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Survival and recovery of longline- and pot-caught cod (*Gadus morhua*) for use in capture-based aquaculture (CBA)

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ABSTRACT

In capture-based aquaculture (CBA) wild cod (*Gadus morhua*) are caught and held in sea cages in order to supply fresh, high-quality fish throughout the year. CBA of cod is attracting growing interest among the Norwegian fishing industry. The most common gear for CBA is the demersal seine net (Danish or Scottish seine). However, there are powerful incentives to increase the extent of CBA, but this will necessitate the participation of fishing vessels from the smaller coastal fleet that utilise commercial pot and longline gear. CBA legislation is fish-welfare oriented and stringent, and documentation of stress, injuries and survival of captured fish is required for new capture methods. Field experiments were performed in order to determine the condition at capture of cod caught by longline and pots, using a combination of behavioural, physical, physiological and reflex-based indicators. Mortality and recovery were recorded in an onboard holding tank. No dead cod were observed at capture and, except for hooking wounds, the fish appeared unharmed. There was a high prevalence of fish that were incapable of submerging (about 40%), which if not dealt with resulted in high mortality (proportion: 0.79; 95% CI: 0.62–0.89). The mortality of fish that were capable of submerging was lower in pot-caught (0.09; 95% CI: 0.04–0.21) than longline-caught (0.39; 95% CI: 0.24–0.58) cod. Physiological and reflex stress measurements indicated that pot-caught cod suffered less stress from capture and handling, which suggests that pots are preferable as CBA gear. However, our knowledge of temporal and spatial variation in the suitability of fish for live storage (e.g. buoyancy status) is currently insufficient to predict the CBA potential of pots and longline outside of experimental conditions. Reflex impairment could predict mortality for pot and longline gears, and the inclusion of buoyancy status as part of a reflex/buoyancy impairment (RBI) score greatly improved model predictability. However, there was evidence that the relationship between RBI and mortality was influenced by the suite of stressors experienced by the fish, and this must be taken into careful consideration when comparing this relationship between fisheries.

1. Introduction

The capture and trade of live cod (*Gadus morhua*) referred to as capture-based aquaculture (CBA, Ottolenghi et al., 2004), is attracting growing interest among the Norwegian fishing industry. Cod aggregate in coastal waters during the spawning season (February–April) and when they feed on capelin (April–May), and huge landings are achieved within short periods. This seasonal and regional fishing pattern creates significant problems for fish quality, product development and marketing for the processing industry (Dreyer et al., 2008). In CBA, wild cod are captured in spring, transported to shore and held and fed in sea cages in order to supply fresh, high-quality fish throughout the year (Dreyer et al., 2008).

There are strong incentives for fishermen to land their catch alive, as they are allocated extra quotas and obtain high prices for better-quality fish. The most usual gear for CBA is the demersal seine net (Danish or Scottish seine), which made annual catches of up to >4000 tonnes of live cod over the last 15 years. In order to increase the extent of CBA in Norway, and reach the annual

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industry-wide target of 30,000 tonnes, it is necessary that smaller fishing vessels from the coastal fleet (longline and pots) that cannot operate seine, can also participate. The current regulations for cod CBA in Norway are aimed at ensuring fish welfare, and participating vessels are subject to stringent regulation by the Norwegian Food Safety Authority. Documentation of stress, injuries, healing and survival (collectively called "welfare issues") are thus required for new potential CBA capture methods and it is essential to have knowledge of the suitability of individual or groups of fish for live storage.

At present, little information is available on post-capture survival from pot and longline gears. However, both are believed to be benign gears, since fish in the catch are often alive and their flesh quality is high, indicative of low capture stress (Botta et al., 1987a,b; Rotabakk et al., 2011; Suuronen et al., 2012; Thomsen et al., 2010). Midling et al. (2005) showed that survival rates of longline-caught cod could be as high as 95% in transport tanks, given good sorting. Nøstvik and Pedersen (1999) found that more than 90% of the cod longer than 20 cm and captured by fish pots, fyke net and hand line were viable and fit for tagging.

