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Original Article

Consequences of catch-and-release angling for black bream *Spondyliosoma cantharus*, during the parental care period: implications for management

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Black sea bream *Spondyliosoma cantharus* is highly valued for its sporting and eating qualities. Due to its inshore spawning aggregations and male nest guarding behaviors, it is considered vulnerable to over-exploitation via recreational angling. Accordingly, greater uptake of the practice of catch-and-release (C&R) may provide some potential to limit the effects of angling on populations. Thus, the consequences of C&R for 40 *S. cantharus* (mean length 306 ± 10 mm) were assessed. Fish were sampled following their capture from charter boats by recreational anglers with varying levels of skill and experience. Of these fish, 17% were deeply hooked (e.g. in esophagus) and considered at high risk of post-release mortality (PRM). Blood lactate levels ranged between 0.40 and 2.60 mmol l^{-1} (mean ± *SE*: 1.25 ± 0.09) and were significantly and positively correlated with fight time. Reflex impairments were observed in 32% of the catch, also suggesting an elevated probability of PRM. Hook damage was the only significant predictor of reflex impairment. The dominance of males (89%) across the catches highlighted the potential for additional indirect impacts of angling via the predation of eggs by conspecifics in the vacated nests of captured males. These results are discussed within the context of post-release performance of individual *S. cantharus*, the potential for C&R to limit impact at the population level and a need to consider future regulation of the fishery to ensure sustainability of stocks.

Keywords: fisheries management, nest guarding, recreational angling, reflex impairment, spawning, stock exploitation.

Introduction

Global participation in recreational angling has been estimated at C.700 million, with the global recreational catch potentially being as high as 47 billion fish per annum (Cooke and Cowx, 2004). Estimates suggest there are approximately six million anglers in England alone, with recent surveys indicating almost 900 000 people (2% of the national population) participate in sea angling, capturing ~10 million fish per annum (Armstrong *et al.*, 2013a). It is thus increasingly apparent that recreational angling might not be benign (Llompart *et al.*, 2012), with potential impacts including selective harvesting (e.g. size, personality), disrupted spawning and individual mortality (Post *et al.*, 2002; Coleman *et al.*, 2004; Cooke and Cowx, 2004; Lewin *et al.*, 2006). Where a species predictably congregates for spawning, then its vulnerability to exploitation is elevated (de Mitcheson and Domeier, 2005; de Mitcheson *et al.*, 2005, 2008; de Mitcheson and Erisman, 2012).

Minimum size limits, bag limits, and temporal and spatial closures are commonly mandated fishery management actions in recreational fisheries (FAO, 2012; Armstrong *et al.*, 2013b). Accompanying such regulations (e.g. for size limits where smaller individuals must be released) or where such regulations are lacking, catch and release angling (C&R) is increasingly promoted as a conservation tool that minimizes angling impacts on target populations (Arlinghaus *et al.*, 2007). The desired conservation benefits of C&R rely on the assumption that a high proportion of released fish will survive (Cooke and Schramm, 2007), with impacts on physiological and behavioral performance not compromising the reproductive potential of individual fish (Bartholomew and Bohnsack, 2005). Probability of sub-lethal effects and/or post-release mortality associated with C&R are influenced by a range of individual and interacting variables such as fish size, hook damage (see Veiga *et al.*, 2011), fight time, air exposure (Arends *et al.*, 1999), general fish handling and environmental conditions (reviewed in Muoneke and Childress, 1994; Cooke and Suski, 2005). These can result in a range of stress responses in captured individuals (Lowe and Wells, 1996; Meka and McCormick, 2005). There a variety of endpoints and research approaches used to study C&R. Physical damage associated with hooking (e.g. wounds, bleeding) or handling (e.g. scale loss) can be assessed visually while secondary (physiological) responses (e.g. changes in glucose or lactate concentrations) can be measured nonlethally from blood samples (Cooke *et al.*, 2013).

In recent years, researchers have also incorporated reflex indicators (e.g. ability to maintain equilibrium, escape response, i.e. whole body, "tertiary" stress response indicators) into assessment of fish vitality and have determined that such reflexes can be predictive of future individual performance and post-release mortality (Davis, 2010; Raby *et al.*, 2012). These predictors (i.e. reflex indicators), can provide a cost-effective means of rapidly assessing fish vitality and the likely future performance (e.g. predator avoidance, nest guarding fitness and general health) of released fish (Davis, 2010).

