The on-board live storage of Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) caught by trawl: Fish behaviour, stress and fillet quality

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Abstract

The aim of the present study was to assess the effects of the short-term live storage of Atlantic cod and haddock on residual blood in fillets. The fillet colour characteristics of fish sampled after 0, 1.5, 3 and 6 h of live storage were compared with fish subjected to current commercial processing procedures. Fish behaviour during live storage was also assessed, along with handling stress, by measuring the blood constituents (cortisol, glucose, lactate, pH and haematocrit), the initial white muscle pH, muscle twitches and length of time to the onset of rigor. The fillet colour in the CIE L*a*b* colour space was determined on fresh fillets (on-board) and the presence of discolouration was quantified by using a modified version of the Fillet Quality Index method. Fish behaviour analysis performed during live storage showed some signs of stress and that the condition of fish caught at greater depths was inferior to fish caught in shallower waters. The survival rate varied between the different trials (48.9 to 92.5 %), and was likely impacted by the fishing depth. The blood chemistry data showed that the captured fish were somewhat stressed, but we were not able to clarify whether the fish were becoming gradually more stressed during the subsequent live storage, or whether the observed increase or lack of recovery were a result of a delayed response for the various stress parameters. The occurrence of blood spots and discolouration was low in fillets cut from both species of fish just after capture. Subsequent live storage did not change this scenario. The colour characteristics of fillets cut from dead fish after 4.5-5.5 h were only marginally inferior to fillets from all the other treatments.

1. Introduction

Atlantic cod (*Gadus morhua*) has traditionally been one of the most important commercial species in the northern part of the Atlantic Ocean, and it is an important species for food production in Norway. In the last five decades, as a result of technological advances the catch capacity of the fishing fleet has increased significantly (Standal and Sønvisen, 2015), and due to high labour costs the number of fishermen on each vessel has been reduced. Therefore, every fisherman has to handle increased quantities of fish, which poses a challenge with respect to both fish quality and human safety. During

the last 30 years, technological progress regarding the processing of whitefish on board trawlers has been very slow. Today, there is a willingness to develop innovative on-board automated catch handling systems that safeguard the initial fish quality as well as the fishermen's HSE (Health, Security and Environment). Fish welfare has also become an issue in wild fisheries in recent years (Lambooij et al., 2012). As stated by the Norwegian Council for Animal Ethics, both the duration of harvesting and the length of time that fish experience high levels of stress, fear or pain should be shortened, aiming for gentle handling and minimal damage during capture.

Capture can affect fish in terms of injuries, excessive stress incidents and product quality. Gear-related injuries can result in compromised welfare as well as inferior product quality (Botta et al., 1987; Lowe et al., 1993; Esaiassen et al., 2004; Özyurt et al., 2007; Digre et al., 2010; Rotabakk et al., 2011; Olsen et al., 2014). Both weather conditions and the duration and size of the haul may affect the quality of fish caught by trawl or Danish seiners (Margeirsson et al., 2006). By the time the catch has been hauled on board, the fish are often stressed due to excessive muscle activity (escape behaviour), as can be identified by a low initial pH and elevated blood lactate levels (Digre, 2011; Olsen et al., 2013). Stress and inadequate on-board handling routines can result in poor bleed-out and thus reduced product quality (Botta et al., 1986; Olsen et al., 2013). In the Norwegian whitefish industry, adequate bleeding of the fish is considered necessary for good product quality. The flesh of poorly bled whitefish such as cod and haddock becomes dark or reddish in appearance and its commercial value can be reduced (Valdimarsson et al., 1984). It has been shown that immediate bleeding of the catch just after capture will improve bleed-out and minimise fillet discolourations (Kelly, 1969; Huss and Asenjo, 1976; Valdimarsson et al., 1984; Botta et al., 1986; Olsen et al., 2014). However, other factors such as the capture conditions, the transfer of fish from sea to vessel and the on-deck handling procedures may also play a role in fillet discolouration. In cases where large catches are taken on board, such as in trawl and seine fisheries, it is difficult to keep the fish alive before the entire catch has been bled, that is, before the blood starts to coagulate. In the present study, we evaluate whether the use of live holding tanks can be a remedy that improves bleed-out and minimises the occurrence of fillet discolouration. However, keeping captured fish in these systems can lead to a number of welfare

considerations related to the condition of the fish after capture. Appropriate welfare standards should be devised for the post-capture holding of fish. In addition to the physiological parameters, fish behaviour can be used to monitor their condition in these cases. Fish can be behaviourally impaired due to a spectrum of sublethal stressors experienced during capture in fisheries (Wilson et al., 2014), and behavioural indicators such as reduced swimming activity, respiratory stress, disorientation or an inability to maintain balance can all be used to quantify the stress response.

The short-term live storage (0, 3 and 6 h) of trawl-caught cod and the impact on fillet quality have been studied by Olsen et al. (2013). They found that the commercial processing method (fish kept in a holding bin without water before processing followed by direct gutting 4-6 h after capture) resulted in a significant increase in muscle discolouration compared to fish that were bled immediately. They also found that live storage for 3 h increased fillet discolouration significantly, whereas after 6 h the fillets became considerably lighter. This effect was explained by the redistribution of the blood away from the muscle during post-capture recovery. They concluded that for the best possible quality, the fish should be bled immediately, or alternatively, stored live for at least 6 h before bleeding. The authors also concluded that more research is necessary before the live-storage concept can be introduced to vessels.

The aim of our research was to compare short-term live storage ($\leq$ 6 h) before bleeding with commercial processing procedures (storage without water before bleeding) from physiological, behavioural and fillet colour perspectives. Therefore, we used similar sampling times (0, 1.5, 3 and 6 h) as Olsen et al. (2013) to allow a direct comparison of the results.

2. Methods

2.1 Fish capture

Atlantic cod (*Gadus morhua)* and haddock (*Melanogrammus aeglefinus*) were caught using a two-belly ALFREDO No. 5 (Refa-Frøystad Group, Tromsø, Norway) trawl on-board the research vessel 'M/S Helmer Hansen' (63.8m LOA and 4080 HP) in March 2014. Thirty-one hauls were conducted during the period 8-14 March 2014 off the coast of Tromsø in northern Norway (70-71° N/ 24-31°E), of which six hauls were selected for physiological and behavioural assessment. The main species in the catch were Atlantic cod, haddock and saithe (*Pollachius virens*). The towing time for the selected six hauls varied between 13 and 55 min with the total catch ranging from 500 to 9000 kg (Table 1). The fishing was mainly conducted at two depths, around 300 m (n=3) and around 70 m (n=3), at a towing speed of 3.6 knots and with a mean water temperature of 5.6 ^{o}C (± 0.3^{o}C, SEM).

2.2 Live fish holding tank

A 2.4-m^3 (1.48 m x 1.48 m x 1.09) live fish holding tank (Melbu Systems AS, Melbu, Norway) filled with seawater (taken from a depth of approximately 4 m, at 97-155 l min^{-1}) was placed on the trawl deck. The seawater was distributed through a perforated bottom plate, and it left the tank via a simple overflow (Figure 1).

The behaviour of the captured fish in the tank was monitored continuously throughout the experimental period using a modified Logitech C910HD camera suspended 75 cm above the surface of the water. The tank was covered with a plastic sheet suspended on a metal frame to minimise disturbances to the fish and light reflections from the water surface. The tank was lit continuously with 8 superbright LED lights (LBIR-850-35), each providing 54 watts of infrared light (850 nm). A second camera was deployed on deck to continuously monitor activities on the vessel that could later be related to changes in fish behaviour. To measure the dissolved oxygen (DO) levels and temperature in the holding tank, we used a DO meter (Model 9010, Royce Instruments Co., New Orleans, USA).

2.3 Fish and sampling

The fish were randomly collected from the codend immediately after the net was hauled onto the deck. They were then transferred in a batch to the water-filled holding tank. Four experiments were conducted for cod and one for haddock. The cod from Trial no. 5 (fish collected from Haul nos. 27 and 29, see Table 1) were only used for survival and fish behaviour studies.

Live fish (n=12-20) were randomly collected from the holding tank just after they were caught and transferred from the codend to the tank, netted and killed with a blow to the head within 5-10 s after netting (0 h group). The same procedure was conducted for the live-stored fish 1.5, 3 and 6 h after capture. After the fish were killed, a blood sample was taken by inserting a heparinised syringe into the caudal vein. The whole blood lactate was measured before the initial white muscle pH, muscle excitability and body temperature had been assessed. Then the throats were cut manually and the fish were exsanguinated for 30 min in a separate tank containing clean seawater. Subsequently, their length and weight were determined. The fish were then labelled, gutted, their sex was determined, and their livers and gonads were weighed before being rinsed in seawater. After that, the fish were placed belly down in Styrofoam boxes containing crushed ice. The development of rigor mortis was monitored for the first 24 h after death. After cold storage for 1 day, the fish were filleted and the right fillets were washed in seawater for 30 s. Excess water was wiped away with tissue paper and the fillets were examined for the possible presence of blood spots, colour, and blood-filled veins, and a picture was taken of each fillet to determine the fillet colour in the CIE L*a*b* colour space. The commercially processed fish were collected from the dry holding tank on board and kept for 4-5 h in plastic buckets after capture before being gutted, and the initial white muscle pH, muscle excitability and body temperature were assessed. Then the same procedure was carried out as for the live-stored fish.

The cod (both sexes, n=170) from Haul nos. 2, 9, 16, 27 and 29 (Table 1) had a weight of 3.8 ± 0.1 kg (mean ± SEM) and a standard length of 74.7 ± 0.9 cm. The condition factor (CF), hepatosomatic index

(HSI) and gonadosomatic index (GSI) were 0.9 ± 0.0, 5.1 ± 0.2 and 2.5 ± 0.3, respectively (calculations based on the whole fish weight). The haddock (both sexes, n=60) from Haul no. 25 weighed 1.1 ± 0.1 kg and had a standard length of 46.1 ± 0.7 cm. Their CF, HSI and GSI were 1.0 ± 0.0, 3.5 ± 0.1 and 0.7 ± 0.1, respectively.

2.4 Analytical methods

2.4.1 Fish behaviour

Seven variables were selected to enable the quantification of the stress response in the study (Table 2). They were designed to reflect the stress behaviour of the captured fish and included measures of activity, balance, respiration and respiratory stress. Two levels of balance loss and three levels of respiratory stress were reflected in the two different measures.

Sampling of video – Trial nos. 2 to 5 were analysed for behaviour as film was not available for Trial no. 1. The behaviour samples were taken at time points (TP) 0, 1.5, 3 and 6 h after capture to match the sampling for the other variables. Five one-minute video samples were taken at each time point and the seven variables listed in Table 2 were measured from each video sample.

