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Resilience of inshore, juvenile snapper *Pagrus auratus* to angling and release

M.K Broadhurst, P.A. Butcher, K.C.Hall, B.R. Cullis and S.P. McGrath

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2	Resilience of inshore, juvenile snapper Pagrus auratus to angling and
3	release
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17	
18	Suggested running headline: Post-release mortality of Pagrus auratus
19	
20	

Abstract

22	This study assessed the mortality of 157 snapper Pagrus auratus (9–29 cm L_T) after being			
23	conventionally angled and then released into cages (along with 48 controls) for 4 days off			
24	southeastern Australia. Fatalities were restricted to 12 angled fish (7.6%) and mostly			
25	attributed to the ingestion of hooks and especially their subsequent removal, which caused			
26	substantial blood loss and immediate death. Hook ingestion was significantly biased towards			
27	smaller fish (<21 cm L_T) and attributed to a lower chance of anglers initially detecting these			
28	individuals on the line (allowing them to consume more of the baits). While mortalities might			
29	be reduced in future via (1) choosing terminal rigs that promote mouth hooking and/or (2)			
30	cutting the line on any-hook ingested fish, the results nevertheless validate releasing unwanted			
31	angled inshore juvenile <i>P. auratus</i> as a means for managing their exploitation.			
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34				
35	Key words: catch-and-release; hook ingestion; post-release mortality; Sparidae.			
36				
37				

38 **INTRODUCTION** 39 40 Sparidae encompasses more than 33 genera and 110 species, with a global distribution across 41 tropical and temperate estuarine and coastal demersal areas (Carpenter & Johnson, 2002). 42 Many sparids are economically important and form the basis of important artisanal, 43 commercial and, in developed countries, recreational fisheries (Broadhurst et al., 2005; Götz 44 et al., 2007; Alós et al., 2008; Overton et al., 2008; Veiga et al., 2011). 45 At least ten sparids (six genera) occur in Australia (Carpenter & Niem, 2001; Grant, 46 47 2008); all of which are recreationally fished for an estimated annual catch of almost 17 48 million individuals (Henry & Lyle, 2003). The exact catch composition is unknown, but the 49 most abundant species include Acanthopagrus spp. [especially yellowfin bream A. australis 50 (Owen 1853) and black bream A. butcheri (Munro 1949); c. 50% of the total] and snapper

51 Pagrus auratus (Bloch & Schneider 1801) (c. 20%) (estimated in 2000/01 by Henry & Lyle,

52 2003). Like most recreationally targeted sparids throughout the world (*e.g.* those described

53 by Götz et al., 2007; Alós et al., 2008; Overton et al., 2008; Veiga et al., 2011), the

54 Australian species are managed by legal sizes and personal quotas. Combined with voluntary

non-consumptive fishing, these regulations result in *c*. 11 million sparids (65% of the total

56 catch) being released per annum; which is among the greatest rate for any family of

- 57 Australian teleosts (Henry & Lyle, 2003).
- 58

Recognition of the need to validate the assumption of few negative impacts to such
large numbers of released fish has resulted in several relevant studies, and mostly for *A*. *australis* (Broadhurst *et al.*, 1999, 2005, 2007; Butcher *et al.*, 2007, 2008, 2010; Reynolds *et al.*, 2009) and *A. butcheri* (Haddy & Pankhurst, 1999, 2000; Grixti *et al.*, 2007, 2008). This

work estimated total short-term (<10 days) mortalities of <28% for both species and, like for
virtually all other studied sparids (*e.g.* Götz *et al.*, 2007; Rudershausen *et al.*, 2007; Overton *et al.*, 2008; Alós *et al.*, 2009*a*; Veiga *et al.*, 2011), identified hook ingestion as a consistent,
key deleterious factor (Broadhurst *et al.*, 2005; Grixti *et al.*, 2008). Consequently, most
efforts at mitigating mortalities have concentrated on promoting shallow hooking, via
modifications to terminal rigs and/or fishing methods (Grixti *et al.*, 2007; Butcher *et al.*, 2008,
2010).