A central step in cod CBA is the gathering of information on fish condition and survival potential, immediately post-capture, and methods to do this will need to be developed. During hauling from depth, the gas in the swimbladder of physoclist species expands in accordance with Boyle's law, and the fish may suffer a range of barotraumas like bloated eyes (exophthalmia), everted stomach/oesophagus and loss of equilibrium/balance (e.g. Parrish and Moffitt, 1992; Rummer and Bennett, 2005). Cod have been shown to have a mechanism for dealing with swimbladder rupture, gas release and healing (Humborstad and Mangor-Jensen 2013; Midling et al., 2012) that counteracts the adverse effects of positive buoyancy and is an important reason for the success of CBA of cod in demersal seine fisheries. Individuals showing signs of positive buoyancy and an inability to submerge (Hochhalter, 2012) cannot be used for live storage purposes and are easily sorted out, as can fish with other visible physical injuries.

Exhaustive swimming during attempts to escape from the capture gear also induces physiological stress that is not visible to the observer. Although physiological measures are widely used to describe stress status, they are intrusive (requiring blood samples), time-consuming and expensive, although new field instruments for rapid measurements are now available (Stoot et al., 2014). The main problem with physiological measures however, is that they do not consistently correlate with mortality (Davis et al., 2001). In the course of the past decade, a new alternative method (RAMP: reflex action mortality predictor) using reflex impairment to evaluate fish condition and survival potential has been developed (Davis, 2010). Humborstad et al. (2009) demonstrated the applicability of the method in cod exposed to rising levels of stress (swimming to exhaustion, exposure to air and abrasion). The RAMP curves indicated that cod with reflex impairment of less than 50% would survive and probably recover from capture stress. However, when the fish are exposed to other types of stressor, the relationship between reflex impairment and mortality may change and new RAMP curves need to be derived for such stressors (Davis, 2010). We performed field experiments in order to determine condition at capture in cod caught by longline and pot using a combination of behavioural, physical, physiological and reflex based indicators. Mortality and recovery after capture were recorded in order to evaluate the potential of these gears for CBA.

2. Material and methods

2.1. Gear deployment and fish sampling

Fishing experiments using collapsible pots (Furevik et al., 2008) and bottom-set longline (multifilament swivel line with EZ-baiter hook and monofilament snood) were performed in the Varangerfjord, near the Russo-Norwegian border, at depths of 114–184 m, in September 2008. Pots were attached to a ground-rope, with 55 m between each pot, while longline hook spacing was 1.8 m. Within the experimental area, two pot fleets (10 pots per fleet) and one longline fleet (250 hooks) were deployed in parallel fleets, with a distance between fleets of minimum 500 m. Fleet positions were systematically switched between consecutive deployment days. Longlines were baited with frozen squid (*Ilex* sp.) pieces, while three squid, each cut into five pieces were put in a single bait bag per pot. Each fleet was set and hauled between 12:00 h and 19:00 h, giving a soak time of about 24 h. Haulback of the buoy-line was done at normal speeds ($\sim$1.2 ms^{1}), while groundrope hauling was slow at less than $\sim$0.3 ms^{-1} (based on retrieval durations of 30–60 min per fleet) and variable both within single fleets and between fleets, depending on catch rates and capacity to handle fish during the onboard measurement process. However, the rate of ascent was not monitored for individual hooks or pots.

During hauling, fish were immediately transferred to a small tank (dimensions 0.5 m × 1.0 m × 0.5 m height). Only fish hooked in the mouth were selected, as other hooking types (deep and foul hooking) inflict injuries that are too severe to leave the fish suitable for live storage purposes, from fish welfare and CBA legislation per-