Data analysis – Six of the seven variables were counts of fish. They were transformed into the proportion of fish in view of the camera in order to standardise for the variable fish density in the tank and the variable visibility of the fish in the tank. The mean and standard error were calculated for five samples at each time point. In order to summarise the behavioural stress response from all the variables in a single value, a simple model was created. The stress indicator model (SIM) included all the proportion variables (i.e. the number of gill movements was excluded). Activity was also excluded as extremely high values in some cases overshadowed the variability in all the other measures. The

measures reflecting positive behaviours were included directly and the measures reflecting negative behaviours were included as their complementary values.

$$SIM = \frac{m + (1-d) + (1-g) + (1-f) + (1-s)}{n}$$

where:

n = number of variables

m = proportion of fish with pectoral movements

d = proportion of fish that lost balance

g = proportion of fish gaping

f = proportion of fish with flared gills

s = proportion of fish with their heads above the surface

2.4.2 Blood chemistry

The measurements of glucose, blood pH and haematocrit (measured as % of the red blood cell packed volume (RBC)) were done using an Epoc© (Epocal Inc., Ottawa, Canada), which can measure several blood parameters simultaneously. The cartridges were stored in a fridge in their original packaging at 4^{o}C. Before use the cartridges were allowed to reach room temperature (about 18 ^{o}C), at which all the analyses were performed. A few drops of whole blood were added to the cartridge, and shortly afterwards the result was displayed directly on the instrument's screen.

Cortisol – The blood was sampled with heparinised syringes and centrifuged (6 000 rpm, 5 min) with a Galaxy Mini Star Silverline C1413-VWR230 centrifuge (Radnor, USA) to extract the blood plasma. The plasma was subsequently stored at -20 °C until later analysis of the cortisol. The cortisol was determined by using a radioimmunoassay method, as described by Iversen et al. (1998).

Blood lactate – The whole blood lactate was measured using a Lactate Scout+ meter (EKF Diagnostics GmbH, Magdeburg, Germany) with a measuring range of 0.8-23.3 mmol L^{-1}. The test

strip was briefly soaked in blood flowing out immediately after the throat was cut, and before it was inserted into the test meter. This method has been tested on cod and is regarded as a reliable method for the assessment of the welfare of farmed fish (Brown et al., 2008).

2.4.3 White muscle biochemistry and rigor mortis

Body and core temperature – A Testo 110 thermometer (Testo AG, Lenzkirch, Germany) was used to measure the fish's body temperature in the epaxial muscle between the lateral line and the dorsal fin.

Initial white muscle pH **–** The pH in the epaxial white muscle between the lateral line and dorsal fin was measured using a shielded glass electrode (WTW SenTix 41, WTW, Weilheim, Germany) connected to a portable pH meter (model WTW 315i). During the measurements, the electrode was frequently rinsed and re-calibrated using pH 4.01 and pH 7.00 buffers.

Muscle twitches **–** The ability of the white muscle to contract immediately after death was determined using a Twitch Tester Quality Assessment Tool (AQUI-S Ltd., Lower Hutt, New Zealand). The instrument measures the electrical excitability of the muscle tissues. An electrical pulse was generated (9V DC) by the instrument every 0.6 s. A few (1-3) measurements were performed on one side of each fish. For each measurement, the electrodes were in contact with the fish for about 1-2 s. The following scale was devised: **3** – Strong tail twitch (electrodes placed along the entire lateral line, behind the head and near the caudal fin); **2** – Weak tail twitch (electrodes placed as above); **1** – Minor muscle contractions in (small) restricted areas of the fish's body surface (electrodes placed a few cm apart); **0** – No contractions whatsoever.

Rigor mortis – The onset of rigor mortis was determined using the Rigor Status Method (**0** = pre- or post-rigor; **1** = rigor onset (first sign of stiffness, for instance in the neck or tail regions); **2** = rigor (a larger area is clearly in rigor); **3** = the whole fish in rigor; **4** = stronger rigor; **5** = very strong rigor (extremely stiff, rod-like fish) (Erikson, 2001).

2.4.4 Residual blood and fillet colour

Visual assessments of residual blood in fillets – Experienced evaluators (n=2) evaluated the right fillets cut from fresh (on-board) fillets according to a modified version of the Fillet Quality Index (FQI) method (Olsen et al., 2013). Four different parameters were assessed and the sum of these attributes represents the FQI; fillet blood spots (0 = no visual blood spots; 1 = 1-2 small blood spots; 2 = several small or big blood spots), discolouration of the loin or belly (0 = homogeneous white; 1 = pink; 2 = red) and blood-filled veins in the belly (1 = no visible blood in veins; 2 = partly filled with blood in less than 3 veins; 3 = partly filled with blood in all veins; 4 = filled with blood in all veins).

Computer vision evaluation of fillet colour – Images of the fillets were taken on the same day that the visual assessments of colour was performed on board, one day after capture. A digital colour camera (Nikon, Coolpix5000, Nikon, Tokyo, Japan) with a 50 mm lens and the following settings was used: Autofocus, shutter speed 1/200 s, ISO 400, aperture F 5.6, manual flash – autometer 5.8. A polarisation filter was placed in front of the flash and a second polarisation filter was placed on the lens. The polarisation angle of the lens polariser was perpendicular to the polarisation on the flash polariser in order to minimise surface specular reflections. The images were taken in RAW format with maximum resolution (6000 x 4000) and stored on a computer for subsequent evaluation. Processing was carried out on the captured images (still). For automated colour analysis of the fillets in the CIE L*a*b* colour space (Erikson and Misimi, 2008), we chose to study the potential effects of poor bleed-out on a portion of the fillet only. The chosen region of interest (ROI) is shown in Figure 2. The fillet images were colour calibrated using the GretagMacbeth ColorChecker chart with 24 colour patches (Colour-Science AG, Hinwil, Switzerland). As both the a* and b* values turned out to be

positive, they represented redness and yellowness, respectively. The chroma (colour saturation, C*), hue angle (0^o = red hue; 90^o = yellow hue, H^o) and whiteness (W) (Park, 1994) were calculated as $C^*_{ab} = (a^{*2} + b^{*2})^{1/2}$, H^o_{ab} = arctan (b*/a*) and W = L* - 3b*, respectively.

2.4.5 Statistical analyses

To test the significance of any differences between the groups, or the impact of the treatment, a one-factor analysis of variance (ANOVA) generally followed by a Tukey's *post hoc* test were used (Minitab Ltd., State College, Pa., U.S.A.). For the discrete variables, survival rate, muscle twitches and visual quality assessments of the fillets, a Mann-Whitney nonparametric test was performed. The results were reported as mean values ± standard error of means (SEM).

3. Results

3.1 Fish survival during live storage

An overview of the different parameters related to the live storage tank (survival rate, fish density, DO level, temperature and pH) is given in Table 3. The DO levels ranged from 60 to 120 % saturation, with an exception of 46 to 60 % saturation for a period of 2 h (Trial no. 3). The pH values were stable at 8.0-8.1, whereas the temperature varied from 4.1 to 6.1^{o}C. For the cod the holding density ranged from 119 to 548 kg m^{-3}, whereas the haddock had a holding density of 87 kg m^{-3}. Under these conditions it became evident that a certain proportion of the fish subjected to live storage eventually died. When the tank was emptied after each trial was terminated, the number of mortalities in the batch (trial) was counted. Therefore, the given survival rates are only valid for the point in time when each trial was terminated. Direct comparisons between the trials are thus not relevant as the length of time before emptying the tank varied between the different trials. For Trial nos. 1, 2 and 3 the survival rate for cod, assessed after 24 to 29 h of live storage, varied from 48.9 % to 68.1 % (Table 3). In Trial no. 4, the survival rate for haddock was 92.5 % after 6-7 h of live storage. In Trial no. 5, for cod collected from Haul nos. 27 and 29 (these two hauls were mixed), the survival rate was 77.3 % after 8 to 22 h of live storage.

3.2 Fish behaviour during live storage

The fish in Trial nos. 4 and 5 demonstrated reduced stress behaviour in comparison to those in Trial nos. 2 and 3 (Figure 3). Trial nos. 4 and 5 were carried out with fish hauled from 70 m, rather than 270 m for Trial nos. 2 and 3 (Table 1). The cod activity in Trial nos. 2 and 3 was near zero during the whole period, with very little variation (Figure 3). On the other hand, swimming activity was exhibited by the cod in Trial no. 5 and to the greatest extent by the haddock in Trial no. 4. There was no trend of increasing or decreasing activity during the 6 h of the trials.

Loss of pectoral movements was considered the mildest indicator of balance loss. The lowest proportion of individuals exhibiting pectoral movements were the cod from the deep trawls (trials 2 and 3), while all fish from the shallow trawls (trials 4 and 5) (Figure 3) exhibited pectoral fin movements. The cod in Trial no. 2 exhibited the least balance maintenance activity. Few increasing or decreasing trends were seen during the trials. Full loss of balance was exhibited in all four trials at TP 0 h, although there was a large variation at this TP (Figure 3). In all four trials the fish demonstrated some balance recovery by TP 1.5 h, and the haddock appeared to be in better condition than the cod (Figure 3).

The respiration and respiratory stress were measured using a count of gill movements and three variables of increasingly negative strength; the proportion of fish with their heads above the surface, the proportion of fish gaping and the proportion of fish with their gills flared. The gill movements were measured only during Trial nos. 2 and 3, as the fish in Trial nos. 4 and 5 were too active to allow counting. The fish in Trial nos. 2 and 3 started with a low number of gill movements per minute at TP 0 h and followed a steady decline (after an initial increase in Trial no. 2 between TP 0 h and 1.5 h) towards TP 6 h (Figure 3d). No fish exhibited the behaviour of holding their heads above the surface in Trial nos. 4 and 5 (Figure 3e). In Trial nos. 2 and 3 at least half the visible fish exhibited this behaviour at TP 1 h, and this increased during the holding period. Likewise, no fish were recorded as gaping during Trial nos. 4 and 5 (Figure 3f). Gaping behaviour increased over time during Trial nos. 2 and 3. When fish were first brought on board at TP 0 h none exhibited flared gills. This behaviour did not develop during Trial nos. 4 and 5, but increased in Trial nos. 2 and 3 (Figure 3g), with nearly all the cod in Trial no. 2 having flared gills by TP 6 h.