70

71 Much less information is available on the post-release fate of the remaining Australian 72 sparids, including the highly valued *P. auratus*. Such bias can be partially attributed to 73 comparatively lower catch and release, although species-specific distributions and the 74 logistics of assessing mortality are also important. For example, A. australis and A. butcheri 75 tolerate a wide range of salinities and occur in coastal rivers, estuaries and near shore areas in 76 large abundances and across all sizes (Grant, 2008). In contrast, P. auratus prefer marine 77 waters with juveniles and small adults ($< c. 40 \text{ cm } L_T$) mostly located in shallow bays, while 78 larger fish are often distributed across the continental shelf down to 200 m (Sumpton et al., 79 2003; Grant, 2008). The cheapest field-based experiments to assess short-term post-release 80 mortality involve angling fish and then 'releasing' and monitoring them in replicate, large 81 surface cages (termed 'confinement' studies; Pollock & Pine, 2007); which need to be moored 82 close to the fishing area, and in low flow with protection from waves. Such logistical 83 requirements have been more suited to the distributions of *Acanthopagrus* spp.

84

Notwithstanding the above, two short-term confinement studies involving *P. auratus*have been published in the primary literature (Broadhurst *et al.*, 2005; Grixti *et al.*, 2010*a*).
Both have estimated mortalities to juveniles, but with various limitations. Specifically,

88	Broadhurst <i>et al.</i> (2005) t-bar tagged 72 angled fish (15–31 cm L_T) in Botany Bay, New South		
89	Wales (NSW) and released them along with controls (caught by seining) into four floating 48		
90	000 l cages for 10 days. Although catch histories were available for each angled fish, there		
91	were insufficient numbers and/or data to attribute causality among the observed fatalities (c.		
92	33%). Grixti et al. (2010a) followed a similar design in Port Phillip Bay, Victoria, but instead		
93	of being tagged, 620 fish (15–26 cm L_T) were fin clipped according to intuitive <i>a priori</i>		
94	treatments and monitored for either 1 h or 3 days. This experimental approach facilitated		
95	relative mortality assessments (e.g. between shallow- and deep-hooked fish of 3 and 52%)		
96	but, because individual fish could not be identified, precluded quantifying the full range of		
97	contributing factors, including any random effects.		
98			
99	Isolating the key deleterious impacts associated with angling (and their mechanisms of		
100	action) is important to prioritise resolution strategies. This study aimed to acquire such		
101	information for inshore juvenile P. auratus by collecting detailed data describing their		
102	conventional angling and handling across a sufficient sample size, and then immediately		
103	releasing them individually (or at densities where they could be subsequently identified by		
104	their $L_{\rm T}$) into cages; most of which were rigid and submerged to the seabed (< 10 m depth)		
105	where they were protected from tide and wave action.		
106			
107	MATERIALS AND METHODS		
108			
109	Twenty-four boat-based anglers were asked to target P. auratus between 06:00 and		
110	14:00 on one day during January 2008 in Botany Bay, NSW (34.0° S; 151.2° E), and then		
111	immediately place their fish into portable 110 l cylindrical cages (provided by researchers)		
112	tethered to their boats. The cages were made from polyvinyl chloride (PVC) buckets with		

113lids, and comprised one top and two lateral 'windows' positioned at 300 mm above the base114(with a combined area of c. 1200 cm²) and covered by 6-mm PVC mesh. Depending on their115sizes, P. auratus were caged at densities of 1–10 so that the total weight was <5 kg 110 l cage⁻¹1161. Anglers completed a data sheet for each fish and placed it into the 110 l cage before117securing the lid and alerting researchers.

