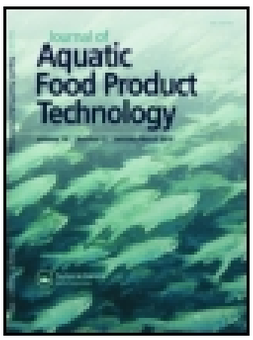

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Effects of Long-Term Feed Deprivation on the Development of *Rigor Mortis* and Aspects of Muscle Quality in Live-Stored Mature Atlantic Cod (*Gadus Morhua* L.)

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ABSTRACT

Fresh Atlantic cod is available in large amounts in Norway during the first 5 months of the year. Live-storage of cod may extend the marketing period of fresh cod products throughout the year. In addition, this concept makes *pre-rigor* processing possible. The main problem of keeping wild cod in captivity is that it does not easily accept formulated dry feed. The purpose of this study was, therefore, to investigate how long-term live-storage of mature Atlantic cod in the absence of feed (79 days) affects the onset and development of *rigor mortis*, as well as fillet quality by assessing hardness and water-holding capacity of the muscle, pH, protein, and water content. The results showed that starvation of Atlantic cod for 23 days reduces the *pre-rigor* time from 29 to 17 h. Further starvation did not decrease this period significantly, suggesting that live-stored cod deprived of feed for 79 days may still be industrially processed before the onset of *rigor mortis*. More than 51 days of starvation reduced protein concentration and increased water content of the muscle. After 51 days, the muscle texture was softer than in fish starved for a shorter period.

KEYWORDS

Atlantic cod; live-storage; feed deprivation; *rigor mortis*; muscle quality

Introduction

The migration pattern of Atlantic cod leads to limited supply of fresh cod in Norway for most of the year, and this causes marketing challenges and considerable variations in price and profit for the fish industry (Brander, 2005; Dreyer et al., 2008; Ottesen and Grønhaug, 2003). Live capture and storage of wild Atlantic cod is a promising solution for these issues. The current regulations state that live-caught fish can be stored alive in sea cages for up to 12 weeks, and during the first 4 weeks, feeding is not required (FOR-2004-12-22-1878, 2005). The main problem of keeping wild cod in captivity is that it does not easily accept formulated dry feed. It may, however, be fed more successfully using frozen pelagic species such as capelin or herring. The availability, quality, and price of such feed suggest that this may not always be a viable alternative (Sæther and Bogevik, 2017). An extended period of live-storage without feeding may be an option, if fish welfare, fillet quality, and processing possibilities are not compromised. Only a few studies have been published on how muscle quality of fish in captivity is affected during long-term storage without feeding. Einen and Thomassen (1998) studied the effects of starving farmed Atlantic salmon up to 12 weeks and found that only small changes in fillet quality occurred. Love (1988) studied several aspects of long-term starvation of Atlantic cod. He reported that the water content in muscle dramatically increased after 8 weeks of starvation and that newly captured starving fish entered *rigor mortis* very quickly after death. A considerable decrease in muscle glycogen during long-term starvation of cod has also been reported (Black and Love, 1986).

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The onset and strength of *rigor mortis* affect fillet quality by having an impact on both texture, gaping, color, shape, water-holding capacity (WHC), and drip loss of the fillets (Bjørnevik and Solbakken, 2010; Kristoffersen et al., 2006, 2007; Ofstad et al., 1996; Skjervold et al., 2001; Sørensen et al., 1997; Tobiassen et al., 2006). The state of *rigor mortis* is also important for processing of fish, since mechanical filleting can only be carried out successfully when the fish is in *pre-* or *post-rigor* condition (Huss, 1995; Love, 1988; Stroud, 1969). It is well-known that *antemortem* stress and activity will reduce the time before the onset of *rigor mortis*, making *pre-rigor* processing difficult (Kristoffersen et al., 2006; Misimi et al., 2008; Roth et al., 2012). Wild-caught cod are commonly in or entering *rigor mortis* when delivered fresh at land-based processing facilities. Such cod have to be stored for 2–4 days to await *rigor mortis* resolution before filleting. This storage will reduce freshness and shelf life of fresh fillet products in retail (Tobiassen et al., 2006). The nonstressful slaughter of fish, including live-stored cod in sea cages, will, however, provide a long enough *pre-rigor* period to process the fish in nearby facilities before entering *rigor mortis*. It has been shown that the onset of *rigor mortis* is closely linked to depletion of adenosine triphosphate and glycogen, i.e., the *post-mortem* energy status in muscle (Cappeln and Jessen, 2002; Love, 1988; Mørkøre et al., 2008).