With all the variables summarised, the stress indicator model clearly demonstrated a pattern of increasing stress in the cod in Trial nos. 2 and 3 and lower stress in Trial nos. 4 and 5 (Figure 4). The cod in Trial no. 2 exhibited a constant decrease in condition throughout the trial, whereas the cod in Trial no. 3 appeared to stabilise at TP 3 h, although no data were available to confirm this for TP 6 h. The cod and haddock in Trial nos. 4 and 5 both showed a slight increase in condition between TP 0 h and TP 1.5 h, after which it was stable. The haddock exhibited the least stress behaviour throughout the trials.

3.3 Blood chemistry and white muscle biochemistry

The mean body temperature at the time of sampling for cod and haddock were 6.0 ± 0.3 and 4.4 ± 0.1^{o}C, respectively.

Effects of live storage – The effects of live storage on blood and muscle chemistry are shown in Table 4. The mean plasma cortisol concentration was significantly lower in the cod sampled immediately after landing on deck (62.6 ng mL^{-1}) than in the cod stored live for 1.5 h, 3 h and 6 h (102.7, 123.3 and 125.4 ng mL^{-1}, respectively, $p<0.001$). A similar trend was seen for the haddock, where the lowest mean plasma cortisol concentration was found in those sampled just after landing on deck (15.4 ng mL^{-1}), whereas the haddock stored live for 6 h exhibited significantly higher values (41.0 ng mL^{-1}, $p<0.005$). The blood pH ranged from 7.2 to 7.4 for the cod, with significant differences between the cod stored live for 1.5 h (pH 7.2) compared to the cod stored live for 6 h (pH 7.4, $p=0.028$). For the haddock, their blood pH ranged from 7.3 to 7.5, with significant differences between the fish sampled just after being brought on board (0 h, pH 7.3) and the fish stored live for 3 h (pH 7.5, $p=0.003$). The whole blood glucose and lactate values had a similar trend to the plasma cortisol concentration values, where the fish from the 0 h treatment had the lowest values. For the cod, the glucose values ranged from 4.7 to 10.2 mmol L^{-1}, with significantly lower values for the cod from the 0 h treatment (4.7 mmol L^{-1}) compared to the 1.5 h (7.3 mmol L^{-1}) and 3 h treatments (10.2 mmol L^{-1}, $p<0.001$). The cod stored live for 6 h were no different from those stored for 1.5 h or 3 h. Similarly, for the haddock the 0 h treatment (3.9 mmol L^{-1}) had significantly lower glucose values than the 3 h (6.6 mmol L^{-1}) and 6 h (8.7 mmol L^{-1}, $p<0.001$) treatments. The mean lactate values varied from 3.4 to 9.6 mmol L^{-1} for the cod, with significantly lower values at 0 h (3.4 mmol L^{-1}) compared to 1.5 h (6.2 mmol L^{-1}), 3 h (8.5 mmol L^{-1}) and 6 h (9.6 mmol L^{-1}). Similarly, the lactate values varied from 3.7 to 9.1 mmol L^{-1} for the haddock, with significantly lower values at 0 h (3.7 mmol L^{-1}), compared to 3 h (7.2 mmol L^{-1}) and 6 h (9.1 mmol L^{-1}). The cod from the 0 h and 6 h treatments had a significantly lower levels of haematocrit (32 % Hct) than the cod stored live for 1.5 h (36 % Hct, $p<0.05$). In the case of the haddock, the haematocrit levels (21-24 % Hct) were similar for all the treatments ($p>0.05$).

338

339 The mean initial white muscle pH of the cod and haddock from all the treatments was 7.1 ± 0.0 and
340 7.0 ± 0.0, respectively (Table 4). The cod stored live for 3 h had a significantly higher initial muscle
341 pH (pH 7.2) compared to the commercially processed cod taken from a dry holding bin and sampled
342 5.5 h after being taken on board (pH 7.0). The haddock stored live for 3 h had a significantly higher
343 initial muscle pH (7.1) than just after capture (0 h, pH 6.9) or when taken from a dry holding bin 4.5 h
344 after landing (pH 6.8).

345

346 The mean muscle twitch scores for both the cod (1.6 – 2.1) and haddock (2.0 – 2.6) after 0, 1.5, 3 and
347 6 h of live storage were no different within each fish species (Table 4). The scores corresponded to 'a
348 weak' to 'a strong' tail twitch. Commercially processed fish that was dead when sampled did not
349 respond to electrical stimulation at all (twitch score 0).

350

351 The onset of rigor was assessed for all the treatments and in general the cod had a shorter pre-rigor
352 time than the haddock (Table 4). In the cod the onset of rigor started within 5 to 8 h, while for the
353 haddock it started 5.5 to 10.5 h after capture.

354

355 *Effect of capture* – As each treatment for the cod consisted of fish from different hauls, we tested for
356 possible statistical differences between hauls during treatment (these data are not shown in Table 4).
357 As can be seen in Table 4, there were indeed some differences in several cases (indicated with an X in
358 Table 4 if there were significant differences between hauls during one treatment, $P>0.05$). The plasma
359 cortisol level in the cod stored live for 6 h from Haul no. 9/Trial no. 2 (107.3 ng mL^{-1}) was
360 significantly lower than in the cod from Haul no. 2/ Trial no. 1 (150.3 ng mL^{-1}). However, the glucose
361 values for the cod stored live for 6 h from Haul no. 9 were significantly higher (10.7 mmol L^{-1}) than
362 the cod from Haul no. 2 (7.9 mmol L^{-1}). There were also some significant differences between the
363 hauls for all the treatments, except for the cod that was stored live for 6 h for the parameter muscle-
364 pH. The initial muscle pH of the cod from Haul no. 16/Trial no. 3 (catch amount 1423 kg, Table 1)
365 always exhibited the highest muscle pH, thus indicating that a lower catch amount yielded a higher

muscle pH. There were also some significant differences between the hauls for the cod stored live for 1.5 h and for the cod sampled immediately after landing on deck for the blood lactate and twitch tester parameters, respectively, although these differences were rather small.

3.4 Visual assessment of residual blood in fillet colour by machine vision

Effect of live storage – The visual assessments of the discolorations and residual blood in the fillets are given in Table 5. The results for the cod showed that there was a tendency for less discolouration in both loin and belly when the fish were processed immediately after landing (0 h treatment). Conversely, there was a tendency that the dead fish taken from the dry holding bins after 5.5 h produced fillets with a slightly higher degree of discolouration. Thus, the fillet colour of all the cod varied between 'homogeneous white' and 'slightly pink'. With regard to the residual blood in the veins and the number of blood spots, there were no differences between treatments ($p>0.05$). The scores of 2.4-2.7 for the amount of residual blood in the veins mean that the belly had veins that were 'partly filled with blood in fewer than 3 veins' or 'partly filled with blood in all the veins'. The low blood spot scores of 0 to 0.3 show that the fillets either had no blood spots or 1-2 spots on average. Regarding the total scores, there was a tendency for the best and the worst fillets to come from the '0 h' and 'dead 5.5 h' treatments, respectively. The same picture was observed for the haddock fillets.

The fillet colour (Figure 2) for the cod and haddock as assessed by machine vision analysis is shown in Figures 5 and 6, respectively. The cod stored live for 6 h produced slightly darker loins (lower L* values) than the loins from all the other treatments ($p<0.05$). However, this was not reflected as a greater degree of whiteness, as all the treatments produced loins with a similar whiteness with mean values of between 76 and 77. Immediate bleeding (0 h) resulted in fewer red loins, where the Δa^* values were 2-3 units lower compared to all the other treatments. Increasing the live storage time led to a gradual increase in redness after 1.5, 3 and 6 h, where the mean a* value was 5 after 6 h, that is, similar to the redness of the fillets (loins) cut from dead cod after 5.5 h. The degree of yellowness, with b*-values of around 3, was similar for all the treatments ($p>0.05$). With regard to the hue, the

most striking feature was that immediate bleeding resulted in higher hue values ($p<0.05$), which corresponds to fewer reddish (more yellowish) loins compared to the other treatments. In line with this, the colour saturation (chroma) of these loins was the lowest out of all the treatments ($p<0.05$).

The fillets (loins) cut from the dead haddock stored in a dry holding bin for 4.5 h were slightly darker (ΔL^* values of 1-2 units) than all the other loins ($p<0.05$). The same was true for the whiteness, where a small reduction in whiteness was also observed after live storage for 6 h ($p<0.05$). The redness values were low for all the treatments, where the loins from the dead fish collected from a dry holding bin had significantly higher a* values (Δa^* of 2 units). The b* values were low and similar for all the treatments ($p>0.05$). The hue angles of the loins from the dead fish were around 45^o, whereas the loins from the other treatments had hue angles of around $80\text{-}90^o$, meaning the latter were clearly more yellowish ($p<0.5$). The chroma values were generally low, with mean values ranging from about 2.5 to 3.3. Only the loins from dead fish and fish stored live for 1.5 h were significantly different from each other. Based on the CIE L*a*b* colour space, Figure 7 illustrates the greatest colour difference observed between the two treatments in the present study. This happened to be dead haddock vs. haddock stored live for 1.5 h. In the loin region, loins from the latter treatment are visibly whiter than those from fish collected after 4.5 h in a bin without water.

The CIE L*a*b* colour measurements showed that the haddock loins were somewhat lighter, whiter, less red, more yellowish (higher hue angles), as well as exhibiting lower colour saturation levels than was the case for the cod loins. The yellowness of the loins (b* values) was similar for both species of fish.

Effect of capture – As stated previously, each treatment for the cod consisted of fish from different hauls, and we tested for possible statistical differences between hauls during treatment (these data are not shown in Table 5). As can be seen in Table 5, there were some significant differences in two cases for the dead cod for the 'residual blood in veins' parameter and the total scores between the hauls (indicated with an X in Table 5 if there were significant differences between hauls during one

treatment, P>0.05). The dead cod from Haul no. 2 exhibited less residual blood in their veins and a lower total score than the dead cod from Haul no. 16, although the differences were small.

Regarding the CIE L*a*b* colour measurements there were indeed some significant differences between the hauls in several cases, as can be seen in Figure 5 (illustrated by a X on the graph). The main difference between these hauls was the total catch amount (See Table 1; 2553 kg/Haul no. 2/Trial no. 1, 4410 kg/Haul no. 9/Trial no. 2, 1423 kg/ Haul no. 16/Trial no. 3). Additionally, the fish density was different between the trials (see Table 3; 118 kg m^{-3}/ Trial no. 1, 405 kg m^{-3}/ Trial no. 2, 410 kg m^{-3}/ Trial no. 3). The cod from Haul no. 2 produced significantly less red loins than the cod from Haul nos. 9 and 16 for all the treatments (except for the cod that had been stored live for 1.5 h), which was reflected as greater whiteness ($p<0.05$). Furthermore, the fillet loins of the cod from Haul no. 2 produced less yellow loins, and the colour saturation (chroma) of these loins was the lowest out of all the treatments, except for the cod that had been stored live for 1.5 h ($p<0.05$).