118

119 Researchers retrieved the 110 l cages and, after removing the datasheets and checking 120 for deaths, transported them to a monitoring site, comprising two 240 m lengths of 12 mm 121 diameter (ø) polyamide (PA) rope buoyed at the surface in a straight line (anchored at either 122 end). The 1101 cages were weighted (2 kg brick), tied to the 12 mm ø rope at 5 m intervals 123 and deployed to the sea bed (3 m). When all of the available 110 l cages (n = 78) were 124 stocked, angled *P. auratus* were still collected as above, but then transferred to one of three 2600 l cylindrical floating cages (made from 22 mm PA mesh attached to PVC frames) 125 126 deployed on the surface between the monitoring sites. All multi-stocked P. auratus were 127 identified by $L_{\rm T}$.

128

After the angled fish were caged, 48 'control' *P. auratus* that were previously trapped or angled in shallow water off Coffs Harbour (30.3° S; 153.1° E), and housed in aquaria for three months were distributed among 41 empty 110 l cages (at comparable stocking densities as the angled fish) and similarly deployed at the monitoring sites on the same day. The controls were handled, transported and housed according to the methods described by Broadhurst *et al.* (1999).

135

All cages were retrieved after four days and any mortalities were recorded. At this
time, 10 angled and 11 control *P. auratus* were randomly selected from their cages and

138	sampled for blood within 1 min of initial disturbance following the methods outlined by
139	Broadhurst et al. (2005). Eleven P. auratus were also angled from Botany Bay and similarly
140	sampled (within 1 min of hooking).

142 DATA COLLECTED AND ANALYSES

143

144 The following general categories of data were collected for all angled *P. auratus*: angler 145 name; hook type and size (absolute; mm²); line strength (kg); trace length (cm); bait and rig 146 types; whether the boat was anchored or drifting; fishing depth (m); period between hooking 147 and landing (*i.e.* playing time in s); landing and restraint methods; period of air exposure 148 during unhooking and 'release' (s); anatomical hook location; whether or not the hook was 149 removed; $L_{\rm T}$ (cm); the presence or absence of fin damage, scale loss, bleeding or hook damage; cage number; and whether they died or survived the experiment. Replicate water 150 temperature (°C) and dissolved oxygen (mg l⁻¹) were recorded on the fishing and monitoring 151 152 days using an Horiba U/10 water quality meter.

153

154 A Fisher's exact test was used to test the hypothesis of no difference in the total 155 numbers of angled and control *P. auratus* surviving at the end of the experiment. All data 156 describing the capture and handling of each angled fish were collated as either fixed 157 'terminal-rig', 'fishing-and-landing' or 'angling-response' factors. Design factors (considered 158 as being random) included 'anglers' and 'cages'. These various terms were then considered 159 for inclusion in generalised linear mixed models (GLMMs) fitted using ASReml-R (Butler et 160 al. 2009) and via penalized quasi-likelihood (Breslow & Clayton, 1993) to the dichotomous 161 status (alive v. dead) of P. saltatrix at the end of the experiment. Total length was included as 162 a co-variate in all models.

164	After assessing the baseline model, two groups of GLMMs were separately fitted using a
165	forward selection approach to ascertain which of the (1) terminal-rig and fishing-and-landing
166	or (2) angling-response factors contributed towards fatalities. Where appropriate, significant
167	fixed effects identified in these analyses were then considered as response variables and
168	GLMMs fitted to isolate their causes. This sequential and structured modelling approach is
169	biologically plausible and avoids many of the statistical challenges and pitfalls associated
170	with variable selection in GLMMs for small data sets. But, the limited sample size and low-
171	frequency binary data mean that all modelling should be considered descriptive, rather than
172	predictive.

173

174 The *P*-values for the various GLMMs were derived via the asymptotic distribution of two 175 test statistics: (1) a pseudo F-to-enter based on a Wald value (from the GLMM), and (2) the 176 change in deviance from a generalised linear model obtained by excluding the random terms. 177 Both approaches were chosen to overcome inherent technical problems. In particular, the 178 Wald test suffers from the Hauck-Donner phenomenon (Hauck & Donner, 1977), while using 179 the change in model deviance to derive *P*-values can be anti-conservative if there is 180 significant extra-binomial variation induced by ignoring sources of variation from the random 181 terms.