The purpose of this study was, therefore, to investigate how long-term live-storage of wild mature Atlantic cod in the absence of feed affects the onset and development of *rigor mortis*, as well as fillet quality by assessing hardness and WHC of the muscle, pH, protein, and water content.

Materials and methods

Fish and sampling

Atlantic cod were caught using Danish seine in March 2015, off the coast of Andenes, Norway. The procedures of capture and handling of the fish and veterinary approval are described by Ageeva et al. (2017). Two days after catch, 10 fish in the sea cage at Bjarkøy were slaughtered. After transport of the live cod to the onshore site at Kraknes, the fish were tagged and placed in two indoor tanks (volume 20,000 L each), as described in the previous article. Ten fish were also slaughtered on days 23, 51, and 79 days after capture by randomly collecting five fish from each tank. The fish were not fed during this live-storage. At slaughter, the fish were stunned by a blow to the head, identified by their tag numbers, and then total weight, length, muscle pH, lactate, and glucose in the blood were measured (Table 1). The fish were then exsanguinated by cutting the ventral and dorsal aorta, followed by bleeding for 30 min in a separate container (600 L) with running seawater (~5°C). During gutting, the weights of gonads, liver, and gutted fish (head-on) were determined. The fish were then gently packed belly down in plastic boxes with ice (8–10 kg ice per 16–18 kg fish) and transported to Nofima, Tromsø (~35 min by car). There, they were stored in a cold room (0–1°C), and the development of *rigor mortis* and muscle pH were monitored for 5 days. *Rigor mortis* and muscle pH development was also monitored in the fish slaughtered 2 days after catch. All fish were hand-filleted 7 days *postmortem*. The left loin (200 g) was used for determination of WHC and water content, while the right loin was wrapped in plastic and frozen at −30°C until protein analysis.

Blood analyses

Blood samples were collected from the heart through an incision in the pericardium immediately after stunning, and whole blood lactate and glucose were determined within 1.5 min. The analyses were performed using handheld digital meters: Lactate Scout+ (SensLab GmbH, Leipzig, Germany) and FreeStyle Lite (Abbot Diabetes Care Inc., Alameda, CA, USA), respectively. When lactate concentration was below detection limit (0.5 mmol L^{-1}), the observations were registered as 0.25 mmol L^{-1}. Calibration of both meters and the blood analysis were carried out according to manufacturers' guidelines.

Table 1. Biological data, muscle pH, blood glucose and lactate of experimental fish at slaughter on days 2, 23, 51 and 79 after capture.

	Feed deprivation			
	2 days (5♀, 5♂)	23 days (3♀, 7♂)	51 days (4♀, 6♂)	79 days (3♀, 7♂)
Body length (cm)	84.2 ± 2.5	87.8 ± 2.1	92.0 ± 2.9	87.3 ± 2.1
Total weight (g)	5201 ± 407	5499 ± 479	5387 ± 443	4704 ± 283
Range	3140 – 6780	3038 – 8340	3168 – 7546	2818 – 5798
Gutted weight (g)	3959 ± 303	4338 ± 353	4743 ± 380	4195 ± 246
Range	2530 – 5360	2678 – 6512	2810 – 6548	2560 – 5182
HSI	5.12 ± 0.58	3.97 ± 0.39	4.96 ± 0.54	3.19 ± 0.5
Range	1.29 – 8.38	2.17 – 5.47	2.11 – 7.47	0.93 – 5.32
GSI	10.81 ± 1.22^{a}	7.38 ± 1.36^{a}	1.45 ± 0.25^{b}	1.14 ± 0.14^{b}
Range	1.8 – 14.9	1.51 – 11.89	0.74 – 3.16	0.49 – 1.70
Glucose (mmol L^{-1})	5.25 ± 0.79^{a}	3.41 ± 0.38^{b}	3.11 ± 0.29^{b}	2.68 ± 0.20^{b}
Lactate (mmol L^{-1})	0.90 ± 0.29^{a}	0.25 ± 0.00^{b}	0.53 ± 0.10^{ab}	0.25 ± 0.00^{b}
Initial muscle pH	7.62 ± 0.08	7.59 ± 0.07	7.74 ± 0.06	7.55 ± 0.03

The data are represented as mean ± SE of mean.
HSI (Hepatosomatic index) = (liver weight/total weight) × 100.
GSI (Gonadosomatic index) = (gonad weight/total weight) × 100.
Different lowercase letters indicate significant differences ($p < 0.05$) between sampling days.