4. Discussion

4.1 Live storage and fish survival

With regard to the water quality in the live storage tank (Table 3), the results show that the fish had adequate access to oxygen (DO 46-120 % saturation) at all times. As a comparison, at 2 to 6 ^{o}C the cod mortality rates are high when the oxygen saturation levels are < 16 to 22 %, whereas no mortalities have been observed at levels > 34 % saturation (Plante et al., 1998). As expected, the water temperature was similar to that of the sea and the typical pH values of fresh seawater (pH 8.0-8.1) showed that metabolically produced carbon dioxide did not accumulate in the tank due to good water exchange. The fish density varied between 87 and 548 kg m^{-3}. We should mention that the adult Atlantic cod were kept in an open system (tank) for 2 days at 8 ^{o}C at a fish density of 549 kg m^{-3}. A general stress response (cortisol and glucose) was measured, but the mortality rates were negligible (Staurnes et al., 1994).

The survival rate varied between the different trials (48.9 to 92.5 %). The cod from Trial no. 2 had the lowest survival rate compared to the cod from Trial nos. 3 and 5, while the haddock had a higher survival rate than all the other trials. There were some important differences between the hauls that probably had an impact on the survival rate during live storage. Plausible factors were: The total catch per haul (ranging from 500 to 9000 kg), the fishing depth (279-333 m and 63-77 m), the weather conditions (wind 7 to 18 m/s) and the duration of the haul (ranging from 15 to 55 min, which may be considered relatively short hauls). These are the factors that have been reported to affect the survival rates of fish (Digre et al., 2010; Olsen et al., 2013). Olsen et al. (2013) reported that cod mortality rates tend to increase when the haul duration and size increase.

As the fish behaviour data indicated (see below), it is likely that the fishing depth has a considerable impact on survival rates during live storage. Our data (Tables 1 and 3) indicated that fish caught at a depth of about 70 m had higher survival rates (77 and 93 %) during live storage than fish caught at about 280 m (survival rates of 49-68 %). As the fish are brought to the surface, the gas in the swim bladder of physoclist species such as cod and haddock expand, and the fish may suffer a range of barotraumas such as swollen eyes, an everted stomach, a damaged swim bladder and loss of equilibrium (Rummer and Bennett, 2005). However, cod have a mechanism for dealing with swim bladder rupture, whereby gas release and healing (Humborstad and Mangor-Jensen, 2013; Midling et al., 2012) eventually counteract the adverse effects of positive buoyancy. However, some individuals that show signs of positive buoyancy and an inability to submerge (Hochhalter, 2012) will die and are therefore not suitable for (long-term) live storage. Hochhalter (2012) identified that the capture depth was the most important variable for predicting the ability of yelloweye rockfish (*Sebastes ruberrimus*) to submerge after capture. The ability to submerge can therefore be a good indicator for predicting whether a fish will survive after capture.

4.2 Fish behaviour

Fish behavioural responses to holding during the course of the 6 h study do not present any clear benefit to short-term holding of fish after capture by trawl. In this study, the condition of the fish appeared to be closely related to the trawl depth. While the cod and haddock trawled at a depth of 70 m demonstrated relatively normal behaviour, the cod trawled at a depth of 270 m indicated symptoms of barotrauma (Olsen et al., 2012; Nichol and Chilton, 2006; Neat et al., 2009) immediately after being placed in a tank. This behaviour occurred throughout the 6-h study. Respiratory problems, apparent at TP 0 h in cod from 270 m, continued, and in fact worsened during the 6-h holding time.

Few studies have been conducted on behavioural responses to trawl capture and the existing studies have focussed on bycatch release and fitness-influencing behaviours (see Wilson et al., 2014). Severe physiological exhaustion has commonly been described as a likely cause for behavioural impairment following capture (Olla et al., 1997; Ryer et al., 2004; Davis and Parker, 2004). Crushing, descaling and barotrauma are also likely causes (Olsen et al., 2012; Nichol and Chilton, 2006; Neat et al., 2009). Gas embolism in the gills resulting from barotrauma may have caused the respiratory problems observed in the cod trawled from 270 m due to a reduced diffusion of oxygen across the gill surface. High lactic acid concentrations following extended burst swimming during the trawling (see below) may have caused an imbalance in the acid base system. This would in turn have affected the metabolic processes and caused the characteristic ‘head up’ swimming behaviour observed in these fish. Recovery from such a severe injury is unlikely, and so it is questionable whether live holding is beneficial. It is more likely to threaten the welfare of the captured fish. It is possible that with slower hauling from great depth less damage will occur as the body will have more time to equilibrate. Further research is required to test this hypothesis.

The cod and haddock captured from a depth of 70 m did not demonstrate any of the damage related to barotrauma. Their behaviour was observed to be relatively normal (at least in terms of the captive wild fish) on their arrival in the tank at TP 0. After settling to TP 1.5, their activity levels stabilised and their disorientation, observed as a loss of balance, was reduced, thus suggesting a fast recovery. The

haddock demonstrated the least impairment in their behaviour, although in this trial their density in the tank was relatively lower than for the cod, so further studies are required to confirm this.

4.3 Stress associated with capture and live storage

The blood chemistry, initial muscle pH, muscle twitch ability and length of time to the onset of rigor indicated that the fish were exposed to considerable stress during the catching process. Cortisol is a widely used indicator in studies on stress in fish, and the baseline levels in unstressed fish are normally low relative to the levels reached during stress, although the concentrations vary between species (Pottinger, 2008). The release of cortisol is slower compared to that of catecholamine, and most fish species show their highest plasma cortisol levels within 0.5-1 h after an incidence of stress (Barton and Iwama, 1991). As our towing times were relatively short (13-55 min), this might be in line with our results, showing a gradual increase in the plasma cortisol values for both the cod and haddock during the subsequent live storage for up to 6 h. Another possibility is that the fish experienced further (additive) stress caused by the live storage per se, perhaps initiated by high fish densities. The water quality in the live storage tank, on the other hand, can be considered adequate (see above), and it can therefore be regarded as a less likely stressor in the current context. Interestingly, the plasma cortisol levels for the haddock were lower than for the cod, which indicates that the haddock were less stressed than the cod after capture. Possible explanations for this could be biological differences between the species in their response to stress, the considerably lower fish density for the haddock in the live storage tank, the differences in the fishing depths between these two species (70 vs. 300 m, just the cod from Trial nos. 1, 2 and 3 were assessed for blood chemistry, initial muscle pH, muscle twitch ability and length of time to the onset of rigor). Moreover, pronounced differences in the haematocrit levels were observed between the cod (33-36 %) and haddock (21-24 %). Although the stress response in fish has been studied extensively (Wendeleaar Bonga, 1997), little information is available on gadoid, and especially haddock (Afonso et al., 2008).

523 Our plasma cortisol (62 ng mL-1) and haematocrit (33%) values for cod caught at a depth of about 300
524 m and sampled at 0 h is comparable to what Brown et al. (2010) found for crowded, commercially
525 reared Atlantic cod (plasma cortisol 15-62 ng mL-1 and haematocrit 26-33 %). Hemre et al. (1991)
526 found an increase in plasma cortisol of <15 ng mL-1 after the handling of Atlantic cod, while a
527 simulated high-density transport of the same species resulted in elevated levels of plasma cortisol
528 (ranging 10.5-199.7 ng mL-1) and glucose (ranging 4.9-12 mM) (Staurnes et al., 1994). Rested cod
529 (anaesthetised using metomidate) showed mean cortisol and haematocrit levels of 18.9 ng mL-1 and
530 31.5 %, respectively. When the fish were chased continuously for 30-130 min, the corresponding
531 values were 127.8 ng mL-1 and 29.3 % (Erikson et al., 2011). Hence, the cortisol values of cod and
532 haddock measured at 0 h indicated pre-peak levels or a modest stress response.

533 Similarly, the glucose levels of both species were at their lowest just after landing, 4.7 (cod) and 3.9
534 (haddock) mmol L-1. The highest values were reached after 3 and 6 h of live storage for cod (10.2
535 mmol L-1) and haddock (8.7 mmol L-1), respectively. In comparison, the maximum blood glucose
536 values in cod after a stress incident have been reported to be reached after 0.5-4 h (Hemre et al., 1991;
537 van Ham et al., 2003; Olsen et al., 2008; Brown et al., 2010), indicating our values at 0 h actually
538 represented pre-peak levels.

539 Moderate variations were observed in the blood-pH for both cod (pH 7.21-7.37) and haddock (pH
540 7.26-7.53). In comparison, the blood pH in rested cod, as measured just after rapid sampling, has been
541 reported as pH 7.69 ± 0.02 (Hultmann et al., 2012), whereas in cod chased for 30-130 min, the mean
542 value was pH 7.28 (Erikson et al., 2011). For haul durations of < 5 h, Olsen et al. (2013) reported a
543 mean pH of 7.20 just after the trawl capture of cod, whereas after live storage for 3 and 6 h the blood
544 pH increased significantly to 7.36 and 7.50, respectively.

545 Just after capture (0 h), the whole blood lactate concentrations for cod and haddock were 3.4 and 3.7
546 mmol L-1, respectively. For both species, a progressive increase during live storage was observed,
547 ending up at 9.6 (cod) and 9.1 mmol L-1 (haddock) after 6 h. In rested farmed cod, typical blood
548 lactate values are <0.5 mmol L-1, whereas crowding in cages for 20-120 min resulted in blood lactate

549 levels of between 2 and 4 mmol L-1 (Brown et al., 2008). Olsen et al. (2013) reported mean lactate
550 values of 3.49 to 5.22 mmol L-1 just after capture, depending on the haul duration <5 to >6h). After 6
551 h of live storage the values ranged from 6.36 to 6.79 mmol L-1. Taken together, our fish seemed to be
552 very stressed after 6 h.

553

554 Immediately after the trawl gear had been hauled onto deck, the mean initial muscle pH values were
555 7.11 (cod) and 6.93 (haddock). The pH values did not change during the subsequent live storage for 6
556 h ($p>0.05$). In comparison, the typical muscle pH in rested cod is pH 7.57 and after chasing for 30-130
557 min the muscle pH reduced to pH 7.09 (Erikson et al., 2011). Since the muscle pH changes rapidly in
558 response to stress, we can conclude that the fish were severely stressed by their capture and they did
559 not recover throughout the entire period they were kept in the live storage tank ($p>0.05$). At best, a
560 slight tendency towards recovery can be observed. In contrast, Olsen et al. (2013) showed that their
561 cod did recover after capture, probably due to the larger haul sizes and longer haul durations compared
562 to those our fish were subjected to. Their mean initial pH values after capture were pH 6.95-7.01, and
563 after live storage for 6 h the fish had partly recovered, as the values then were pH 7.11-7.32. The pH
564 of the dead fish was pH 7.05 (cod) and pH 6.80 (haddock), as measured after 5.5 and 4.5 h,
565 respectively. The muscle pH during live storage tended to increase as the size of the haul decreased.
566 Similar effects were found by Olsen et al. (2013) in their study.