182

183 The blood samples were analysed for concentrations of cortisol (ng ml⁻¹) and plasma 184 glucose (mM) by direct chemiluminescent immunoassay and using an enzymatic 185 spectrophotometric assay, respectively, according to the manufacturers' instructions. Owing 186 to low levels of both parameters (below the detectable range – see Results) among baseline 187 and control fish, formal statistical analyses were not done to test the hypothesis of no

188	differences among the groups of fish. Rather, the extent of censored data and mean levels of
189	both parameters for which there were recordable data are presented.
190	
191	RESULTS
192	
193	In total, 157 <i>P. auratus</i> (mean $L_T \pm$ S.D. of 18.4 ± 4.2 cm) were caught by 15 of the 24
194	anglers using various terminal rig configurations (but all comprising baited, J or circle hooks),
195	played for mostly <1 min, and then, within an additional 1 min, typically landed without a net,
196	restrained by hand while the hook was either removed (most fish) or the line cut, and released
197	into the cages (Table I). Of these fish, 150 were subsequently deployed and monitored
198	alongside the controls (25.8 \pm 2.4 cm $L_{\rm T}$). Water temperature (mean \pm S.D. of 22.5 \pm 0.4 °C),
199	salinity (36.0 \pm 0.0 psu) and DO (8.5 \pm 0.4 mg $l^{-1})$ remained similar during the angling and
200	subsequent monitoring days.
201	
202	FATALITIES AND CAUSES
203	
204	There were no fatalities among the controls, but seven of the angled P. auratus died
205	immediately after being placed in the cages (and prior to their deployment—within 5 min of
206	capture), while another five fish were dead at the end of the monitoring period, providing a
207	total, non-significant anger-induced mortality of 7.6% (Fisher's exact test, $P > 0.05$). The
208	initial fatalities and solitary confinement of most fish precluded the coherent inclusion of
209	cages as a random term; restricting the baseline model to the intercept and random effect of
210	anglers.
211	

212 Because nine of the 12 fatalities were caught by two of the 15 anglers, this term 213 explained nearly 30% of the total variation in the baseline model, although the residual also 214 clearly indicated the influence of other factors. The first GLMMs fitted to those fixed factors 215 describing the terminal rig and fishing and landing processes (and with $L_{\rm T}$ as a co-variate) 216 identified that only hook removal was significant, with both P(Wald and deviance) < 0.01217 (Tables I and II). But this treatment was clearly confounded by anatomical hook location, 218 with hooks removed from all 142 mouth-caught individuals (with only two deaths), but left in 219 11 hook-ingested fish (of which six died) and removed from three (all died). No other 220 variables, including the $L_{\rm T}$ of fish were significant after hook removal was included as a term 221 and the model refitted (P > 0.05; Table II).

222

223 The importance of anatomical hook location in determining fatalities (*i.e.* nine of 14 224 hook-ingested v. two of 142 mouth-hooked fish; Table I) was subsequently explored in the 225 second group of GLMMs assessing the influence of just the angling-response factors. Both 226 this factor and bleeding were the only significant main effects; returning P < 0.01 for both the 227 Wald and change in deviance test statistics (Table II). However, all of the bleeding fatalities (four of 12 inflicted fish; Table I) had ingested their hooks, suggesting some co-dependency 228 229 between anatomical hook location and the presence of blood. A GLMM refitted accounting 230 for anatomical hook location supports this conclusion, with a P(Wald) < 0.05, but a 231 P(deviance) > 0.05 for bleeding. Subsequent assessment of the interaction between bleeding 232 and anatomical hook location also returned conflicting levels of significance [P(Wald) > 0.05]233 and P(deviance) < 0.05]. These analyses, combined with a lack of any significant effects of 234 $L_{\rm T}$ or hook damage (P > 0.05; Table II), suggest that anatomical hook location was the most 235 important predictor of fatalities.