Rigor mortis *and muscle pH*

The development of *rigor mortis* was assessed by measuring compression force (CF [g]) during the first 5 days after slaughter using a digital force gauge SAUTER FK 250 (SAUTER GmbH, Albstadt, Germany) modified with a flat-ended, circular piston (diameter 11 mm) placed 5 mm under a ring-shaped stopper. The compression test was performed by pressing the piston vertically into the fish muscle until the ring-shaped stopper touched the skin, and the CF applied, which indicates the level of muscle hardness, was recorded. The first measurement was within 30 min after stunning each fish and subsequently during ice storage at time intervals 4, 6, 10, 14, 24, 36, 48, 60, 72, 90, and 120 h *postmortem*. To ensure minimal fish handling during *rigor* development, CF was determined without removing the iced fish from the boxes. The first measurement was performed on the left side on each fish about 6 cm behind the gill arch and 1 cm above the lateral line. The subsequent measurements were carried out about 0.5 cm behind the previous one. For each measurement point, the recording was repeated five times, and the average values were used in the results.

Pre-rigor time for each individual fish (t_{CF100g} [h]) was determined as the time when CF (muscle hardness) was equal to 100 g, using linear interpolation between the values closest to 100 g. The time before maximum *rigor* (t_{CFmax} [h]) was the time elapsed when maximum CF (CF_{max} [g]) for each individual was registered. Then, the mean values of each variable of the individuals in the batch were calculated. The rate of *rigor mortis* resolution (r_{res} [g h^{-1}]) was determined according to Li et al. (2010). Since the CF values did not approach a constant level, the *rigor* resolution was determined to be complete when the change in CF was less than ±50 g ($CF_{\pm 50g}$ [g]) from the end-point value.

Muscle pH was recorded on the right side of fish at the same time points as muscle hardness was determined. In addition, the ultimate muscle pH was determined 7 days after slaughter. The measurements were carried out through an incision in the skin, and subsequent measurements were about 0.5 cm away from the previous cut. A portable WTW 330/set-1 pH-meter (Wissenscaftliche-Technische Werkstätten GmbH, Weilheim, Germany) equipped with a Hamilton double pore glass electrode (Hamilton Bonaduz AG, Bonaduz, Switzerland) was used.

Physicochemical analysis

The loins were minced and WHC was determined as described by Herland et al. (2011). WHC was expressed as the percentage liquid loss released from the sample after centrifugation. Three replicates

(10 g) of each mince were dried at 103 ± 2°C for 16–18 h to estimate water content. Muscle protein was determined as described by Ageeva et al. (2017).

Statistical analysis

The statistical interpretation of data was carried out using SYSTAT 13 for Windows version 13.1 (Systat Software Inc., San Jose, CA, USA). The results are given as mean ± standard error of the mean (mean ± SE of mean). Analysis of variance (ANOVA) (one-way ANOVA) was used to explore the differences in calculated and measured variables between different sampling days.

Results and discussion

Quality changes during the trial

The fish were not sorted by size before the experiment; thus, a wide range of fish sizes was included in each group (Table 1). Individual tracking of changes in total weight from tagging day (day 9 after capture) to trial termination (day 79) showed a decrease in total weight by 26.9 ± 1.4% (results not shown). Furthermore, the main weight loss of 24.5 ± 2.8% occurred from tagging to day 51 post-capture and was caused by the significant reduction of gonads. There were, however, no significant changes in HSI during the starvation period (Table 1).

The concentration of blood glucose was highest in fish sampled 2 days after capture and decreased during the starvation period. The change was significantly different in fish slaughtered on subsequent sampling days (Table 1). Black and Love (1986) observed a significant reduction of blood glucose in wild cod after 73 days of feed deprivation. A small but significant decline in plasma glucose has been shown to occur during early stages of food deprivation in farmed cod (Olsen et al., 2008) and salmon (Waagbø et al., 2017). This reduction can be explained by the lower amount of glycogen in the liver during the starvation (Black and Love, 1986). Unfortunately, the amount of glycogen in liver and muscle during the feed deprivation was not determined in the present study.