567

568 The twitch ability of the white muscle confirmed the initial pH values as the twitch scores (1.6-2.6) for
569 both species were no different except for the dead fish, where their twitch ability had practically
570 ceased altogether. The twitch scores of anaesthetised fish are 3.0 ± 0, and scores of 2.6 ± 0.5 have
571 been measured in stressed fish (Erikson et al., 2011).

572

573 It is well known that the length of time to the onset of rigor is longer for rested fish than for exhausted
574 ones (see Robb, 2001). In the present study, rigor started a little earlier for the cod (5-8 h) compared to
575 the haddock (8-11 h). All the same, the results show that there was ample time for on-board processing
576 before the onset of rigor mortis. As the initial pH, a measure of the depletion of energy in the muscle,
577 is directly linked to the onset of rigor, it could be expected that in haddock it should have occurred
578 somewhat earlier than for cod. However, these results are in line with Digre et al. (2010). They
579 observed that trawl-caught haddock entered rigor a little later than cod even if the initial pH was lower
580 in haddock (Digre et al., 2010). A plausible explanation for this opposite trend might be explained by
581 differences between species. Misimi et al. (2008) reported that the length of time to the onset of rigor
582 for unstressed and stressed Atlantic cod was about 6 and 12 h, respectively.

583

584 The blood glucose, blood lactate, blood pH and muscle pH levels observed in this study are close to
585 those reported previously for wild cod caught by trawl and longlining (Olsen et al., 2008; 2013; Digre
586 et al., 2010; Roth and Rotabakk, 2012). During stress and muscle activity prior to slaughter, white
587 muscle is predominantly used and large amounts of lactic acid in the muscle are produced. Together
588 with H+ from ATP degradation this results in a low initial white muscle pH and the muscle cells go
589 into rigor. The development of rigor starts in parts of the fish and progressively includes the whole
590 fish.

591 The plasma cortisol, blood glucose and blood lactate increased significantly during live storage for
592 both the cod and haddock compared to the fish slaughtered immediately after landing on board (0h).
593 These results are in line with Olsen et al. (2013), who found an increase in blood glucose and blood
594 lactate values for wild-caught Atlantic cod during live storage of up to 6 h. The blood pH and muscle
595 pH for haddock increased significantly after live storage for 3 h, indicating that the fish had started to
596 recover. This trend was not observed for cod. The main difference between the trials on haddock and
597 cod was the fish density during live storage in water-filled tanks, 87 kg m^{-3} vs. 119-411 kg m^{-3} for the
598 haddock and cod, respectively.

In summary, our stress assessment based on blood chemistry showed that the fish were stressed, but due to the short haul durations we were unable to distinguish between capture stress and a possible additional stress effect caused by live storage. However, the muscle biochemistry unequivocally revealed that the fish were in fact severely stressed by their capture and they hardly recovered during the entire live storage period.

4.4 Blood spots and discolouration of fillets

For both the cod and haddock the frequency of the discolouration of their loins and bellies, as well as for their fillets, the blood spots were low and unaffected by live storage (Table 5). Each fillet generally had a few veins filled with blood. Therefore, even though the fish were stressed by their capture, the fillet colour characteristics were still good. Furthermore, under the experimental conditions of the present study, live storage as a concept for improving fillet colour characteristics would be a superfluous processing step. The commercial processing of fish that have been dead for 4.4-5.5 h, produce marginally inferior fillets. Olsen et al. (2013), on the other hand, who compared live storage with bleeding immediately after capture, reported that live storage for 3 h increased muscle discolouration significantly. After 6 h, however, most of the red discolouration was gone and the fillets became considerably lighter. Compared with our results just after capture, their scores for the discolouration of loins and bellies, and bruise/blood spot parameters were higher than ours. However, our total scores were higher as we included an extra parameter, a 'residual blood in veins' score of 1-4 vs. 0-2. One explanation for our lower scores could be the considerably longer haul durations and the bigger haul sizes in the study by Olsen et al. (2013). On the other hand, our fish were just as stressed as their fish, as determined just after landing. Another difference between the two studies was that our fillets were evaluated fresh the day after capture, while Olsen et al. (2013) evaluated their fillets after frozen storage.

In practice, our data suggest that live fish can be withdrawn continuously for bleeding and processing during the interval of 0-6 h post-capture, as there were no significant differences between live storages from 0 to 6 h. Similar effects were found for the haddock. However, there was a trend that the cod stored live for 6 h had a lower total score than after 1.5 and 3 h of live storage, but the differences were not significant. The commercially produced cod and haddock had higher scores than the live-stored fish or fish processed immediately after capture, which is in accordance with Olsen et al. (2013).

4.5 Loin colour

With regard to the colour of the cod loins (Figure 5), the effects of live storage were that their lightness decreased after 6 h, their whiteness and yellowness were unaffected, their redness and chroma increased with storage time, and their hue angle decreased (towards a more reddish tint). Therefore, compared with immediate bleeding after capture, live storage had a predominantly inferior effect on loin colour as the optimal colour of cod in the market is shiny white with no discolourations such as a reddish tint.

Dead cod processed after 5.5 h had a similar, or better (lightness), loin colour compared to fish stored live for 6 h ($p>0.05$). However, the differences in colour were small and it is questionable whether in practice they are of importance for fish processors or consumers.

In terms of haddock (Figure 6), live storage led to a decrease in loin whiteness after 6 h, whereas their redness, yellowness, hue and chroma were unaffected by live storage. The consequence of delaying processing by 4.5 h (dead fish) were darker and less white loins, more redness, a lower hue (a more reddish tint) and a tendency for higher chroma, whereas their yellowness was unaffected. Therefore, it seems that the effect of delayed processing (bleeding) was somewhat more severe for the haddock than for the cod. Moreover, the haddock could be processed with similar results throughout the live storage period (0 to 6 h).

5. Conclusions

The fish behaviour analysis performed during live storage showed that there were more signs of stress and the condition of the fish caught at greater depths was inferior to those caught in shallower waters. The survival rate varied between the different trials (48.9 to 92.5 %), and was likely impacted by the fishing depth. The blood chemistry data showed that the captured fish were somewhat stressed. However, we were not able to clarify whether the fish were becoming gradually more stressed during the subsequent live storage, or whether the observed increase, or lack of recovery, regarding the blood chemistry parameters were in fact a result of a delayed response to the various stress parameters. In terms of muscle biochemistry, our data showed that the fish were stressed by capture. Moreover, the fish did not recover during 6 h of live storage.

The occurrence of blood spots and discolouration was low in the fillets cut from both species of fish just after capture. Subsequent live storage did not change this result. The colour characteristics of the fillets cut from dead fish after 4.5-5.5 h were only marginally inferior to those from all the other treatments. The live storage of cod led to a slight reddish tint in their loins, whereas the haddock's loin colour was largely unaffected by live storage. The loin colour of the cod stored live for 6 h was similar to that of the dead fish (5.5 h post-capture), whereas the loin colour of the dead haddock (4.5 h post-capture) was somewhat inferior to the cases where the fish were processed just after killing.

Under the prevailing fishing and processing conditions we cannot unambiguously recommend live storage as a concept to improve the fillet colour characteristics of fish caught by trawl. The factors that suggested avoiding live storage were delayed mortality, questionable animal welfare and no recovery from stress. On the other hand, the colour characteristics of fillets from surviving fish can be maintained (similar to those just after capture). To justify this alternative, the colour of these fillets should be clearly superior to those cut from the remaining dead fish from the storage bin (not yet processed by the fishermen).

675

676

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Figures:

Figure 1 – The live holding tank designed and built by Melbu Systems AS (Melbu, Norway). Dimensions in mm.

Figure 2 – The CIE L*a*b* colour parameters of the Atlantic cod and haddock loins were determined just after capture (0 h), after live storage for 1.5, 3 and 6 h, as well as in the fillet loins cut from dead fish kept in a bin without water (commercial processing) for 4.5 h (haddock) and 5.5 h (cod). Colour analysis was done by machine vision, where the green rectangle corresponds to the chosen loin region of interest.

Figure 3 – Different fish behaviour measurements of cod (Trial nos. 1, 2 , 3 and 5) and haddock (Trial no. 4) during live storage; a) proportions of fish with their heads above the water surface; b) proportion of fish gaping; c) activity, number of fish crossing a fixed point/minute; d) proportion of disbalanced fish visible; e) number of gill movements/minute; f) proportion of fish with flared gills; g) proportion of fish with pectoral movements; h) number of gapes per fish per minute.

Figure 4 – a) Stress Indicator Model 1; b) Stress Indicator Model 2; c) Stress Indicator Model 2 without activity. In order to summarise the behavioural stress response from all the variables in a single value a simple model was created called the Stress Indicator Model.

Figure 5 – Loin colour of cod stored live for 0, 1.5, 3 and 6 h, or collected dead from a bin without water (commercial processing) 5.5 h post-capture. The different letters (a, b or c) represent significant differences between the treatments ($p < 0.05$, mean ± SEM, n=22-46). The X represents a significant

877 difference between the hauls during the treatment. Each treatment consisted of fish from different
878 hauls.

879

880 Figure 6 – Loin colour of haddock stored live for 0, 1.5, 3 and 6 h, or collected dead from a bin
881 without water (commercial processing) 4.5 h post-capture. The different letters (a, b or c) represent
882 significant differences between the treatments ($p < 0.05$, mean ± SEM, n=11-12). The X represents a
883 significant difference between the hauls during the treatment. Each treatment consisted of fish from
884 different hauls.

885

886 Figure 7 – The picture illustrates the largest observed colour difference between the two treatments in
887 the present study. Fish #1513 represents a haddock stored live for 1.5 h, whereas Fish #1538
888 represents a haddock collected dead 4.5 h post-capture from a bin without water.

Table 1

Table 1 - Catching data, fishing conditions and catch amount for the sampled fish from 6 different hauls. Trial no 5 consisted of cod from haul no 27 and 29, and were only used for survival and fish behavior studies.