237	Based on these results, anatomical hook location was then considered as a binary			
238	response variable (mouth v. ingested) and GLMMs fitted in an attempt to isolate explanatory			
239	factors (Table III). The only significant factor was L_T , which returned a $P(Wald) < 0.01$, but a			
240	highly non-significant $P(\text{deviance}) > 0.05$ (Table III). Because the $P(\text{deviance})$ ignores			
241	random effects, such disparity in significance indicated a strong dependency on angler. This			
242	relationship was explored in a conditional scatter (jittered) plot of anatomical hook location			
243	against L_T for each angler, which revealed that for most of the anglers ($n = 9$) that caught			
244	hook-ingested fish, there was a bias towards this occurring among smaller individuals (Fig.			
245	1).			
246				
247	PHYSIOLOGICAL RESPONSE OF ANGLED FISH			
248				
249	The chemiluminescent immunoassay was unable to detect plasma concentrations of			
250	cortisol <3.6 ng ml ⁻¹ among either those <i>P. auratus</i> that were immediately sampled after			
251	angling, or the caged controls ($n = 11$ for both). Similarly, four of the caged angled fish had			
252	cortisol concentrations below the detectable range of the assay. The remaining six caged			
253	angled fish had a mean (\pm S.D.) concentration of 4.3 \pm 0.4 ng ml ⁻¹ . Comparatively fewer			
254	censored data were recorded for plasma glucose (<1.0 mM) among baseline ($n = 8$), controls			
255	(4) and angled (4) fish using the enzymatic spectrophotometric assay. The remaining means			
256	(± S.D.) were 1.7 \pm 0.6, 1.9 \pm 0.3 and 2.2 \pm 0.6 mM, respectively.			
257				
258	DISCUSSION			
259				
260	The c. 8% mortality of <i>P. auratus</i> in this study is lower than the c. 33% recorded by			

262 estimate of c. 11% (pooled across treatments) for more southern stocks. This estimate is also 263 within the range of other sparids angled from the same depths (<10 m), including A. australis 264 (5-28%; Broadhurst et al., 2005; Butcher et al., 2007), A. butcheri (8%; Grixti et al., 2008), 265 black seabream Spondyliosoma cantharus L. 1758 (2.8%; Veiga et al., 2011), gilthead 266 seabream Sparus aurata L. 1758 (11.7%; Veiga et al., 2011), two-banded seabream Diplodus 267 vulgaris (Geoffroy Saint-Hilaire 1817) (0%; 2011) and striped seabream Lithognathus 268 mormyrus L. 1758 (33%; Alós et al., 2009a). Further, like for many assessed sparids, 269 including those angled from deep water and incurring the cumulative impacts of barotrauma 270 (e.g. C. laticeps - Götz et al., 2007; P. pagrus - Rudershausen et al., 2007; Overton et al., 271 2008 and annular seabream Diplodus annularis L. 1758 – Alós et al., 2009a), a large 272 proportion of the variability among mortalities to P. auratus here was explained by the 273 anatomical hook location (Broadhurst et al., 2005; Butcher et al., 2007; Grixti et al., 2008, 274 2010a; Veiga et al., 2011). This factor manifested as disproportionally greater deaths among 275 individuals that ingested hooks (64%) than those hooked in the mouth (1.4%); a relationship comparable to that (52 v. 3%) observed by Grixti et al. (2010a). 276

277

278 There are at least two factors contributing towards such apparent consistency in the 279 importance of anatomical hook location in deciding the fate of sparids. First, in all of the 280 above cited experiments fish were angled on hooks with natural baits. It is well established 281 that such configurations typically are ingested at a greater rate than artificial baits or lures 282 (Bartholomew & Bohnsack, 2005). Second, juvenile sparids (*i.e.* typically comprising the 283 greatest proportion of released individuals) often school, which might increase competition 284 for baits as a perceived source of food and therefore contribute towards an aggressive hooking 285 response. Most sparids are targeted with constant tension on the line (termed 'active fishing', 286 but see Alós et al., 2009a) which usually limits the depth of hooking (Bartholomew &