Antemortem stress of fish leads to accumulation of blood lactate (Brown et al., 2010; Digre et al., 2017; Olsen et al., 2008), lower initial muscle pH (Kristoffersen et al., 2006; Roth et al., 2012), and accelerated onset of *rigor mortis* (Bjørnevik and Solbakken, 2010; Erikson et al., 2011; Mørkøre et al., 2008; Strasburg et al., 2008). In the present study, the individual lactate levels varied from below detection limit to 2.70 mmol L^{-1} (results not shown). The fish slaughtered 2 days after capture had the highest blood lactate concentration (Table 1). This is lower than previously published by Digre et al. (2017) and Olsen et al. (2013), who reported lactate values in the blood of stressed cod between 3.4 and 9.6 mmol $L^{-1}$and 6.45 to 9.29 mmol L^{-1}, respectively. Hence, the results indicate that the cod slaughtered in the present study were not stressed, which is also reaffirmed by high initial muscle pH (Table 1).

The ultimate muscle pH determined 7 days *postmortem* was high at all 4 sampling days, around 6.8–6.9, suggesting a low muscle glycogen content even at the time of capture (Table 2). This can probably be explained by suppressed feeding behavior during the start of the spawning, as suggested by Fordham and Trippel (1999), and is in accordance with our previous observations that the cod slaughtered 2 days after capture had empty gastrointestinal tracts (Ageeva et al., 2017).

Feed deprivation significantly reduced the protein concentration and increased the water content in the muscle during the last 28 days of the experiment (Table 2). These changes in muscle quality during long-term starvation of cod are well-known (Black and Love, 1986; Eliassen and Vahl, 1982; Ingolfsdottir et al., 1998; Love, 1988) and were also found in studies on gender-specific responses to starvation (Ageeva et al., 2017; Hagen and Solberg, 2010). The feed deprivation did not cause significant changes in WHC, despite a tendency to decrease toward the termination of the experiment (Table 2). This slight reduction in WHC may partly be due to the increased water content and reduced protein concentration in the muscle.

Table 2. Muscle pH, water-holding capacity (WHC) determined as liquid loss, protein- and water contents in cod fillets determined 7 days *postmortem* on sampling days 2, 23, 51, and 79 after capture.

	Feed deprivation			
	2 days	23 days	51 days	79 days
Muscle pH	6.91 ± 0.06	6.85 ± 0.06	6.83 ± 0.07	6.97 ± 0.05
WHC (%)	5.54 ± 1.03	6.83 ± 0.58	6.56 ± 0.87	8.82 ± 0.95
Protein (%)	17.38 ± 0.26^{a}	16.76 ± 0.41^{a}	16.49 ± 0.34^{ab}	14.92 ± 0.59^{b}
Water (%)	82.37 ± 0.3^{a}	82.77 ± 0.42^{a}	83.23 ± 0.44^{ab}	84.62 ± 0.53^{b}

The data are represented as mean ± SE of mean.
Different lowercase letters indicate significant differences ($p < 0.05$) between sampling days.

Development of rigor mortis and muscle pH

Rigor mortis

The assessment of *rigor mortis* was based on the same measurements principles as described by Sørensen et al. (1999), Botta (1991), Berg et al. (1997), and Amlacher (1961). However, in contrast to previous studies, our instrument was portable and could be used during fieldwork.

Figure 1A shows the development of *rigor mortis* in fish subjected to feed deprivation for 2, 23, 51, and 79 days. The results are shown as the average CF (g) applied on each batch (n = 10) at different time points. According to this, the muscle hardness of all batches remained low during the initial 10 h *postmortem*, independent of starvation time. The first significant difference was registered 14 h *postmortem* ($F(3, 36) = 3.986$, $p = 0.015$), when the fish starved for 79 days started to enter *rigor mortis*.