Despite a relatively small body size ($<$ 40 cm), black bream *Spondyliosoma cantharus* is a highly valued recreational sport fish (Lewis, 2016). In contrast to other UK marine fishes and typical global fishery management practises, recreational anglers primarily target *S. cantharus* during their breeding period when large shoals aggregate on inshore spawning grounds (Pajuelo and Lorenzo, 1999). They are demersal spawners, with eggs laid in a nest excavated by the male as he creates a depression in a sandy gravel substrate, which exposes bedrock and gravel on which the eggs are deposited (Collins and Mallinson, 2012). For fish that engage in sole paternal care, should males be displaced from nests, there is an elevated risk of egg predation (Gonçalves and Erzini, 2000; Suski *et al.*, 2003). Spawning aggregations that are predictable in timing (spring) and location (inshore rough ground), can make fish vulnerable to high angling pressure (de Mitcheson *et al.*, 2008; Donaldson *et al.*, 2011). Despite this, there is no minimum landing size in many regions, no total allowable catch and there is no stock assessment required by The International Council for the Exploration of the Sea (Collins and Mallinson, 2012). Given its reputation as a good food fish, *S. cantharus* is consequently harvested in large numbers; of an estimated total annual catch by anglers of $>$100 000 individuals ($\sim$70 tonnes) in the English Channel, over 65% are removed (Armstrong *et al.*, 2013a). Some anglers release captured gravid females on the assumption that capture will not impact on their reproductive potential, and thus selectivity remove males (S. Cumming, pers. comm.).

The aim of this study was to use a suite of emerging rapid assessment tools (e.g. reflex assessment (Davis, 2010) and field diagnostic tools for analysing blood samples in the field (Stoot *et al.*, 2014) to provide an initial assessment of the response of individual *S. cantharus* to C&R, with consideration for the future survival and reproductive potential of released fish. The rapid assessment approach used here has been applied to several different recreational fisheries around the world (e.g. *Esox lucius*, Arlinghaus *et al.*, 2009; *Cichla ocellaris*, Bower *et al.*, 2016a; *Albula vulpes*, Suski *et al.*, 2007; *Negaprion brevirostris*, Danylchuk *et al.*, 2014). Objectives were to: (i) assess injury and stress indicators in captured individuals and test these against a range of angling and environmental metrics; (ii) identify other patterns in fish catch data, including sex ratios and stomach contents (to assess egg predation from nests with displaced males), to more fully assess angling impacts; and (iii) evaluate these outputs in the context of the sustainable management of *S. cantharus.*

Material and methods

Study sites

Between 7 May and 16 June 2015, angler catches were surveyed across three inshore areas ("marks") where spawning aggregations of bream are consistently targeted by private recreational boats and the local charter angling fleets operating from the Dorset ports of Poole, Swanage and Weymouth, Southern England (Figure 1). Of the three marks targeted, the most westerly mark was located off the coastal landmark of "Dancing Ledge" (50°34′97.1″N 2°00′48.8″W). Here, depths were in excess of 19.5 m with the substrate composed of patches of sand, boulders and gravel. Located to the east and $\sim$1.6 km NE of Swanage Pier, a mark known as "Dogs Bone" (50°35′01.4″N 2°00′46.3″W) was characterized by a mixed substrate composed of rock and sand and a depth of 19.8 m. The most westerly mark surveyed was "Poole Rocks" located in Poole Bay (50°41′41.2″N 001°52′92.3″W). Depths here did not exceed 12 m with a substrate composed of mud and rock. At all sites, angling was conducted across a range of tidal conditions, ranging from slack water to maximum tidal flows of two knots.

Fish capture

On three separate sampling events (7th May, 4th June, 16th June), researchers accompanied recreational anglers aboard *Silver Spray II*, a Poole based angling charter boat. Across the three trips, there were between three and eight anglers with each using one rod. The angling style, hook choice (e.g. overall size, gape, and style) and baits (typically bottom fishing using squid and mackerel as bait on relatively small hooks) were as selected by each angler and was independent of the scientific data collection. Similarly, each angler was responsible for unhooking their own catch and handling fish (sometimes including photography) until the moment the fish would either be released or dispatched for harvest. It was at this point that fish were intercepted for study and placed into a water filled holding tank of 50 l volume ("RAMP" tank) in which the fish were subsequently tested for reflex impairment.

Rapid assessment protocol

Based on the Reflex Action Mortality Predictor (RAMP) methodology developed by Davis (2010), the rapid assessment data collection started when each individual bream was hooked. There were two time recordings made. Firstly, the time taken between the fish being hooked and being removed from the water was recorded as "fight time" (s). Secondly, the time between removal from the water and up to being placed into the "RAMP tank" was recorded as total "air exposure" time (s).