Bohnsack, 2005; Grixti *et al.*, 2007, 2010*a*), so presumably those that manage to ingest hooks, do so with sufficient force to cause considerable damage. Such impacts are supported here by most of the hook-ingested *P. auratus* dying within 5 min, (four of which bled profusely), and similar rapid fatalities among hook-ingested *A. australis* angled across comparable space and time (Broadhurst *et al.*, 2005; Butcher *et al.*, 2007).

292

293 While anatomical hook location (and associated bleeding) explained most of the 294 fatalities in this study, the deaths of two mouth-hooked P. auratus indicates the influence of at 295 least some other impacts; albeit nowhere near the extent observed by Broadhurst et al. (2005). 296 Two unexamined factors that might have contributed to more *P. auratus* dying during this 297 earlier work were (1) relatively warmer water temperatures (mean \pm S.D. of 24.1 \pm 1.5 v. 22.5 298 $\pm 0.4^{\circ}$ C here) and (2) tagging. More specifically, previous research has identified positive 299 relationships between temperature and post-release mortality for several species (reviewed by 300 Bartholomew & Bohnsack, 2005; Arlinghaus et al., 2007) which are often attributed to a 301 range of physiological disturbances, including a greater metabolic rate and demand for 302 oxygen (Pörtner, 2002). Further, although tagging did not cause mortalities among the 303 controls monitored by Broadhurst et al. (2005) or similar-sized P. auratus in other studies 304 (e.g. Quartararo & Kearney, 1996; Sumpton et al., 2003), undoubtedly this would have had 305 some cumulative impact on angling stressors. Either of the above factors ultimately could 306 have contributed towards mortality. The potential for such effects illustrates the need to 307 carefully design experiments and to collect sufficient data to attribute causality.

308

309 Irrespective of differences in results between the present and the earlier studies, it is
310 clear from the data presented here and by Grixti *et al.* (2010*a*), that limiting hook ingestion in
311 juvenile *P. auratus* would concomitantly reduce fatalities. In addition to actively fishing the

312 line (discussed above), several factors have been identified to affect hook ingestion among 313 sparids, including $L_{\rm T}$, the hook type (circle v. J-hooks) and mass/size, trace length and bait 314 type (Götz et al., 2007; Grixti et al., 2007, 2008, 2010a,b; Alós et al., 2008, 2009b,c; Butcher 315 et al., 2008; Veiga et al., 2011). Of these variables, $L_{\rm T}$ had the greatest influence here. But, 316 unlike for many other teleosts (discussed by Grixti et al., 2010b), including the sparids, A. 317 australis (Butcher et al., 2008), C. laticeps (Götz et al., 2007), D. annularis (Alós et al., 318 2008) and S. aurata (Veiga et al., 2011) and, contrary might be considered intuitive, hook 319 ingestion was biased towards smaller P. auratus (Fig. 1).

320

321 The few data mean that the above relationship between anatomical hook location and $L_{\rm T}$ 322 should be treated with caution. Nevertheless, one plausible explanation is that even though 323 the lines were actively fished, smaller fish may have been able to consume baits before the 324 anglers could detect their presence, which could have allowed some of them to be hooked 325 more deeply. Additional trials would be required to validate this hypothesis and to more 326 closely investigate the importance of other, more controllable, factors affecting hook ingestion 327 so that coherent mitigation strategies can be implemented. In particular, previous studies have 328 shown that changes to terminal rigs, including larger hooks and or subtle modifications (e.g. 329 Butcher et al., 2008) are effective in promoting mouth hooking among sparids (Butcher et al., 330 2008; Alós et al., 2009b; Grixti et al., 2010b).