Pre-rigor time (t_{CF100g} [h]) and the time before maximum *rigor mortis* appeared (t_{CFmax} [h]) as well as the rate of *rigor* resolution (r_{res} [g h^{-1}]) were studied for each individual, and the average values of the individuals in the batches were calculated (Table 3). The cod sampled 2 days after capture remained flexible for around 29 h after slaughtering, which was significantly longer compared to that of fish sampled on subsequent sampling days. The onset of *rigor mortis*, as defined by a CF >100 g, for fish deprived of feed for 23, 51, and 79 days started at around 17, 16, and 15 h after slaughtering, respectively. These relatively long *pre-rigor* periods indicate that even prolonged feed deprivation do not deplete the energy stores in cod muscle completely, as may be seen in cod exposed to extensive preslaughter stress or activity (Kristoffersen et al., 2006). Mørkøre et al. (2008) studied the *rigor mortis* development in Atlantic salmon starved for 35 days and found that only *antemortem* stress accelerated *rigor mortis* development, not the starvation. Despite our indication of decreased *pre-rigor* time with prolonged starvation, which is in accordance with statements made by Love (1988), no significant differences between the fish sampled on the last three sampling days were found.

The time to reach CF_{max} (maximum muscle hardness) was found to be 53, 49, 45, and 40 h *postmortem* for the fish deprived of feed for 2, 23, 51, and 79 days, respectively (Table 3). When comparing muscle hardness (CF) for fish starved for 23, 51, and 79 days after capture, it appeared that the maximum muscle hardness obtained *postmortem* decreased with the increased duration of feed deprivation (Figure 1A; Table 3). The rate of resolution of *rigor mortis* was lowest in the least starved fish (Table 3). This suggests a less rapid proteolytic degradation of the fish muscle proteins initially during the starvation.

There were no significant changes in the muscle hardness measured 120 h *postmortem* (CF_{term}) during the first 51 days, but the muscle was significantly softer in the fish starved for 79 days (Figure 1A; Table 3). Olsson et al. (2006) reported that muscle texture, measured as shear force, in farmed Atlantic cod becomes firmer after 3 weeks starvation prior to slaughter. Our results are in agreement with Bjørnevik et al. (2016), who found that increased muscle hardness after 32 days starvation of farmed cod was not significant. A possible explanation for the changes in muscle hardness during long-term starvation is probably linked to the sequential utilization of muscle