Trial No.	*Haul no.*	*Species*	*Date, March 2014*	*Towing time (min)*	*Total catch (kg)*	*Position start*	*Position finish*	*Fishing depth (m)*	*Wind (m/s)*	*Sea temp (^{o}C)*
1	2	Cod	08	15	2553	71° 14.80' N / 24°13.43' E	71° 14.85' N / 24°20.63' E	316-333	7-8	5.7
2	9	Cod	10	13	4410	71° 16.91' N / 26°53.33' E	71° 16.88' N / 26°50.79' E	279-281	13	5.4
3	16	Cod	11	16	1423	71° 16.64' N / 26°23.76' E	71° 16.93' N / 26°20.80' E	285-287	11-13	5.1
4	25	Haddock	13	23	9000	70° 28.50' N / 30°58.08' E	70° 29.32' N / 30°55.14' E	63-70	8-10	4.1
5	27	Cod	13	25	500	70° 28.82' N / 30°57.63' E	70° 29.77' N / 30°53.92' E	65-74	11-12	4.3
	29	Cod	14	55	1300	70° 32.35' N / 30°46.46' E	70° 31.57' N / 30°46.99' E	63-77	15-18	4.4

Table 2

Table 2 - Variables measured during video analysis of fish behaviour during short term holding of fish on board a trawl vessel.

Indicator	*Measurements*
Activity	Proportion of fish crossing a fixed point per minute
Balance	Proportion of fish with pectoral movements
	Proportion of fish that lost balance
Respiration	Number of gill movements per minute
Respiratory stress	Proportion of fish gaping
	Proportion of fish with head above the water surface
	Proportion of fish with flared gills

Table 3

Table 3 – Overview of the different trials including species, fish survival rate after live storage for 24-29 hours for Trial no. 1-3, 6-7 hours for Trial no. 4 and 8-22 hours for Trial no. 5, fish density and water quality (dissolved oxygen (DO), water temperature and pH). Different letters (A-D) represent significant differences between the treatments regarding survival rate ($p < 0.05$).

Trial No.	*Fish*			*Water Quality*		
	Species	*Survival rate (%)*	*Fish density (kg/m^3)*	*DO%*	*Temp ^oC*	*pH*
1	Cod	58.9^{AB}	118.6	99-113	5.2-6.1	8.1
2	Cod	48.9^{A}	405.2	76-120	5.2-5.6	8.0
3	Cod	68.1^{BC}	410.6	46*-107	4.2-5.0	8.0
4	Haddock	92.5^{D}	87.1	104-116	4.1-4.3	8.1
5	Cod	77.3^{C}	548.1	67-117	4.1-4.4	8.0

*46-60% in a period of 2 hours

Table 4

Table 4 – Blood chemistry (plasma cortisol, whole blood pH, blood glucose, blood lactate and haematocrit) and white muscle biochemistry (initial muscle pH and muscle twitch ability) of live stored cod and haddock (0, 1.5, 3 and 6 hours). Additionally, time to rigor onset was measured. Muscle pH, muscle twitch ability and rigor onset were also measured for fish that had been stored in holding bins without water for 4.5 h (haddock) and 5.5 h (cod).

Live storage (h)	*Blood*					*Muscle*		
	Cortisol (ng ml L^{-1})	*Blood pH*	*Glucose (mmol L^{-1})*	*Lactate (mmol L^{-1})*	*Hct (%)*	*Initial pH*	*Twitch ability (Score 0-3)*	*Rigor onset (h)*
				Cod (n=19-55)				
0 h	62.6 ± 6.1^{A}	7.29 ± 0.04^{AB}	4.72 ± 0.34^{C}	3.41 ± 0.20^{C}	32.88 ± 0.71^{B}	7.11 ± 0.03^{ABX}	2.1 ± 0.1^{AX}	< 8.0 h
1.5 h	102.7 ± 7.6^{B}	7.21 ± 0.04^{B}	7.27 ± 0.67^{B}	6.18 ± 0.35^{BX}	36.32 ± 0.85^{A}	7.18 ± 0.04^{ABX}	1.6 ± 0.2^{A}	< 6.0 h
3 h	123.3 ± 7.9^{B}	7.30 ± 0.03^{AB}	10.15 ± 0.74^{A}	8.46 ± 0.35^{A}	35.59 ± 0.76^{AB}	7.20 ± 0.04^{AX}	1.8 ± 0.2^{A}	< 5.0 h
6 h	125.4 ± 10.0^{BX}	7.37 ± 0.04^{A}	9.56 ± 0.63^{ABX}	9.64 ± 0.74^{A}	32.70 ± 1.26^{B}	7.20 ± 0.04^{AB}	2.1 ± 0.2^{A}	< 5.0 h
Dead 5.5h	n.a.	n.a.	n.a.	n.a.	n.a.	7.05 ± 0.03^{BX}	0.1 ± 0.0^{B}	< 5.0 h
p-value	*0.000*	*0.028*	*0.000*	*0.000*	*0.007*	*0.008*	*0.000*	
				Haddock (7-12)				
0 h	15.4 ± 4.2^{A}	7.26 ± 0.04^{B}	3.91 ± 0.31^{C}	3.66 ± 0.40^{C}	24.38 ± 1.24^{ns}	6.93 ± 0.03^{BC}	2.6 ± 0.2^{A}	9.5 h
1.5 h	26.7 ± 4.4^{AB}	7.37 ± 0.07^{AB}	5.21 ± 0.46^{BC}	4.80 ± 0.53^{BC}	22.14 ± 1.22^{ns}	6.96 ± 0.04^{AB}	2.0 ± 0.3^{A}	10.5 h
3 h	32.5 ± 7.6^{AB}	7.53 ± 0.04^{A}	6.63 ± 0.53^{B}	7.15 ± 0.65^{AB}	21.57 ± 1.27^{ns}	7.10 ± 0.04^{A}	2.2 ± 0.2^{A}	> 10.5h
6 h	41.0 ± 2.3^{B}	7.44 ± 0.04^{AB}	8.66 ± 0.49^{A}	9.12 ± 1.31^{A}	21.43 ± 0.97^{ns}	7.00 ± 0.03^{AB}	2.1 ± 0.3^{A}	> 7.5 h
Dead 4.5h	n.a.	n.a.	n.a.	n.a.	n.a.	6.80 ± 0.03^{C}	0.0 ± 0.0^{B}	5.5 h
p-value	*0.004*	*0.003*	*0.000*	*0.000*	*n.s.*	*0.000*	*0.000*	

Different letters (A, B or C) represent significant differences between the treatments ($p < 0.05$, mean ± SEM). X represent significant difference between hauls within the treatment. Each treatment consisted of fish from different hauls. n.a. = not analyzed; n.s. = not significant.

R1_Table 5

Table 5 – Visual assessments of cod and haddock fillet colour characteristics from fish stored live for 0, 1.5, 3 and 6 h and fish that stored in a bin without water for 4.5 h (haddock) or 5.5 h (cod).

Live storage (h)	*Discolouration loin (0-2)*	*Discolouration belly (0-2)*	*Residual blood in veins (1-4)*	*Blood spots (0-2)*	*Total scores (FQI*) (1-10)*
Cod (n = 26 – 44)					
0 h	0.0 ± 0.0 ^{B}	0.5 ± 0.1 ^{B}	2.5 ± 0.1	0.3 ± 0.1	3.4 ± 0.2 ^{B}
1.5 h	0.1 ± 0.1 ^{AB}	0.7 ± 0.1 ^{AB}	2.7 ± 0.1	0.2 ± 0.1	3.7 ± 0.2 ^{AB}
3 h	0.3 ± 0.1 ^{AB}	0.7 ± 0.1 ^{AB}	2.5 ± 0.1	0.1 ± 0.1	3.6 ± 0.2 ^{AB}
6 h	0.2 ± 0.1 ^{AB}	0.5 ± 0.1 ^{B}	2.4 ± 0.1	0.0 ± 0.0	3.0 ± 0.3 ^{B}
Dead 5.5h	0.3 ± 0.1 ^{A}	0.9 ± 0.1 ^{A}	2.7 ± 0.1 ^{X}	0.2 ± 0.1	4.1 ± 0.2 ^{AX}
p-value	*0,008*	*0.000*	*n.s.*	*n.s.*	*0.004*
Haddock (n = 12)					
0 h	0.0 ± 0.0	0.5 ± 0.1 ^{B}	2.3 ± 0.1	0.4 ± 0.2	3.3 ± 0.2 ^{AB}
1.5 h	0.1 ± 0.1	0.6 ± 0.1 ^{AB}	2.2 ± 0.2	0.3 ± 0.1	3.3 ± 0.3 ^{AB}
3 h	0.0 ± 0.0	0.5 ± 0.1 ^{B}	2.1 ± 0.2	0.3 ± 0.1	3.0 ± 0.3 ^{B}
6 h	0.0 ± 0.0	0.3 ± 0.1 ^{B}	2.1 ± 0.1	0.5 ± 0.2	3.0 ± 0.3 ^{B}
Dead 4.5h	0.2 ± 0.1	1.0 ± 0.1 ^{A}	2.6 ± 0.1	0.3 ± 0.2	4.1 ± 0.3 ^{A}
p-value	*n.s*	*0.000*	*n.s. (0.053)*	*n.s*	*0.037*

*Different letters (A or B) represent a significant difference between the treatments ($p < 0.05$, mean ± SEM). X represent significant difference between hauls within the treatment. For cod, each treatment consisted of fish from different hauls. n.s. = not significant. *FQI – Fillet Quality Index*