Following the protocols developed by Bower *et al.* (2016b), the anatomical hooking location for each fish was also recorded, and

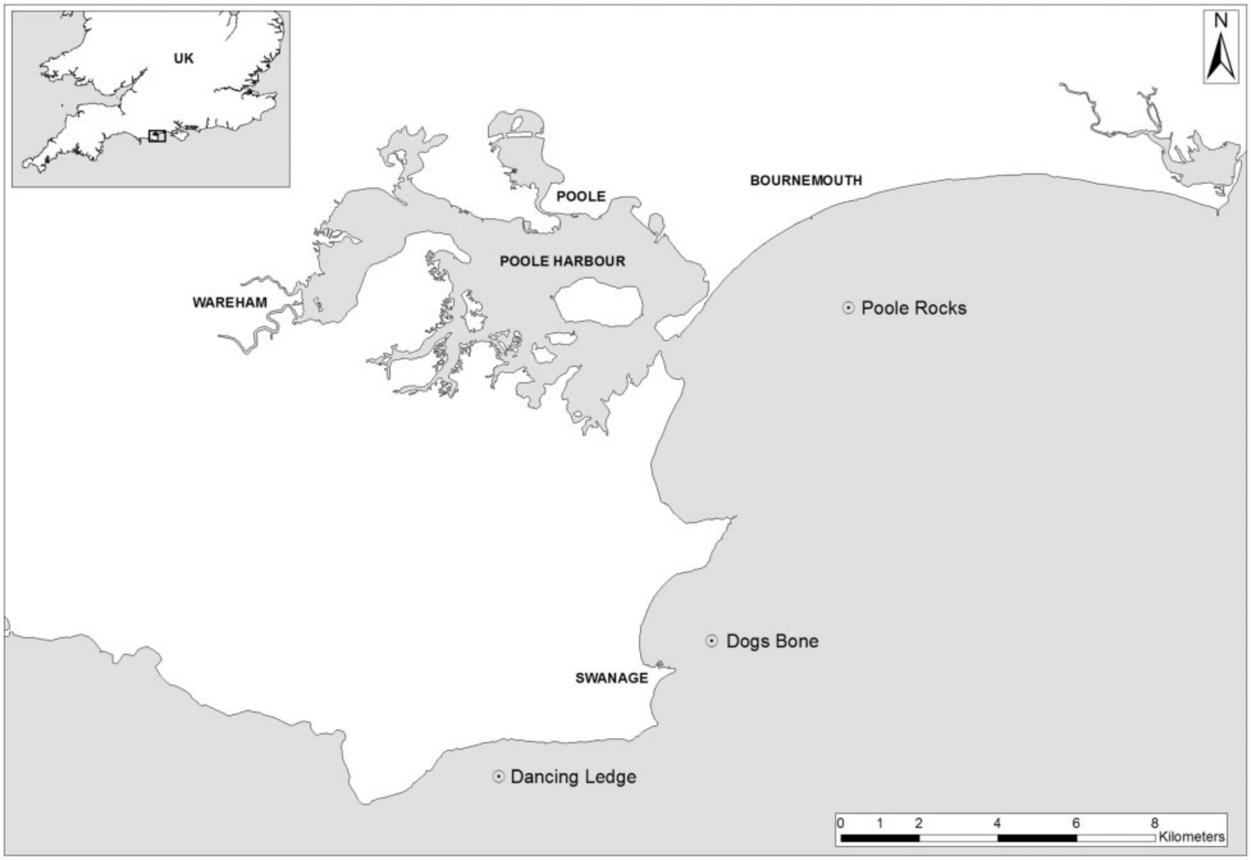

Figure 1. Map of study area showing the three survey locations. Clear areas are land, shaded areas are sea and the survey locations are shown as circles.

scored for the presence of injury (i.e. primary response) using a standardized objective scoring system. A score of 0 indicated no discernible injury; 1 indicated a minor injury (a small tissue tear $<$ 5 mm in length, including any visible tissue tear or abrasion resulting from hooking); 2 indicated moderate injury such as the presence of bleeding, bruising or a tissue tear $>$ 5 mm in length; and a score of 3 indicated major injury that occurred from the hook position. This included ocular or gill damage with significant pulsatile bleeding that resulted from the fish being hooked in the esophagus; in the event of deep hooking, hooks were left *in situ* by cutting the line to prevent further damage accruing from the unhooking procedure. Similarly, a standardized scoring system was also applied to describe the ease of hook removal. A score of 0 was for a hook that was removed easily and in $<$10 s; 1 was for a hook requiring between 10 and 20 s for removal; and 2 indicated a hook required $>$ 20 s to remove or could not be removed and the line cut (Cooke *et al.*, 2000). Any additional potential cause for stress, such as an angler dropping a fish on the boat deck during unhooking or photographing their catch, was also recorded.