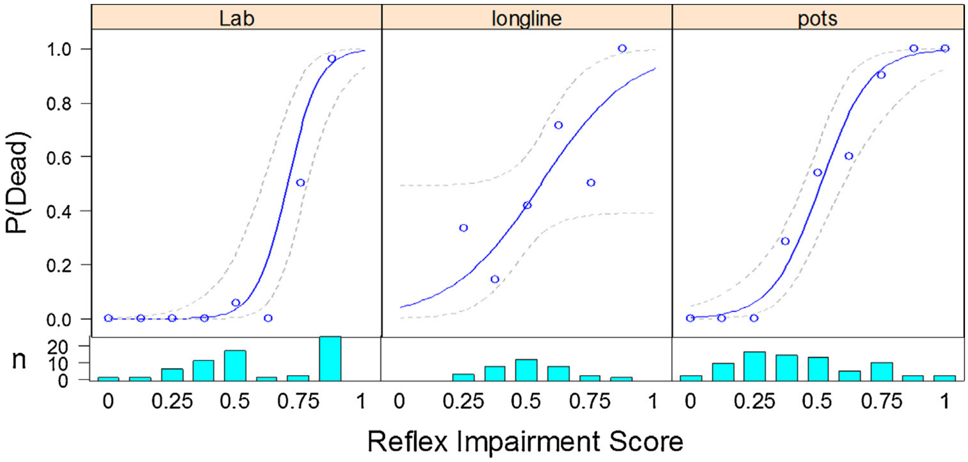

Fig. 1. Reflex/buoyancy impairment (RBI) and mortality relationships for cod captured by longline and pot, and data from a previous laboratory study (Humborstad et al., 2009). Solid lines are fitted values (with 95% confidence intervals; dashed lines) from GLM model. Lower panels show the number of fish per reflex impairment score.

spectives. The hook was gently removed by reversing the hooking action. Fish caught by pots were visually inspected for any injuries, and fish with snout abrasions (present, absent) were not included in the sample. The rationale for fish selection was to compare fish which were seemingly unharmed by the capture and process as observed by visual inspection, in agreement with current CBA legislation.

2.2. Buoyancy status, reflex impairment and physiological status

Buoyancy status was determined for all fish destined for live storage, and was observed in the small tank immediately after capture, based on the individual fish's movements, orientation and ability to dive. The small tank was analogous to the water-filled sorting table that is utilised to remove fish that are not fit for live storage before viable fish are transferred to larger transport tanks in the CBA seine fishery. Up to four fish were put in the small tank at the same time in order to enable unobstructed observations of behaviour by conspecifics during buoyancy determination. A subset of longline-caught cod that were unable to submerge (hereafter "floaters") was randomly selected and surplus gas was gently pushed out (i.e. venting by mimicking the motion of stripping eggs) through the two holes at the side of the anus (Humborstad and Mangor-Jensen, 2013). The fish was submerged and held diagonally head-down, belly-up in the small tank during venting. The venting procedure was completed in less than 1 min, after which the fish either righted themselves and swam downwards or became negatively buoyant and sank.

In order to determine the extent of capture-related impairment, reflex testing was performed immediately after buoyancy status determination. The reflex testing used the seven reflexes which have been shown to be consistently present in unstressed fish (Humborstad et al., 2009): restrained and unrestrained body flex, head complex, operculum closure, gag, vestibular-ocular response and tail grab. After reflex testing, each fish was tagged (T-bar tag; www.floytag.com) and released into a large holding tank (2 m × 2 m × 4 m height). The large holding tank had continuous water flow that ensured oxygen saturation above 90%. Oxygen concentrations were monitored using an Oxyguard Handy Polaris (OxyGuard International, Birkerød, Denmark) oxygen probe. Water was provided through a perforated double bottom (one 8 mm hole every 10 cm). The fish were held in the holding tank for up to fourteen days (i.e. maximum holding times employed during fishing for CBA) to observe mortality. At the termination of the experiment, fish were tested again, in order to determine any change in status (i.e. recovery or deterioration) while in the tank.

A total of 80 fish (40 fish per gear) were selected at random to determine physiological status. Immediately after capture, these were killed by a blow to the head. Blood samples were collected from the caudal vein using heparinized needles and syringes. Plasma was prepared in 2 ml Eppendorf tubes at 10,000 x g for 5 min and frozen at −20 °C for later measurement of alkaline phosphatase (ALP), aspartate aminotransferase (AST), glucose and lactate using the MAXMAT PLII autoanalyzer (ERBA Diagnostics, Montpellier, France). Plasma chloride was quantified using chloride-selective electrodes (COBAS c111 Autoanalyzer, Roche, Indianapolis, USA).