Figure 1

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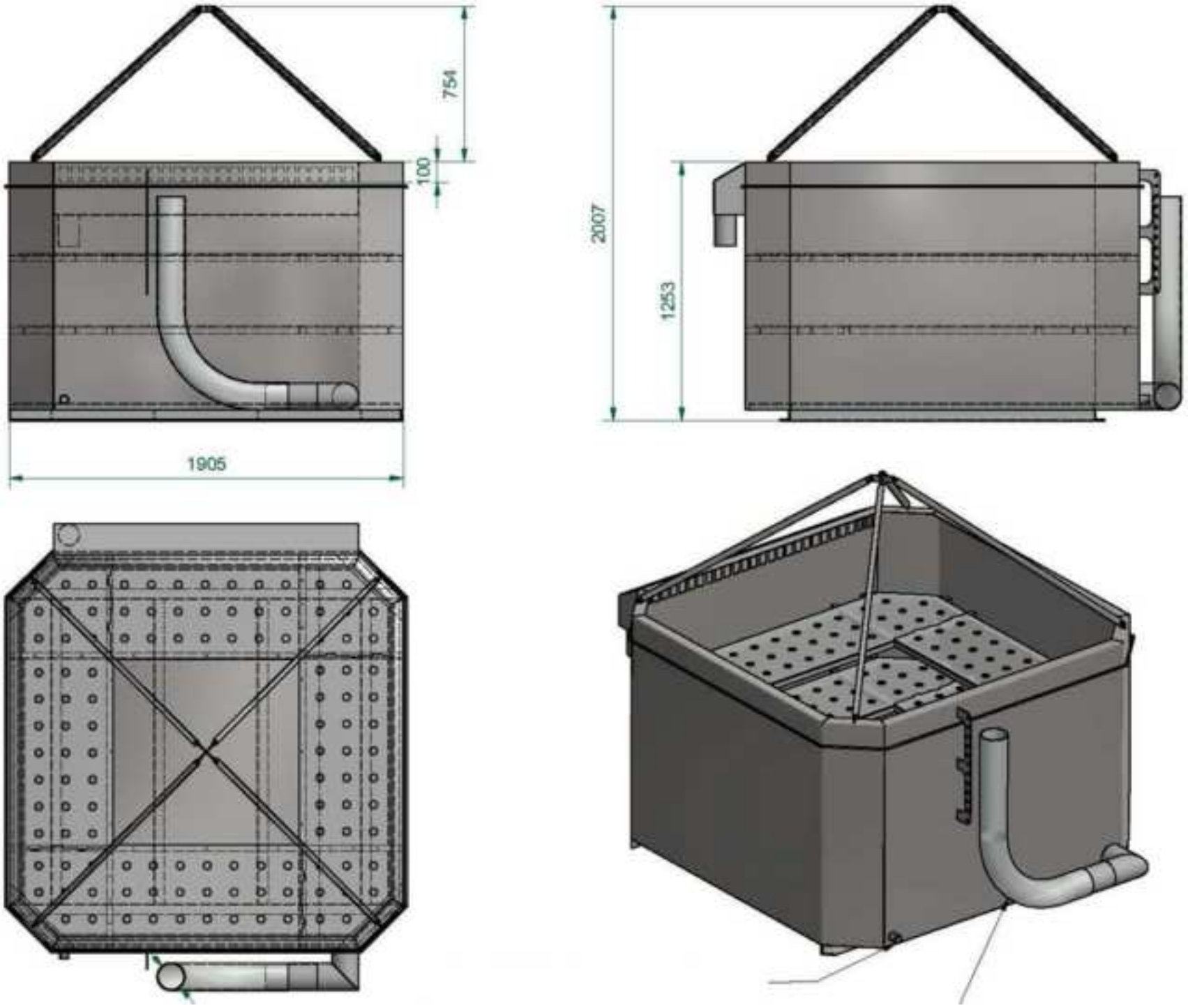

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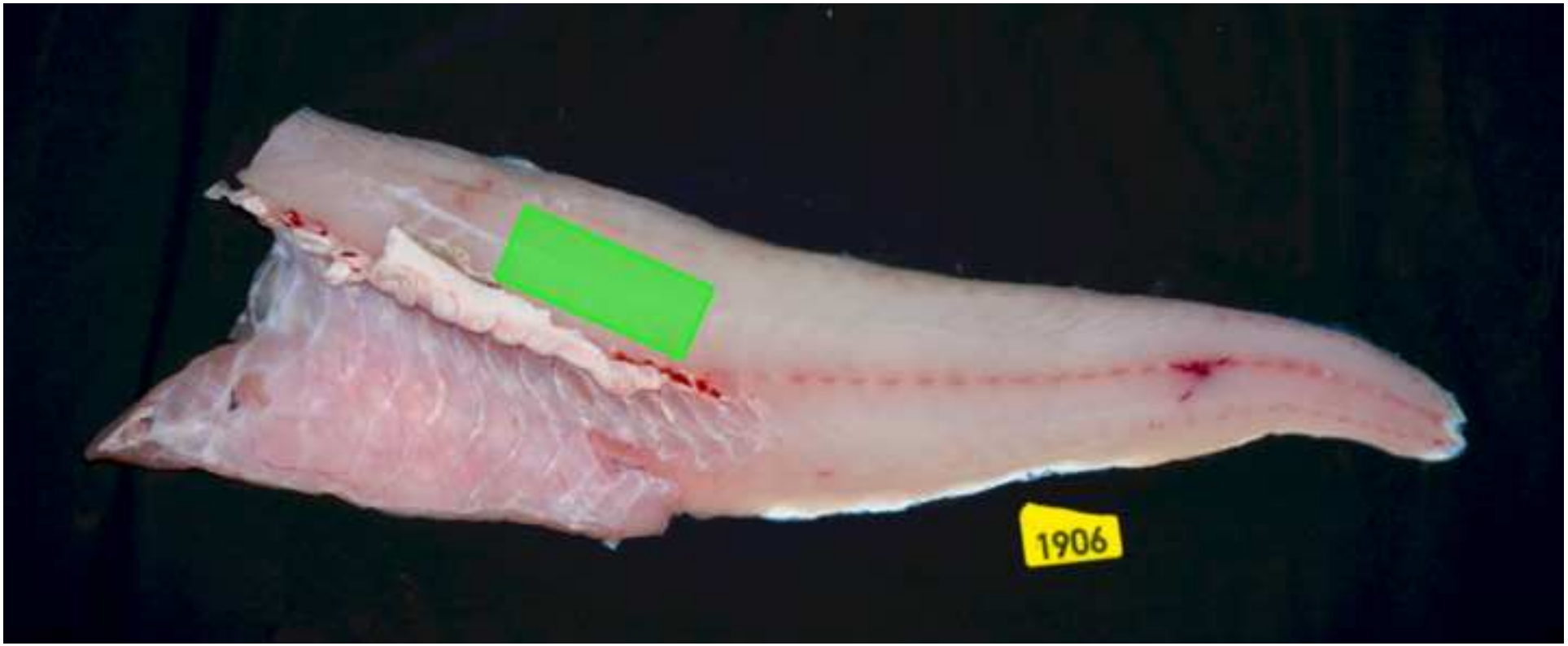

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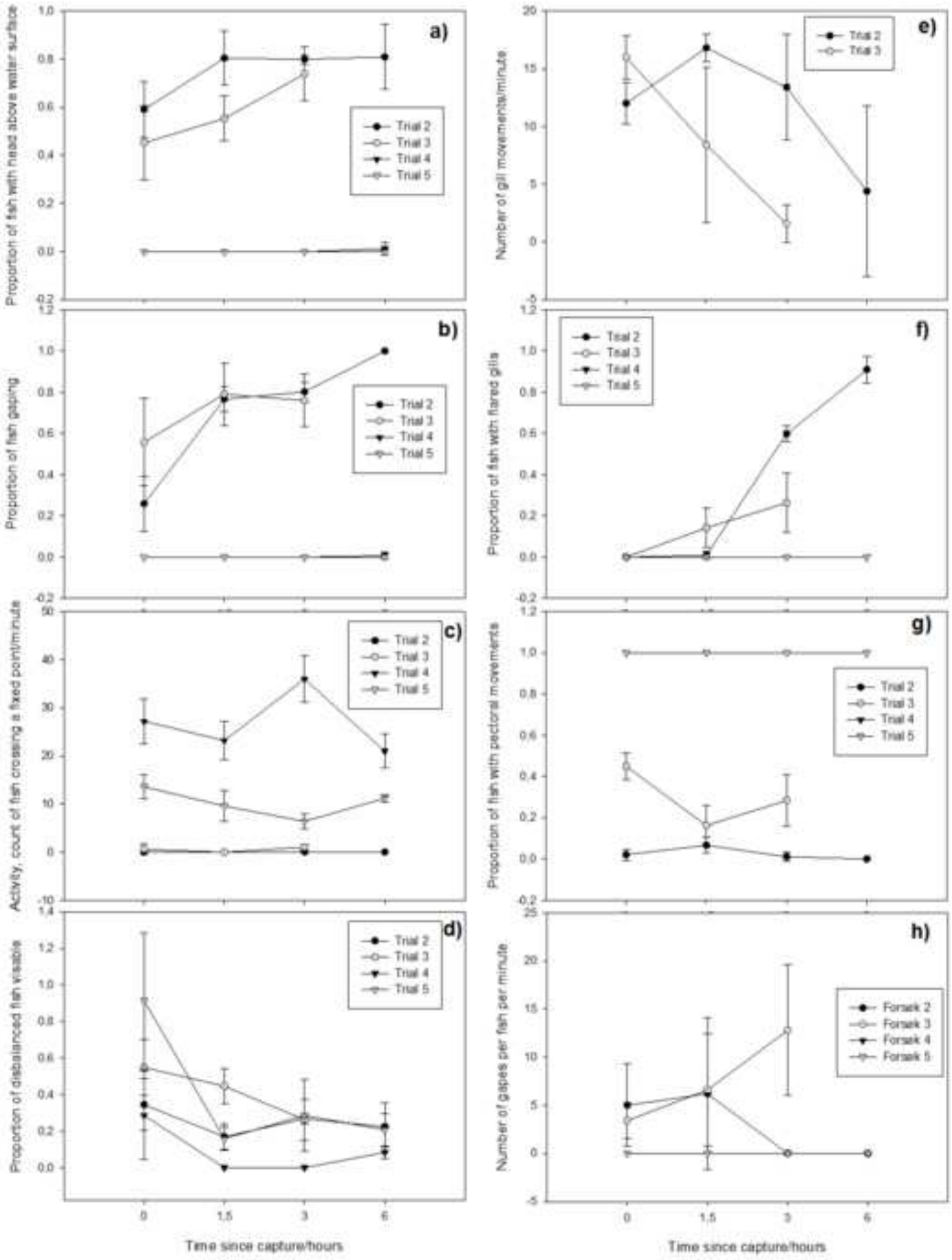