Inhibition of reflex behaviors was then measured using reflex action mortality predictors (RAMP), indicators developed by Davis (2010). Immediately after being placed in the RAMP tank, four reflex indicators were tested in the following order of sequence:

(1) "Equilibrium" (fish rights itself within 3 s after being placed upside-down in water);

(2) "Tail grab" (fish exhibits burst swimming reflex when held by the caudal peduncle);

(3) "Body flex" (fish flexes torso when held along the dorso-ventral axis);

(4) "Head complex" (fish exhibits steady operculum beats during handling) (Davis, 2010).

Binary RAMP scores of 0 (reflex present) or 1 (reflex absent) were assigned to each indicator measurement, and then combined to produce a proportional impairment score ranging from 0 to 1 for each fish, where 0 indicated no overall impairment and a score of 1 would indicate impairment of all four reflexes. Immediately after the reflex response tests were complete, all fish were measured (fork length, nearest 0.1 cm), weighed (g) and either released overboard or dispatched by humane cerebral percussion (Van De Vis *et al.*, 2003; Poli *et al.*, 2005) to facilitate blood sampling and further biological data collection.

Blood sampling

Blood samples were obtained from a randomly selected sub-set of fish that provided a total sample size of a minimum of 30 fish per blood parameter. Blood was taken from the dispatched fish by drawing ~2 ml of blood from the caudal vasculature (Barton, 2002) using a 22-G needle and 5.0 ml collection tube. Bloods were collected as quickly as possible following death, (typically <60 s) and never exceeding the 3-min threshold determined by Romero and Reed (2005).

The blood samples were analysed immediately for their lactate and glucose concentrations using pre-calibrated portable point-of-care (PoC) devices. Lactate concentration was determined using a Nova Lactate Plus Meter (Nova Biomedical, MA) that had a detection range of 0.3–25.0 mmol l^{-1} and an ambient operating temperature range of 5–45°C; its accuracy had been pre-demonstrated to be consistent with other PoC devices and plasma-based laboratory methods (Karon *et al.*, 2007). Glucose concentration was determined using a SD CodeFree™ Blood Glucose Monitoring System (SD Biosensor, Inc, GyeongGi-do, Korea). The device had a detection range of 0.6–33.3 mmol l^{-1} and an ambient operating temperature range of 10–45 °C. While these PoC devices were designed for human use, the general utility and accuracy of a range of PoC devices, similar to the ones used here, have been successfully tested and validated for analysing blood chemistry parameters relevant to fisheries research (Wells and Pankhurst, 1999; Beecham *et al.*, 2006; Stoot *et al.*, 2014). Moreover, PoC devices have been used in this manner to measure blood chemistry parameters in a broad range of fishes, including Perciformes [e.g. peacock bass (Bower *et al.*, 2016a); *Micropterus* spp. (White *et al.*, 2008); barracuda (O'Toole *et al.*, 2010)], Carcharhiniformes (e.g. lemon shark; Danylchuk et al., 2014), Cypriniformes (e.g. *Tor* spp.; Bower *et al.*, 2016b), Salmoniformes (e.g. European grayling; Lennox *et al.*, 2016), and Albuliformes (e.g. bonefish; Cooke *et al.*, 2008). Correspondingly, the study used the assumption that the PoC devices used produced valid relative estimates of blood lactate and glucose concentrations for the sampled fish (Beecham *et al.*, 2006).

Prior to harvested fish being returned to their captors, the peritoneal cavity was dissected to determine sex, along with qualitative assessment of gonad condition and gut contents. The latter categorized stomach contents into four groups: macroalgae, Ctenophera, hydroids and the eggs of conspecifics.

Statistical analysis

Initial analyses used linear regression to determine the significance of relationships between fish length and the angling variables of fight time and air exposure. Testing of the proportions of captured fish in the different categories of unhooking ease and hook damage used using a chi-squared test of independence. The expected distribution was a 50:50 split between fish easy to unhook with no damage (scores of 0) and fish more difficult to unhook with some damage (score of 1 and above). Testing the effect of the angling related variables on lactate and glucose concentrations used general linear models (GLM) as per Bower *et al.* (2016b). The blood chemistry values were log-transformed to normalize the residuals in the model (Bower *et al.*, 2016b). All of the variables and their interactions were included in the initial model, with the final model chosen through the lowest Akaike Information Criterion (AIC) value and parsimony, where the fewest variables explain the most variation.