2.3. Statistical analyses

Individual reflex actions, buoyancy status ("floater" or "diver") and mortality (dead or alive) were scored as present (1) or absent (0). Reflex/Buoyancy Impairment (RBI) was calculated as follows: 1- (sum of individual reflex and buoyancy scores/ total possible score of 8). A Welch two-sample *t*-test was used to compare mean reflex scores between longline and pots. A paired two sample *t*-test was used to compare reflex impairment at capture and termination (for surviving fish) of the experiment.

Table 1
Model coefficients for the GLM describing the relationship between reflex/buoyancy impairment (RBI) and mortality for cod captured by longline and pot, and data from a previous laboratory study (Humborstad et al., 2009).

	Estimate	SE	*z* value	p
Intercept	−3.125	1.581	−1.977	0.0480
RAMP	5.648	2.998	1.884	0.0596
Class (pots)	−2.235	1.972	−1.133	0.2570
Class (Lab)	−8.309	3.280	−2.533	0.0113
RAMP: pots interaction	4.841	3.843	1.260	0.2077
RAMP: Lab interaction	10.717	4.857	2.207	0.0273

Table 2
Analysis of Deviance of model parameters for the GLM describing the relationship between reflex/buoyancy impairment (RBI) and mortality for cod captured by longline and pot, and data from a previous laboratory study (Humborstad et al., 2009).

	Df.	Deviance	Resid.Df	Resid.Deviance	Pr(>Chi)
NULL	22	123.268			
RAMP	1	97.239	21	26.030	<0.0001
Class (Lab, longline and pots)	2	12.662	19	13.368	0.0018
RAMP:Class interaction	2	5.436	17	7.932	0.0660

Laboratory reflex impairment data from Humborstad et al. (2009) was used as an additional suite of stressors (forced swimming, air exposure and net abrasion) for comparison with the capture-related stressors caused by the longline and pot fisheries. The laboratory fish experienced no decompression stressors, so no buoyancy impairment was observed in this group. A total of 169 farmed cod (range 31–49 cm total length) were tested for reflex impairment and held to observe mortality after stressor exposure in indoor tanks (145 cm × 145 cm × 100 cm deep) supplied with aerated sea water at Austevoll Research Station, Norway.

Mortality results are presented as proportions with 95% confidence intervals estimated using the Wilson score method (Wilson, 1927; Newcombe, 2013). The relationship between RBI and mortality was modelled for three different suites of capture-related stressors (longline, pot and laboratory), using Generalised Linear Model (GLM, see Fig. 1, Tables 1 and 2). Mortality was expressed as the proportion of fish dying per RBI score. The residual error distribution within the model was assumed to be binomial and the model was fitted using a logit linking function. There was no evidence of over-dispersion in the final model, so the dispersion parameter (Φ) was set to 1. Kruskal–Wallis one-way analysis of variance of ranks was used to test for whether physiological parameters differed between pot-caught and longline-caught cod. All statistical analyses used the "*R*" statistical software package (version: 2.15.2; R Development Core Team, 2012).

3. Results

No dead cod were observed at capture, and except for hooking wounds, the visual appearance of fish from both gears almost entirely lacked signs of abrasion, discolouring or bleeding. Only a few fish (not quantified but estimated at <1% of the total) were excluded due to foul hooking or snout abrasion (pots).

A range of buoyancy states were observed in the small tank. Positively buoyant fish were observed to lie motionless while belly-up or vertically oriented head-up, or to swim on their side or upside–down at the surface. Fish were also observed to submerge briefly before returning to the surface once swimming had stopped. Negatively buoyant fish also showed a range of behaviours from

Table 3
Physiological parameter values for cod immediately after capture by longline and pot (Kruskal-Wallis rank sum test).

