be then scheduled or regulated accordingly.

Angler behaviour also varied according to the environmental conditions and perceived distribution of fish within the lakes. Although both tournaments were part of the same series with similar participants, the fishing methods, depths and lure types all differed significantly between events and between barotrauma and non-barotrauma fish. For example, fish caught from deeper water during the first tournament were predominantly jigged with soft plastics, whereas during the second tournament more fish were caught from shallow water by cast or trolled lures. Encouraging anglers to adopt, and tournament organizers to promote or regulate for, particular behaviours or gear configurations (*e.g.* restricting the use of soft plastics in tournaments at certain times of the year) may help decrease the incidence of barotrauma (and ingested hooks) among *M. novemaculeata*, and thereby further minimize the potential adverse effects of catch and release on this species.

The results from this study extend the information base to encompass more angling scenarios for *M. novemaculeata* and suggest that while post-release mortality is undoubtedly the result of various cumulative effects, two of the most important factors are clearly anatomical hook location and barotrauma. It is also clear that the short-term effects of both factors (and therefore fatalities) can be considerably minimized through the simple handling methods discussed above and in previous papers (Hall *et al.*, 2009*a*, *b*; Dowling *et al.*, 2010) and through the promotion of angling behaviours and gears that reduce their incidence among angled-and-released fish. These findings may also be applicable to other endemic physoclistic freshwater species, *e.g.* golden perch *Macquaria ambigua* (Richardson 1845), silver perch *Bidyanus bidyanus* (Mitchell 1838), Murray cod *Maccullochella peelii* (Mitchell 1838) and freshwater catfish *Tandanus tandanus* Mitchell 1838, commonly angled and released during tournaments in deep rivers and impoundments, although, ultimately, their validation requires species-specific assessment. Future research with *M. novemaculeata*, possibly involving more complex experimental designs (such as tagging), is also required to determine if the benefits of these methods are maintained across the longer term. As in this study, any such future work will require appropriate experimental protocols to facilitate the accurate attribution of causality for any observed mortality or sublethal effects.

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