331

Irrespective of any modifications to terminal rigs to increase mouth hooking, a
concomitant strategy that also should be promoted is to release all hook-ingested fish with
their line cut (Broadhurst *et al.*, 2007; Butcher *et al.*, 2007; Alós *et al.*, 2009*a*; Grixti *et al.*,
2010*a*). Broadhurst *et al.* (2007) and Butcher *et al.* (2007) demonstrated that such a practice
was appropriate for improving the fate of *A. australis*, with up to 85% of line-cut hook-

ingested individuals surviving (over up to three months); most of which subsequently ejected their hooks. More recently, McGrath *et al.*, (2011) observed 25% mortality among 108 hookingested *P. auratus* monitored in aquaria tanks for six weeks, with 77% of survivors ejecting their hooks over an average of *c*. 9 days. By comparison, there were 100% fatalities among fish (n = 3) that had their ingested hooks removed here.

342

343 The results from this study indicate minimal post-release mortalities to P. auratus after 344 being angled and released during conventional fishing in shallow water. Furthermore, the 345 impacts to survivors appeared to be fairly limited with few differences in blood plasma 346 glucose and cortisol between treatments and controls at the end of monitoring, and 347 immediately sampled wild-caught individuals. Both parameters (across all groups) were 348 within the ranges for unstressed *P. auratus* (e.g. Cleary et al., 2000). However, these data are 349 limited to the conditions examined. Like several other sparids (e.g. C. laticeps – Götz et al., 350 2007, D. annularis – Alós et al., 2009a; and P. pagrus – Stephen & Harris, 2010) larger P. 351 *auratus* inhabit deeper water, where they are extensively targeted by anglers. In addition to 352 any impacts of terminal rigs, are the ancillary effects of barotrauma. This factor has been 353 implicated as contributing towards high mortalities among angled C. laticeps (Götz et al., 354 2007) and P. pagrus (Stephen & Harris, 2010), and trap-caught P. auratus (Stewart, 2008). 355

Clearly, the occurrence of barotrauma, along with associated impacts and methods by which these might be mitigated for angled *P. auratus*, need to be assessed to more comprehensively describe the post-release fate of this species and facilitate its future management. Based on the uniformity among known factors affecting the mortality of sparids angled-and-released from shallow water, it is likely that any such assessments would have broader application across the entire family.

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367

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486	TABLE I. Summary of categorical and, where applicable, mean (\pm S.D.) continuous random				
487	and fixed ('terminal-rig', 'fishing-and-landing' and 'angling-response') factors collected for				
488	the live and dead angled-and-released Pagrus auratus. ¹ seven fish died immediately and				
489	were not caged.				
490					
491	Variables	Alive	Dead		
492	Design/random factors				
493	Angler				
494	1	20	5		
495	2	21	0		
496	3	20	0		
497	4	16	4		
498	5	18	0		
499	6	11	1		
500	7	11	1		
501	8	8	0		
502	9	7	1		
503	10	6	0		
504	11	3	0		
505	12	1	0		
506	13	1	0		
507	14	1	0		
508	15	1	0		
509					
510	Cages ¹				

511	110-1 individual	69	4
512	110-1 mixed 1	10	0
513	110-1 mixed 2	5	0
514	110-1 mixed 3	4	0
515	110-1 mixed 4	4	0
516	110-1 mixed 5	4	0
517	110-1 mixed 6	3	0
518	110-1 mixed 7	2	0
519	110-1 mixed 8	2	0
520	110-1 mixed 9	2	0
521	2600-1 mixed 1	19	0
522	2600-1 mixed 2	18	0
523	2600-1 mixed 3	3	0
524			
525	Terminal-rig factors		
526	Hook type		
527	J	98	7
528	Circle	46	5
529			
530	Absolute hook size (mm ²)	312.7 (117.0)	356.4 (65.9)
531			
532	Line strength (kg)	2.8 (0.7)	2.6 (0.6)
533			
534	Trace length (cm)	73.2 (42.9)	63.6 (24.4)
535			