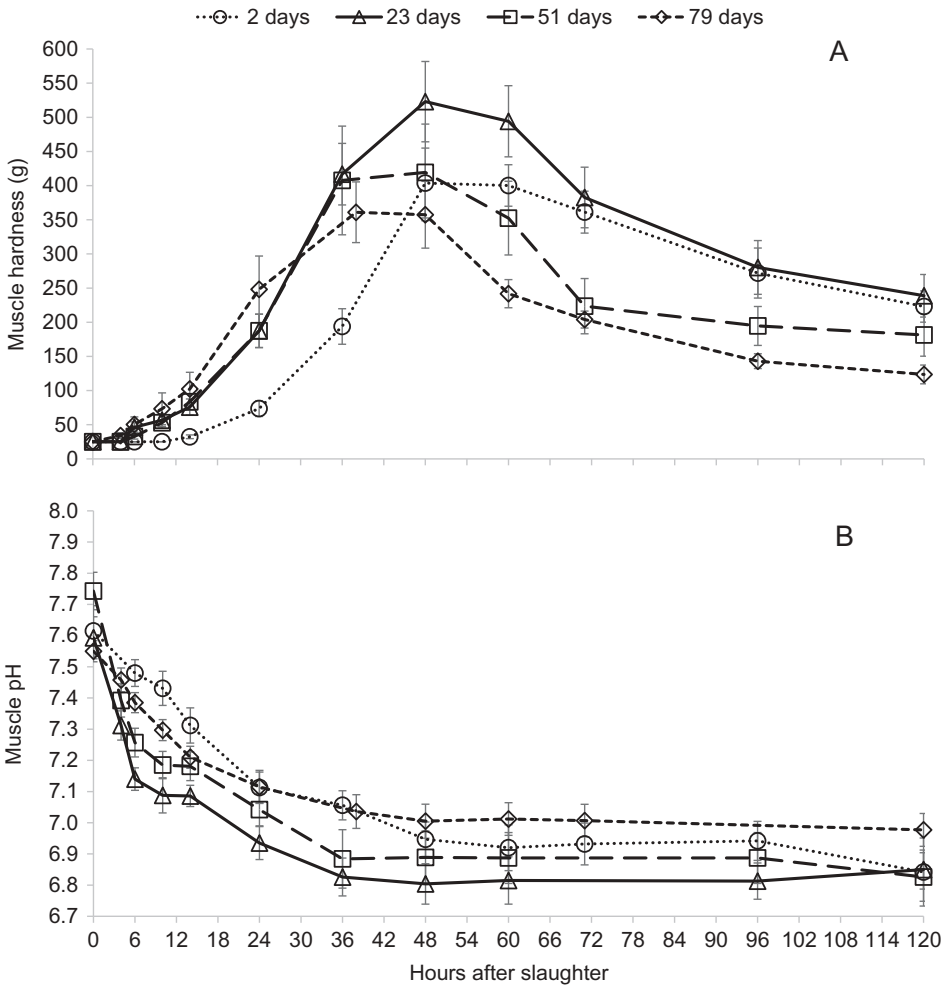

Figure 1. Changes in muscle hardness measured as compression force (A) and muscle pH (B) during 120 h ice storage of Atlantic cod sampled on days 2, 23, 51, and 79 of feed deprivation. Each point is represented as mean ± SE of mean (n = 10).

Table 3. *Pre-rigor* time (t_{CF100g} [h]) and *rigor mortis* development at each sampling day assessed on individual basis as maximal compression force (CF_{max} [g]), time elapsed before maximal compression force (t_{CFmax} [h]), rate of *rigor mortis* resolution (r_{res} [g h^{-1}]) and compression force determined 5 days *postmortem* (CF_{term} [g]).

Sampling days	t_{CF100g}	t_{CFmax}	CF_{max}	r_{res}	CF_{term}
2	28.7 ± 2.1[a]	53.4 ± 1.9[a]	455.2 ± 39.7	4.4 ± 0.3	223.0 ± 22.8[a]
23	17.1 ± 1.7[b]	49.2 ± 2.8[ab]	543.6 ± 57.1	5.4 ± 1.2	238.8 ± 31.1[a]
51	16.0 ± 1.3[b]	45.7 ± 3.9[ab]	499.0 ± 74.2	8.5 ± 1.9	181.4 ± 31.1[ab]
79	14.9 ± 1.9[b]	40.4 ± 3.5[b]	397.0 ± 45.7	6.7 ± 2.2	123.6 ± 13.7[b]
Significant difference between days	$F(3,36) = 13.350$ $p = 0.000$	$F(3,36) = 3.110$ $p = 0.038$	$F(3,36) = 1.261$ $p = 0.302$	$F(3,36) = 1.217$ $p = 0.318$	$F(3,36) = 4.003$ $p = 0.015$

(Mean ± SE of mean).
$r_{res} = (CF_{max} - CF_{\pm 50g})/(t_{CF\pm 50g} - t_{CFmax})$.
CF constant ($CF_{\pm 50g}$ [g]) is the compression force when individual change was less than ±50 g.
$t_{CF\pm 50g}$ = time elapsed before CF constant.
Different lowercase letters indicate significant differences ($p < 0.05$) between sampling days.

nutrients, increased proteolytic activities, and increased water content in muscle. Love (1988) suggested that severe starvation of cod leads to disappearance of contractile proteins (actin and myosin), increasing the proportion of connective tissue (collagen).

Muscle pH

Postmortem muscle pH is shown as the average pH-value for each group (n = 10) at different time points in Figure 1B. The initial muscle pH was in the range of pH 7.7–7.5 (Figure 1B; Table 1), suggesting that the cod was slaughtered in a non-stressful manner at all sampling days (Kristoffersen et al., 2006). The main drop in muscle pH occurred during the first 14 h *postmortem* in all groups (Figure 1B). The decline in muscle pH in cod starved for 23, 51, and 79 days levelled off at 36 h after slaughter. The cod starved for 2 days obtained pH-stabilization at about 48 h *postmortem*, suggesting a higher potential for anaerobic muscle metabolism. Similar high pH-values measured 120 h after slaughter were found in all groups of cod. The time of muscle pH stabilization coincided with the time of maximal muscle hardness in all groups (Figure 1A and B), which is consistent with published results (Amlacher, 1961; Foegeding et al., 1996; Kristoffersen et al., 2006; López-Luna et al., 2014).

Conclusions

The study showed that starvation of live-caught mature cod for 23 days reduces the *pre-rigor* time from 29 to 17 h. Further starvation did not decrease this period significantly. This suggests that live-stored cod deprived of feed for 79 days may still be industrially processed *pre-rigor*. However, more than 51 days of starvation resulted in a lower protein concentration and higher water content in the muscle. In addition, after 51 days, the muscle texture was softer than in fish starved for a shorter period.

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