The reflex impairment responses across the sampled fish were initially compared for differences in their RAMP scores. Due to the relatively low proportion of fish showing impairment, and none with scores >0.50, the data were then restructured into two groups, unimpaired fish (RAMP = 0) and impaired fish (RAMP = 0.25, 0.50), to provide a more balanced data set for subsequent tests, with the difference in the number of fish in the two groups tested using chi-square. As impairment was now grouped into two categories (i.e. binomial grouping, where 0 = unimpaired, 1 = impaired), forward stepwise binary logistic regression was then used to explore the predictor variables that contributed most to RAMP impairment. The predictor variables were all angling related data (fight time, air exposure, hook damage and ease of unhooking), with the final model retaining the most significant predictors.

Throughout analyses, compliance of data with assumptions of homogeneity of variance and normality of distribution were tested using Levene and Shapiro–Wilk tests on each variable prior to analysis. Where the assumptions were met then testing used general linear models as described earlier. Where they were not met then these data were tested using the nonparametric tests outlined. All data are presented as mean ± *SE* unless stated. Bournemouth University Ethical Review Committee granted ethical approval. No research procedures regulated by the UK Home Office were used on live fish.

Results

A total of 40 fish were captured by anglers of mean length 306 ± 10 mm. All captured fish were sexually mature, with significantly more males captured than females (ratio: 1 M; 0.18 F; $\chi^2 = 19.60$, $p < 0.01$). Differences between the lengths of the sexes were not significant (male: 308 ± 5 mm; female: 288 ± 4 mm; Mann–Whitney *U* test; $Z = -1.90$, $p = 0.06$). Across all fish, mean fight time was 59 ± 6 s and mean air exposure was 75 ± 9 s. The relationships between fish length and both fight time and air exposure were significant, with larger fish having longer fight times and extended air exposure (linear regression: fight time $R^2 = 0.29$, $F_{1,38} = 15.29$, $p < 0.01$; air exposure $R^2 = 0.15$, $F_{1,38} = 6.92$, $p = 0.01$; Figure 2). Due to these significant relationships, fish length was excluded from all subsequent analyses other than where it was used as a covariate in general linear models.

Significantly more fish were easy to unhook (score = 0; $n = 34$) than difficult (scores of 1 and 2; $n = 6$) ($\chi^2 = 19.60$, $p < 0.01$). Most fish incurred only minimal damage from being hooked, with the difference between the number of fish with minimal damage (score = 1; $n = 32$) and some damage (scores of 2 and 3; $n = 8$) being significant ($\chi^2 = 14.40$, $p < 0.01$). Of the fish with scores >1 for hook damage, 7 were scored at 3, indicating the location of the hook was in the esophagus and the attempts at removal resulted in considerable damage, including bleeding from the gills for 5 of these fish.

Blood chemistry

A total of 30 fish had blood lactate levels recorded (mean length 309 ± 5 mm), with a mean lactate concentration of 1.25 ± 0.09 mmol l^{-1} (range 0.40–2.60). For blood glucose, 34 fish were sampled (mean length 310 ± 5 mm), with a mean glucose concentration of 2.97 ± 0.13 mmol l^{-1} (range 0.70–4.20). For blood lactate concentration, the best model according to AIC and parsimony was when all independent variables except fight time were excluded from the model; this revealed that elevated lactate levels were correlated with extended fight time ($F = 4.04$, d.f. = 28, $p = 0.04$). For blood glucose concentration, the best model was when all variables were retained but their interactions removed, although this model was not significant ($F = 0.94$, d.f. = 32, $p > 0.06$), with lengthened fight time and air exposure not resulting in increased blood glucose concentrations ($t = 0.09$,