536	Bait type		
537	Trachurus sp	10	0
538	Mugil cephalus	7	0
539	Sardinops neopilchardus	11	0
540	Metapenaeus macleyi	58	6
541	Loliginidae	59	6
542			
543	Rig type		
544	Hook only	36	5
545	>50-cm trace	33	2
546	<50-cm trace	14	0
547	Paternoster	50	5
548	Sinker on hook	5	0
549			
550	Fishing-and-landing factors		
551	Fishing method		
552	Anchored	86	5
553	Drifting	59	7
554			
555	Fishing depth (m)	7.4 (2.2)	7.3 (2.2)
556			
557	Playing time (s)		
558	<10	63	5
559	11–30	79	7
560	31–60	2	0

561	>61	1	0
562			
563	Landing method		
564	Knotless net	2	0
565	Knotted net	4	0
566	No net	139	12
567			
568	Restraint method		
569	Dry bare hand	26	1
570	Wet bare hand	117	11
571	Towel	1	0
572	Not restrained	1	0
573			
574	Air exposure (s)		
575	<15	41	3
576	16–30	98	7
577	31–60	5	2
578			
579	Hook removed		
580	No	5	6
581	Yes	140	6
582			
583	Angling response factors		
584	Hook location		
585	Ingested	5	9

586	Mouth	140	2
587	Body	0	1
588			
589	Hook damage		
590	No	137	10
591	Yes	8	2
592			
593	Bleeding		
594	No	137	8
595	Yes	8	4
596 597			

598	TABLE II. Wald- and deviance-derived P-values, and variance component ratios for the			
599	random effect of angler, associated with fixed variables tested in generalized linear mixed			
600	models (GLMMs) for their independence on the mortality of angled-and-released Pagrus			
601	auratus. Two groups of models were applied: the first to just the terminal-rig and fishing-			
602	and-landing variables; and the second to only those data describing the angling responses of			
603	fish. $L_{\rm T}$ was fitted as a co-variate in all GLMMs, and in all cases returned P(Wald) and			
604	P(deviance) > 0.05.			
605				
606		Р		Variance component ratio
607	Variables	Wald	Deviance	for angler
608	Terminal-rig and			
609	fishing-and-landing GLMMs			
610	Hook type	0.980	0.695	1.711
611	Absolute hook size	0.480	0.246	0.692
612	Line strength	0.696	0.418	1.597
613	Trace length	0.499	0.466	1.539
614	Bait type	0.879	0.298	2.868
615	Rig type	1.000	0.342	2.145
616	Playing time	0.999	0.917	1.516
617	Water depth	0.447	0.921	1.883
618	Fishing method	0.279	0.171	1.523
619	Landing net	0.991	0.623	1.266
620	Restraint method	0.976	0.746	1.404
621	Air exposure	0.132	0.382	2.308
622	Hook removed	0.000	0.000	0.412

624 Angling-response GLMMs

625	Hook location	0.000	0.000	0.210
626	Hook damage	0.146	0.192	1.407
627	Bleeding	0.004	0.006	1.478

TABLE III. Wald- and deviance-derived *P*-values, and variance component ratios for the random effect
 of angler, associated with fixed variables tested in generalized linear mixed models for their
 independence on the anatomical hook location of angled *Pagrus auratus*

633			Р	Variance component ratio
634	Variables	Wald	Deviance	for angler
635	Hook type	0.904	0.653	0.768
636	Absolute hook size	0.868	0.673	0.340
637	Line strength	0.541	0.352	0.708
638	Trace length	0.992	0.611	0.938
639	Bait type	0.927	0.454	1.545
640	Rig type	0.856	0.105	0.537
641	$L_{ m T}$	0.046	0.501	1.617
642				

644 Caption to Fig

- 645 Fig. 1. Jitter plots of the total length of *Pagrus auratus v*. anatomical hook location for each of the
- 646 six anglers that caught hook-ingested fish.