	Pots			Longline			
	Median	*n*	SE	Median	*n*	SE	*p*
ALP (U L^{-1})	5.50	40	0.95	7.80	40	0.96	<0.05
AST (U L^{-1})	6.90	40	2.91	13.35	40	4.53	<0.05
Chloride (mmol L^{-1})	160.8	40	1.30	169.6	39	1.67	<0.001
Lactate (mmol L^{-1})	2.57	40	0.21	4.95	40	0.33	<0.001
Glucose (mmol L^{-1})	2.91	40	0.16	6.84	40	0.58	<0.001

Note: n = Number of fish in the sample, SE = standard error, ALP = alkaline phosphatase, AST = aspartate aminotransferase, U L^{1} = units per liter, where U = amount of enzyme that converts one micro mole of substrate per minute.

motionless to swimming on their belly, side or back on the bottom. The percentages of positive buoyant fish (floaters) were similar for cod caught by longline (43%, 95% CI: 30–57%) and pots (40%, 95% CI: 29–51%).

Overall mortality for floaters was 0.79 (95% CI: 0.62–0.89). In a subset of 17 floaters from longline that were vented, mortality dropped to 0.35 (95% CI: 0.17–0.59). Mortality for diving fish (i.e. excluding floaters and evacuated fish) was 0.09 (95% CI: 0.04–0.21) for pots and 0.39 (95% CI: 0.24–0.58) for longline, where 0.91 (95% CI: 0.80–0.97) of the observed mortality occurred within 24 h in captivity (range 0–68 h).

Reflex testing was performed on 73 cod (mean length ± SD: 55 ± 13 cm) caught by pot and 49 cod (mean length ± SD: 67 ± 14 cm) caught by longline. Mean reflex impairment at the time of capture was higher in longline-caught than pot-caught cod ($p < 0.01$, Welch two sample *t*-test, longline: 0.55 (0.16 SD, range 0.14–0.86, $n = 49$), pot: 0.43 (0.23 SD, range 0–1, $n = 73$)), while there was no significant difference in reflex impairment at termination ($p = 0.53$, longline: 0.33 (0.14 SD, $n = 28$) and pot: 0.30 (0.14 SD, $n = 44$)). For both gears, reflex impairment was significantly lower at termination than at the time of capture ($p < 0.001$, paired (survivors) two-sample *t*-test). The mean reflex impairment of the diving fish that died during the experiment was 0.65 (0.19 SD, $n = 15$).

With both gears, mortality increased with increasing RBI score, which was modelled using logistic regression (Fig. 1, Table 1). There was also a significant effect of capture/captivity class (levels: longline, pot and lab) on this relationship (Table 2). RBI-related mortality for pot and longline was significantly different from the laboratory data, as demonstrated by the Wald *Z*-test of the model coefficients (Table 1), as well as the difference in the model confidence intervals for the fitted values (Fig. 1). The main difference was that the increase in mortality occurs at lower RBI-scores for pot- and longline-caught cod than for laboratory cod. There was no evidence that pot and longline curves were significantly different, which suggests there was no gear specificity in the reflex impairment-mortality relationships. However, there were few data-points at low and high reflex impairment scores for longline, and the observed variation in mortality produced large residual deviances from the fitted model across all RBI scores, which resulted in wide confidence intervals for the longline model. In contrast, all reflex outcomes were observed in pot-caught fish, producing a complete curve from zero to full impairment with narrow confidence bands.

Their physiological status at capture revealed that pot-caught fish (mean length ± SD: 63 ± 11 cm) were less stressed than longline-caught fish (mean length ± SD: 65 ± 17 cm, Table 3). Fish caught by longline had significantly higher plasma levels of leakage enzymes (ALP and AST) ($p < 0.05$), glucose ($p < 0.001$), lactate ($p < 0.001$) and chloride ($p < 0.001$) than fish caught by pots.

4. Discussion

It is generally believed that passive gear, and especially pots, produce live and vital fish that would be suitable for CBA. Our results show that this assumption needs closer examination.