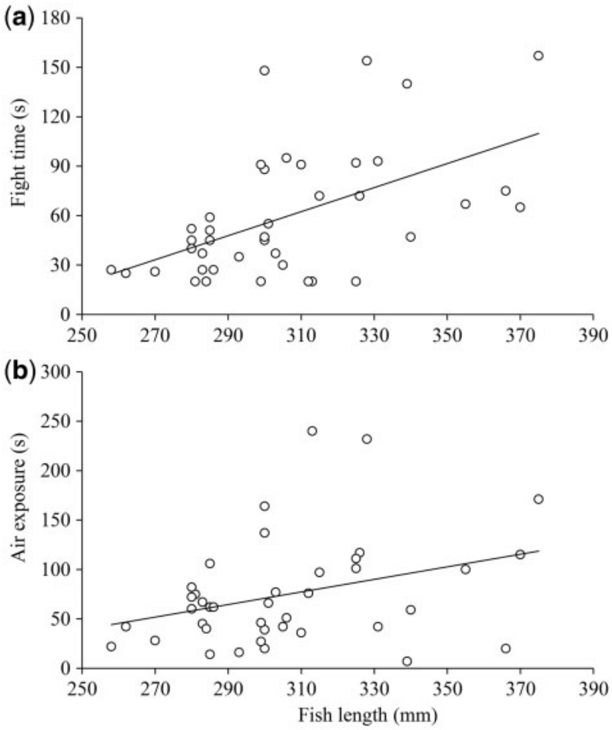

Figure 2. Relationships of fish length versus (a) fight time and (b) air exposure, where the solid lines represent the significant relationships according to linear regression (cf. "Results" section).

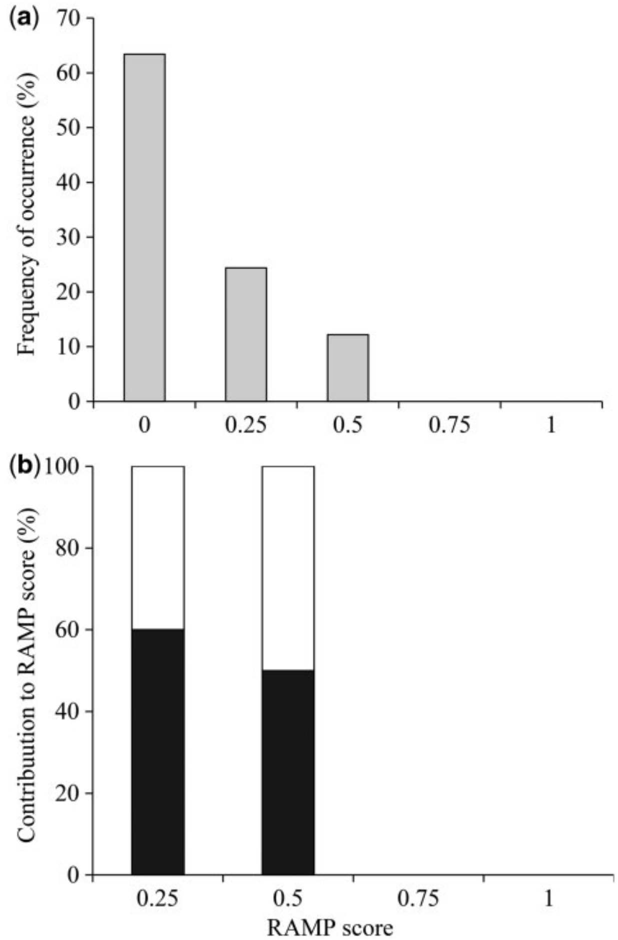

Figure 3. (a) Frequency of occurrence per RAMP score across the 40 sampled fish; (b) proportion of reflex impairments contributing to the RAMP scores >0, where clear bars represent orientation and filled bars represent tail grab. There were nine fish with RAMP scores of 0.25 and four fish with scores of 0.50.

$p > 0.05$; $t = -1.27$, $p > 0.05$, respectively). The effect of fish length as a covariate in this model was also not significant ($p > 0.05$).

Reflex impairment (RAMP)

The mean RAMP score across the 40 sampled fish was 0.11 ± 0.03, with 13 (32%) testing positive for impairment in at least one of the four RAMP indicators tested, with the difference in the number of unimpaired versus impaired fish being significant ($\chi^2 = 4.90$, $p = 0.03$). Of the 13 impaired fish, 9 scored 0.25 (impairment of a single reflex behavior) and 4 scored 0.50 (impairment of two reflex behaviors) (Figure 3a). The two impairments recorded were "orientation" and "tail grab"; the proportions of fish showing these impairments were similar (Figure 3b). The final binary logistic regression model only retained hook damage as a significant predictor of reflex impairment ($p = 0.05$); all but one fish with a score of 3 for hook damage showed some reflex impairment. Fight time ($p = 0.18$), air exposure ($p = 0.22$) and ease of unhooking ($p = 0.53$) were all removed from the final model. The final model correctly predicted 92% of the unimpaired fish into their correct group and 57% of the impaired fish, with the overall model predictions being 80% correct.