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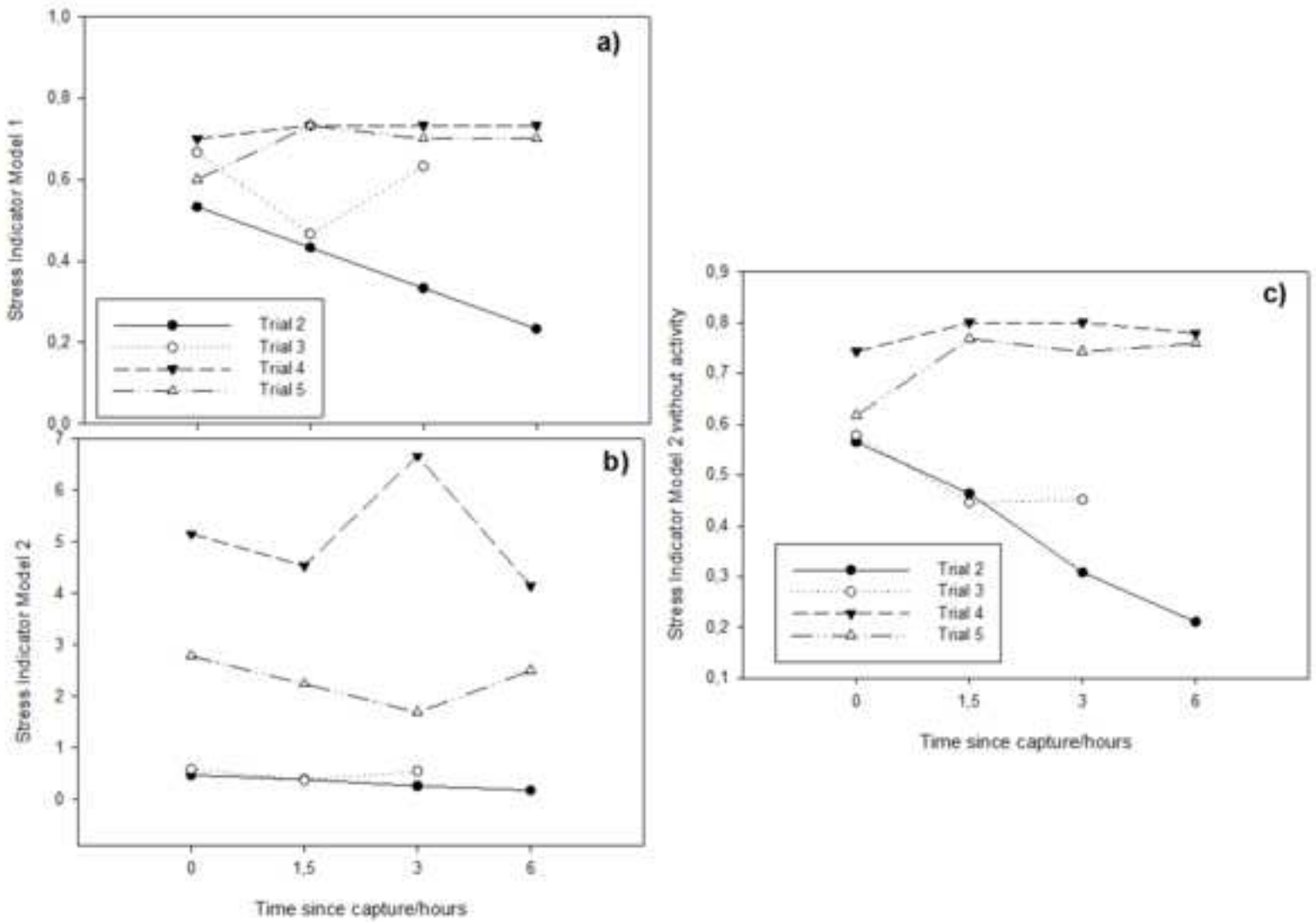

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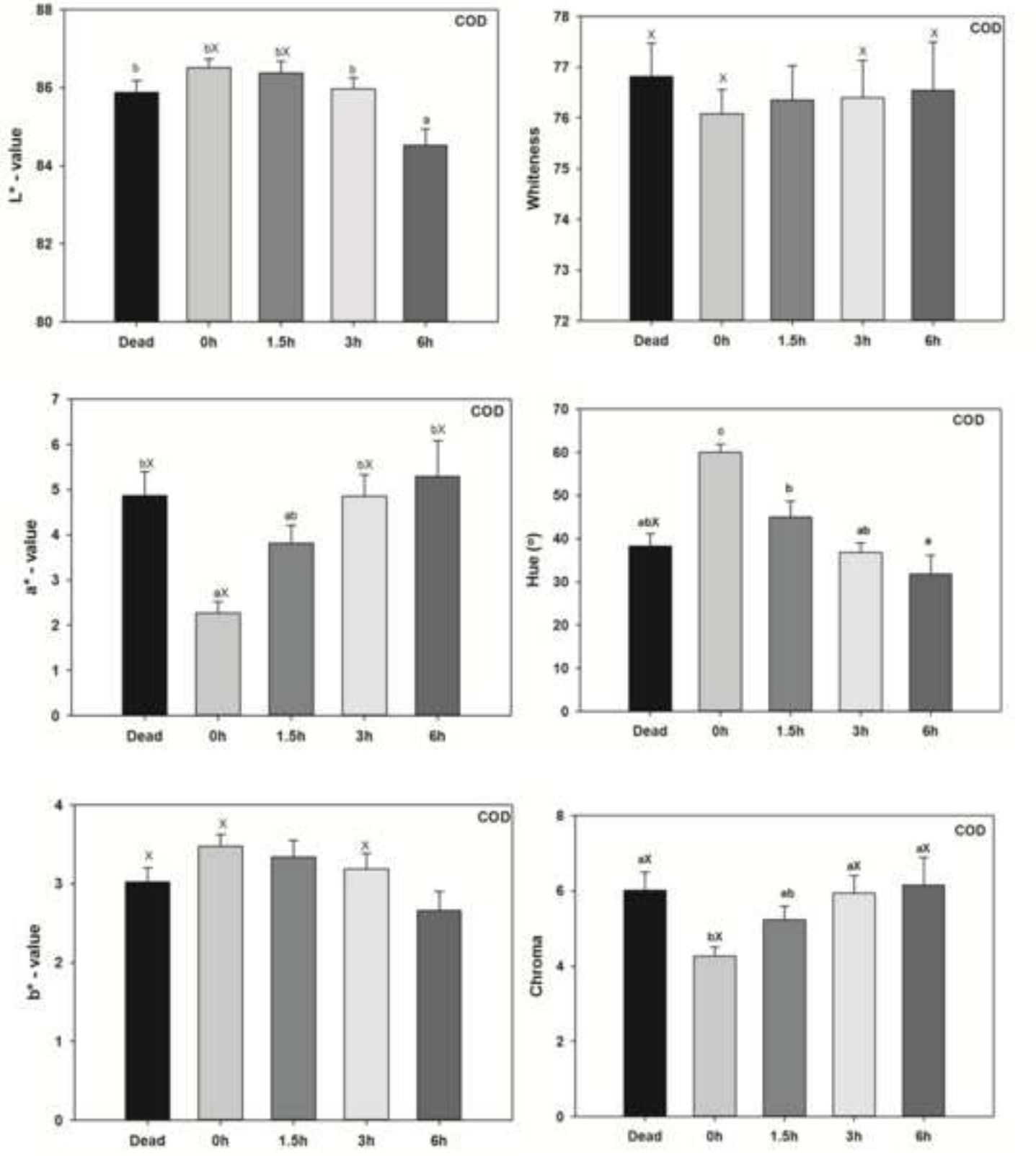

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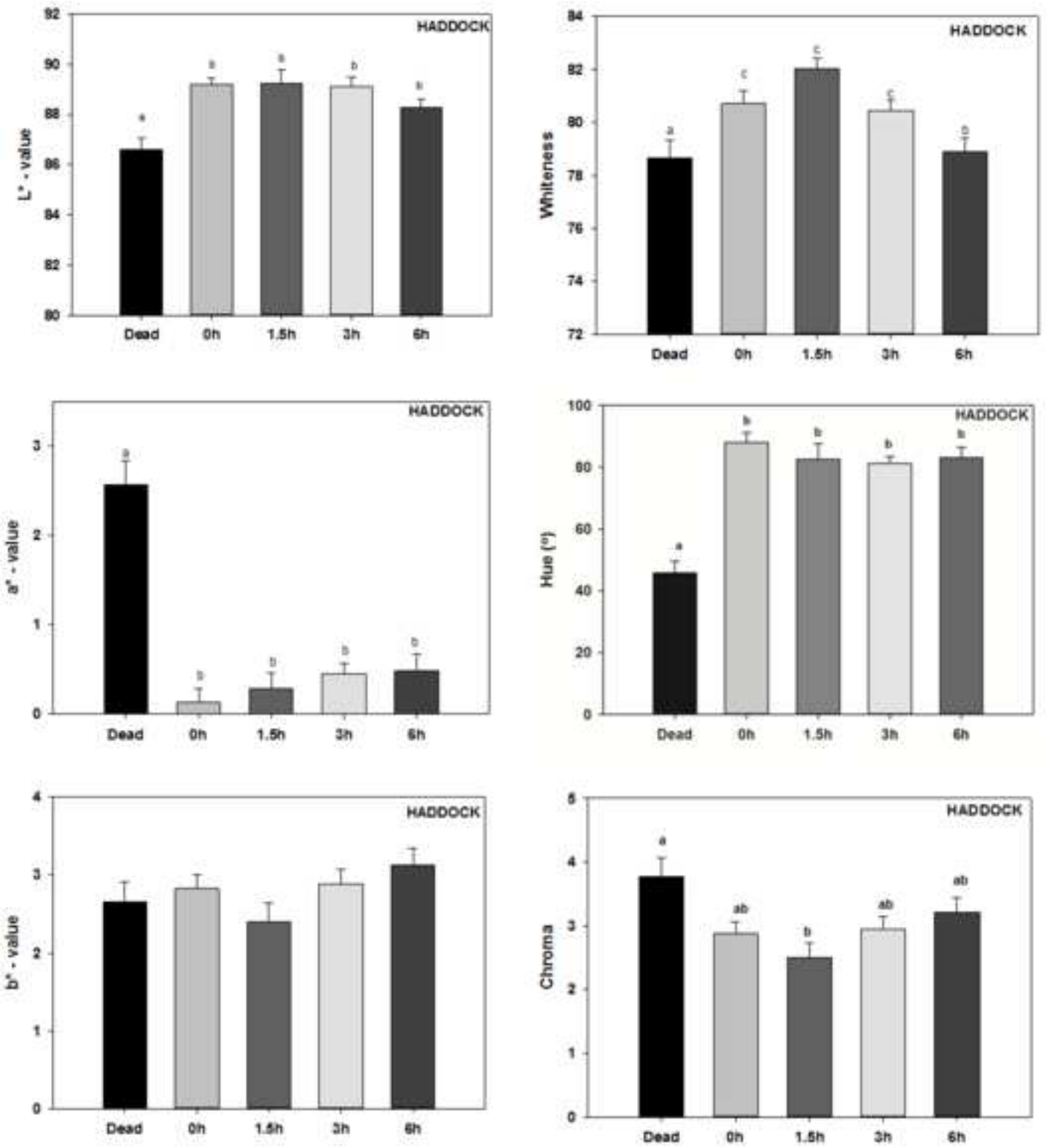

Figure 7

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