The percentage of fish with a compromised buoyancy status (i.e. floaters) in pot and longline gears was high (~40%) compared to demersal seine and trawl, which are normally around 1–20% (unpublished data; Midling et al., 2012). It was also high in comparison with earlier studies on pots, in which 22% floaters were observed in Ramfjorden (northern Norway) at depths of 50–130 m (Løkkeborg et al., 2014) and “very few” floaters were reported by Furevik et al. (2010) at a depth of 50 m at Smøla (western Norway). Floaters are susceptible to avian predation, solar radiation, unfavourable temperatures and are assumed to be poor candidates for live capture with high mortality in net pens (Midling et al., 2012). Our observed mortality of floaters (0.79; 95% CI: 0.62–0.89) confirms this and, combined with the high floater prevalence of about 40% in both gears, is a poor CBA result, which may or may not be extrapolated to other areas and seasons (see below). We did, however, show that if proper venting is administered, as carried out in several other species (e.g. McLennan et al., 2014), survival rates can be improved. This could be done in the smaller coastal fleet, where fish enter the vessel at a low rate and individual treatment is possible. However few data are available on fish performance in terms of feeding success and long-term welfare effects after manual venting.

In CBA for cod with demersal seine, it is essential to ensure a fishing depth that causes rupture of the swimbladder and ascent rate that allows the evacuation of surplus gas (e.g. Midling et al., 2012; depth 130–200 m, haulback speed 1–2.5 ms^{-1}). With regards to a minimum capture depth of 114 m, as in our study, assuming that the fish were neutrally buoyant close to the capture depth, the pressure reduction to surface (~92%) exceeded the threshold for swimbladder puncture (~70%, Humborstad and Mangor-Jensen, 2013; Tytler and Blaxter, 1973). On retrieval, gas was observed to be released from cod in both gears. Ascent rate was not monitored in our study, but this will be variable for fish caught at different locations on the ground-line. Fish caught close to the anchor will be hauled rapidly to the surface during buoy-line hauling. After this, the speed will decrease, on average to less than 0.3 ms^{-1}, and include stops dependent on catch rates, onboard processing capacity, hook/pot distance and fishing depth. Manipulation of ascent rate and simultaneous fishing with Danish seine would be a logical next step in the study of buoyancy status and gear effects.

Buoyancy status is intrinsically linked to vertical behaviour (Arnold and Walker, 1992; Godø and Michalsen, 2000), which in turn is related to a large number of interacting internal (e.g. gonad development and fat cycle, Ona, 1990; swimbladder filling, Strand et al., 2005; stock effects, e.g. Righton et al., 2001) and external factors (light, food availability, hydrostatic pressure, temperature, Strand and Huse, 2007). Differential buoyancy states when cod are retrieved from depth at varying temporal and spatial scales are therefore to be expected. The cod caught for CBA with demersal seine are mainly smaller migratory cod feeding on capelin or larger spent cod on their way back to the Barents Sea (April–June), whereas our experiments were probably based on fish from the Norwegian coastal cod component in Varanger. Coastal cod show little seasonal variation in depth distribution, while Northeast Arctic cod undertake large-scale migrations between deep overwintering grounds and shallow summer feeding grounds (Michalsen et al., 2014), differences that could influence swimbladder/buoyancy status. We suggest enlarged spatial coverage in order to evaluate hypothesised population differences in vertical migration and swimbladder dynamics.