Additional observations

The gut contents of 28 male and five female fish were also examined. While the guts of 13 individual males were void of contents, 15 males displayed variable degrees of gut fullness, with dietary items of individual fish being dominated by macroalgae, Ctenophera, hydroids or the eggs of conspecifics. In the case of the latter, the guts of three males (lengths, 325, 339, 305 mm) were full. Of the five female fish examined, all guts were empty. With the exception of two males, all were running milt. One of the female fish appeared to have spawned while the remaining four were heavily laden with spawn with gonads protruding from the vent.

Discussion

The primary goal of this study was to assess the injury and stress responses of *S. cantharus* to catch and release angling in order to identify the nonlethal responses to capture. It also provided the opportunity to investigate two other aspects related to their angling: the sex ratio of the catches and the selective removal of males from the population of a fish whose reproductive strategy involves male nest guarding (i.e. sole paternal care). These are both discussed in turn.

Effects of angling-metrics on secondary and tertiary stress responses

The reflex impairment tests applied to this study provide reliable indicators of the elevated risk of an individual being removed from a population through post-release mortality, or through delayed population level responses such as compromised reproductive fitness (Philipp *et al.*, 1997). Of the fish sampled, 32% had an impairment score of 0.25 or higher, with the remaining catch being assessed as having no impairment, indicating some potential for C&R to impact negatively on *S. cantharus*. While hook damage was revealed to be a significant predictor of impairment, it was likely that over the data set there was a range of interacting variables that were unable to be separated out in a field situation where high variability in individual fish responses and angler behaviors can be apparent. For example, aspects of the data collection that were unable to be controlled for included individual variability in angler behavior, the gear they utilized and the distance down-tide of the boat from which fish were captured. All of these could have had some individual or additive effect on the extent of change in blood chemistry concentrations and the extent of reflex impairment.

The significant relationship between hook damage and reflex impairment score corresponds with other work on this species. For example, when examining the effect of hook location on three *Sparidae* spp. including *S. cantharus*, Veiga *et al.* (2011) concluded that anatomical hook location was the main cause of post-release mortality (PRM) and, across other species, damage caused by deep hooking has been described as the most important factor affecting PRM (Muoneke and Childress, 1994; Bartholomew and Bohnsack, 2005; Alós *et al.*, 2008). Interestingly, only one deep-hooked fish (score = 3) was captured on a "circle" hook pattern, with all others taken on "J" hooks. The conservation benefits of circle hooks in limiting deep hooking have been widely acknowledged across many recreationally and commercially targeted fish species (Cooke and Suski, 2004; Kerstetter and Graves, 2006). This suggests that a minor adjustment in current angler behavior could limit the number of deep-hooked *S. cantharus*, along with the associated risks of those individuals being removed from the population through PRM.

Elevated levels of glucose and lactate in blood have been shown to provide rapid qualification of normal physiological disruption (Barton, 2002) and where baseline data are available, shifts in blood chemistry can be quantified (Cooke *et al.*, 2013; Bower *et al.*, 2016a). Analysis of blood chemistry was thus incorporated into this study on *S. cantharus*, with data obtained via PoC devices. Although these devices were designed for human use, they were used here for fish as other studies suggest they produce valid and accurate data (e.g. Beecham *et al.*, 2006; Danylchuk et al., 2014; Stoot *et al.*, 2014; Bower *et al.*, 2016a, b; Lennox *et al.*, 2016). The assumption used was that the PoC devices produced accurate data for the blood chemistry parameters of *S. cantharus*. While all the collected data were within the devices' detection range, it is nevertheless acknowledged that the use of the PoC devices were based on an assumption of accuracy that was not tested further in the study, warranting some caution in interpretations. The results for *S. cantharus* revealed that the significant correlation between fight time (anaerobic exercise) and elevated lactate was not reflected in a significant correlation between fight time and RAMP impairment. Other studies focusing on marine fishes (e.g. bonefish, *Albula vulpes*) and freshwater species (e.g. peacock bass, *Cichla ocellaris*) have, however, demonstrated that blood lactate can take between 2 and 4 h to return to baseline levels (Suski *et al.*, 2007; Bower *et al.*, 2016a). This indicates that post-release recovery of otherwise unimpaired fish might translate into an individual's behavior being compromised during an extended recovery process. Indeed, with reference to nest guarding largemouth bass *Micropterus salmoides*, C&R has been shown to result in impaired locomotory activity and reduced level of care to offspring for up to 24 h (Cooke *et al.*, 2000). The varied responses measured and observed in these *S. catharus* individuals thus support the utility and necessity of a multi-method approach to C&R stress assessment. As such, focusing on RAMP scores alone was considered unlikely to account for all fish exhibiting a stress response and thus was likely to have underestimated the post-release physiological and behavioral impacts of C&R.

Potential effects of selective removal of nest-guarding males from spawning areas

The strong dominance of males in the fish catches, along with the behavior of anglers selectively removing males in preference to females, also indicates some important management perspectives. Fishes with life history strategies involving nest preparation and paternal care of gametes have evolved to balance associated bioenergetic costs against the increased survival of offspring (Sargent and Gross, 1986; Knapp and Warner, 1991; Sargent, 1997). Associated male behaviors (e.g. courtship and aggression) are also energy demanding but necessary expenditures to ensure a male's reproductive success (Gozlan *et al.*, 2003). Such is the importance of these qualities in attracting a mate, the females of some fish species have paradoxically been shown to attempt to predate their own fertilized eggs to test the paternal fitness of their choice of male (Ridley, 1978). In light of these behaviors it is perhaps not surprising that fitter (i.e. more aggressive), strongly territorial males have been shown to be more susceptible to capture by recreational angling (Sutter *et al.*, 2012).

In assessing the utility of C&R as a conservation tool for any population which is exploited during reproduction, the complexity of potential effects at the population level become amplified. With respect to *S. cantharus*, the temporary displacement of a male from his nest potentially results in an immediate risk of conspecific nest invasion and brood predation (Suski *et al.*, 2003). That the dissected stomachs of five male fish (15% of all males captured) were filled with the eggs of conspecifics during the present study, suggests there is an immediate risk of brood loss, irrespective of whether the captured male was then released and navigated back to its nest. Due to most managed fisheries affording some level of protection during reproductive periods, it is not surprising that there are relatively few studies focused on the impacts of C&R on nest guarding fishes. However, controlled experiments conducted on the freshwater smallmouth bass *Micropterus dolomieu*, a species with a relatively similar reproductive strategy and associated behaviors, indicated that where released males did return to their nest, subsequent parental care conformed to parental investment theory, with remaining brood size influencing both paternal effort and brood abandonment decisions (Suski *et al.*, 2003). Although the ability of *S. canthaus* males to successfully navigate back to their nests following capture could not be investigated here, it was apparent that due to the mechanics of angling from an anchored boat in depths of ∼20 m and strong tidal currents, it was not untypical to land and release fish 50 m or more up-tide of their nests. Under these circumstances, males which do overcome the navigational challenge of finding their nests may be faced with a decision to either continue guarding or abandon the brood based on predation rates during their absence. For the previously mentioned smallmouth bass and the congeneric largemouth bass, research has shown ability of displaced fish to return to the nest but during their absence the nests are depredated (Hanson *et al.*, 2007; Dufour *et al.*, 2015). It is unclear whether *S. canthaus* has similar navigational abilities or the consequences of leaving the nest untended for a period of time.

Concluding remarks

The stress responses observed across the 40 sampled fishes provided some evidence that direct and probable delayed impairment on their post-release performance and survival were likely. However, of arguably greater importance in the context of angling impacts was the current practice of harvesting males, as it was suggested that this resulted in at least some nests being depredated of their eggs. Therefore, the act of removing an individual male from a spawning aggregation may not be comparable to removing the same individual outside of the spawning period, due to its effect on reproductive output (de Mitcheson, 2016). Although untested here and thus speculative, the anaerobic energy expenditure and associated stressors during capture means there is high uncertainty as to whether released males have the ability to navigate back to their nests, salvage their remaining brood and still have sufficient energy reserves to provide effective parental care until hatching. The observation of the limited numbers of captured females shedding eggs during the process of unhooking and handling also suggested an immediate impact on the reproductive potential of released females.

Based on calculations from data collated in 2013, best estimates of recreational exploitation of *S. cantharus* suggest annual capture to have been in the region of >100 000 individuals (~70 tonnes) from inshore areas along the English Channel (Armstrong *et al.*, 2013a). Commercial landing records from the same area and time period revealed catches totaling 203 tonnes (MMO, 2016). As the recreational catch thus represented ~25% of the total annual catch of *S. cantharus*, it represents a significant contribution to total stock exploitation. As a high proportion of these fish are then harvested, especially males with subsequent probabilities of brood loss, then some protection of these fish is suggested via fishery regulation until population size is demonstrated as stable, with consistent inter-annual catch rates not artificially propped up by the aggregated and aggressive vulnerability of the species to recreational capture (Erisman *et al.*, 2011). Indeed, to ensure the sustainability of *S. cantharus* stocks, existing attitudes of spawning aggregations as providing easy opportunities for exploitation need to shift towards acknowledgement that these critical life history stages need to be better understood and managed accordingly.

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