Physiological indicators immediately after capture indicated that pots are more benign than longline. The fish experienced some level of capture stress in both gears, compared to resting glucose and lactate values (Brown et al., 2008; Olsen et al., 2008). Although there are large individual differences in hooking behaviour (Fernö and Huse, 1983) and behaviour inside a pot (Thomsen et al., 2010), some major gear-related patterns are evident. Furevik and Løkkeborg (1994) reported that cod were active when they first entered the pot, and frequently butted against the netting. After this initial activity, they were observed to calm down and mill around inside the pot. During haulback, an increase in burst speed reactions was observed, especially as the fish experienced buoyancy problems (authors' observations, unpublished data). Cole et al. (2003) observed that fish activity during hauling and as the pot left the water was sufficient to compromise flesh quality of blue cod (*Parapercis colias*). The higher levels of leakage enzymes in longline-caught fish shows that this fishing method caused more tissue damage, probably resulting from hooking. Furthermore, as both glucose and lactate levels were increased, it is likely that these fish were under more continuous exhaustive swimming stress than the pot-caught fish. Compared to those of fish taken by towed gears, longline glucose and lactate values in our study were closer to values observed following haul durations of more than five hours and for haul sizes above 20 tonnes, while values as low as for the pots were not observed even for short haul durations or low haul sizes (Olsen et al., 2013). Compared to pre-stress values (~50 mmol L^{-1}, Larsen et al., 1997; Olsen et al., 2008), chloride was elevated in both pot- (160.8 mmol L^{-1}) and longline- (169.6 mmol L^{-1}) caught cod, where the stress magnitude in longline-caught cod (significantly higher than for pot-caught fish) was indicative of partially impaired osmoregulatory ability. Information on post-hooking behaviour is scarce. However, once hooked, cod displayed a rapid rush and a more intense struggle during initial escape attempts (Løkkeborg et al., 1989), than fish captured in a pot. This difference in behaviour on capture might explain the observed differences in post-capture physiological indicators between fish taken by the two gears.

It is assumed that reflex impairment has its basis in physiological stress (Davis, 2010). Stressors differ in both presence and intensity between gears, and the observed difference in mean reflex status may well be related to the observed differences in physiology. At a mean post-capture reflex impairment of 0.55 (longline), a mortality probability range of 0–0.2 is predictable from laboratory data (Humborstad et al., 2009 and Fig. 1), which is less than 0.39 (95% CI: 0.24–0.58) observed in our study. For pots at 0.42 mean post-capture reflex impairment, a mortality probability of between 0 and 0.1 is predicted, which is comparable with the mortality that we observed (0.09; 95% CI: 0.04–0.21). Differences in RAMP curves among lab, pot, and longline conditions may be associated with stressor differences and the effects of different captive-observation holding conditions on delayed mortality in both laboratory and field. The lack of barotrauma in the laboratory fish may have altered their impairment response curve, relative to longline and pot fish. Laboratory holding conditions are expected to be less stressful than holding fish on board a fishing vessel, and this is consistent with the higher observed mortality of pot and longline fish than of laboratory fish with similar reflex impairment scores. It appears that specific RAMP curves (Fig. 1, Table 1) may be needed for gears that involve different stressors, including consideration of any additional stress associated with captive observation of delayed mortality. Differences in stressors and holding conditions certainly reduce the general applicability of RAMP across different stressors and fisheries. However, once a RAMP curve has been established for a specific set of stressors or gears, the strong relationship between reflex impairment and mortality shows the potential for predicting mortality outcomes, especially at high and low levels of impairment.

In CBA, failure to submerge is a strong sorting criterion (Midling et al., 2012), and our inclusion of buoyancy status greatly improved the fit in the GLM analysis. Hochhalter (2012) showed that the impairment index and barotrauma indicators, both associated with maximum gas retention, were identified as important predictor variables for both yellow eye (*Sebastes ruberrimus*) and quillback rockfish (*Sebastes maliger*) submergence success. The ability to submerge is thus intuitively coupled to buoyancy status and the vitality of the fish, as a strong and vital fish may be able to dive while an exhausted fish may not, given the same positive buoyancy status.

5. Conclusions

Our study revealed a poor CBA result from both pot and longline due to a high incidence of floaters which, if these were left untreated, resulted in high mortality. A wide range of internal and external factors (including gear type) may explain buoyancy status, and our knowledge of temporal and spatial variation is currently insufficient to predict suitability for CBA outside of experimental conditions. Of those fish that were able to submerge, pot-caught cod suffered much lower mortality than longline-caught-fish, a result supported by both physiological and reflexive stress measurements. Reflex impairment could predict mortality among fish caught by pot and longline. However, different RAMP curves were observed between laboratory and field conditions, indicating that careful consideration must be given to the types of stressors present and captive-observation conditions for delayed mortality when comparing RAMP curves for different fisheries. The inclusion of buoyancy status in modelling greatly improved mortality predictability.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fishres.2015.09.001.

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