



# Pre mortem capturing stress of Atlantic herring (*Clupea harengus*) in purse seine and subsequent effect on welfare and flesh quality

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## ARTICLE INFO

Handled by Dr Niels Madsen

**Keywords:**  
Crowding  
Fisheries  
Pelagic  
Lactate  
Texture  
Colour

## ABSTRACT

Atlantic herring was commercially captured with purse seine in catches of 100–400 Mt. During crowding 0–30 min individual fish were sampled from the purse seine, killed by a percussive blow to the head and blood lactate was measured. Muscle pH and rigor index was measured over 24 h. Additionally, 100 fish sampled before and after crowding were stored in tanks, filleted, and analyzed for flesh quality (texture, gaping, blood content, colour and appearance), prior to and after freezing and thawing. Results show that the pre mortem stress associated with capture caused anaerobic muscle activity and the formation of lactic acid both in muscle and blood, elevating with crowding duration. The onset of rigor mortis accelerated with increasing crowding duration. Crowding in the purse seine did lead to lower quality scores of the fillets as seen in softer texture, increased blood content and gaping. Except for blood content, freezing and thawing amplified all measured quality parameters related to the level of stress. We conclude that stress associated with capture and duration of crowding affect the animal's welfare and will have negative effect on the fillet quality of herring.

## 1. Introduction

Over the past decades, the market dynamics for Atlantic herring (*Clupea harengus*) has shifted from being a major raw material source for the fish meal industry to mainly being used for human consumption. As a result, Atlantic herring, in particular the Norwegian spring-spawning herring (NSH), has become one of Norway's most economically valuable specie within fisheries, next after Atlantic mackerel (*Scomber scombrus*) and Atlantic cod (*Gadus morhua*). In 2020, Norway exported 317.418 Mt of Atlantic herring, worth roughly € 380 million. In line with this development, the average prices on first-hand sales of Atlantic herring have increased gradually from 1998 to 2020 from 0.77 to 1.1 €/kg (SSB, 2021). An increasing proportion of the Norwegian herring catch is processed into fillets, which in recent years has comprised approximately 40%, by volume. Although prices of Atlantic herring is dependent on size distribution (Zimmermann and Heino, 2013), the overall pricing after retail market is a good indicator that an overall high quality of products is an important driving force (Bronnmann and Bittmann, 2019).

It is well known that flesh quality traits like color and proximal composition of Atlantic herring varies with season and maturity (Hamre et al., 2003; Hyldig et al., 2012; Jensen et al., 2005). These variations are

quite predictable. More challenging are sudden changes in quality between different catches that can occur simultaneously at the same or at different fishing grounds. On some occasions, these changes can easily be explained by the fish's prey content at time of death. The latter affects enzyme activity and can involve leakage and subsequent belly burst (Felberg et al., 2010, 2009; Veliyulin et al., 2007). Also, the storage conditions such as temperature and time elapsed between capture and processing or varying freezing conditions are of key importance (Dang et al., 2018; Losada et al., 2007). Of major importance is also the fishing gear used. Previous research on Baltic herring shows that herring caught by gillnet had an earlier onset of *rigor mortis* and inosin mono phosphate (IMP) as compared to trawl and trap-net (Hattula et al., 1995), whereas pelagic trawling is known to cause mortality due to physical damage (Suuronen et al., 1996).

Fishing with purse seine involves surrounding a school of fish with a seine, tightening the gap from the bottom such that the net forms a purse. Thereafter the fish is crowded on the longside of the vessel and pumped onboard. For the purse seine, one challenging phase could be crowding into high densities (excess of 200 kg/m<sup>3</sup>) lasting one hour or longer (Digre et al., 2016; Tenningen et al., 2012). Crowding can involve several physiological and environmental challenges for the fish resulting in panic followed by exhaustion, hypoxia and death (Anders et al.,

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<https://doi.org/10.1016/j.fishres.2021.106124>

Received 13 April 2021; Received in revised form 26 August 2021; Accepted 30 August 2021

Available online 6 September 2021

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2019a; Olsen et al., 2012; Tenningen et al., 2012). The physical strain caused by the pump itself when pumping fish onboard the vessel or when pumping fish between vessels when the volume of fish must be reduced, is also of importance for the quality (Digre et al., 2016).

In addition to fish welfare, the pre mortem stress associated with crowding influences the fillet quality in a wide range of aquaculture (Daskalova, 2019) and white fish species (Olsen et al., 2013; Svalheim et al., 2020). For wild caught, and for pelagic species in particular, few studies exist. For Skipjack tuna it has been reported that stress influence the quality of canned products (Crawford et al., 1970), while on Bluefin tuna (*Thynnus thynnus*), the associated effects of stress caused no color changes of the flesh (Addis et al., 2013). More recent studies also show detrimental effects of stress on the flesh quality of Atlantic mackerel (Anders et al., 2020).

Recent studies on herring show that the fish do respond with stress towards crowding and can be exhausted as rapidly as within 10 min, followed by a risk of mortality as a result of scale loss (Olsen et al., 2012). The effects of crowding of herring in the purse seine on the flesh quality have not been studied. It would therefore be of paramount interest to examine whether the stress associated with crowding could explain quality differences within a catch. The aim of this study was therefore to investigate how herring respond to crowding during commercial operation and the subsequent effect on flesh quality on both fresh and frozen products.

## 2. Material and methods

In February 2011, on the west coast of Norway, a total of 1000 tons of migrating Atlantic herring (*Clupea harengus*) from the Norwegian spring-spawning herring stock (NSH), were captured with purse seine by a commercial fishing vessel (MS Birkeland). The fish were caught in 4 catches, each between 100 and 400 tons, within one fishing trip lasting 24 h. The total duration of crowding ( $> 200 \text{ kg/m}^3$ ) varied from 0 to 30 min, before the fish were pumped onboard into tanks containing refrigerated sea water (RSW) with a temperature of  $-1 \text{ }^\circ\text{C}$ . The seawater temperature was approximately  $8 \text{ }^\circ\text{C}$ .

The sampling of fish started the moment the fish were crowded alongside the vessel in such amount that single fish could be caught using a long dipnet. The fish were sampled one at the time and immediately killed by a percussive blow to the head. Fish were sampled from the start of the crowding and approximately every 5 min until the end of the crowding, resulting in a total of 17 fish over 4 catches. For each fish, blood was drawn from the caudal vein immediately after killing before measuring muscle pH and rigor index and placed into polystyrene boxes containing ice. Subsequently muscle pH and rigor index were measured on the same fish over 24 h.

For quality analysis a total of 200 herring were sampled from the last and largest catch, at the beginning of crowding (Control,  $n = 100$ ) and at the end of the catch 30 min later (Stress,  $n = 100$ ). The fish were killed by a percussive blow to the head and stored in RSW tanks at  $-1 \text{ }^\circ\text{C}$  for 24 h, before being packed with ice in polystyrene boxes and shipped by air cargo to laboratories at Nofima, Stavanger. There the fish were stored on ice in a chill room until quality analysis. Six days *post mortem* all fish were filleted; from each fish one fillet was used to measure texture hardness and color in fresh condition, while the other fillet was measured equally after being vacuum packed with salt brine (34‰), frozen at  $-28 \text{ }^\circ\text{C}$  and thawed after 3 months of frozen storage.

### 2.1. Blood analysis

Unheparized whole blood was extracted from the caudal vessels of the fish and analyzed using two i-STAT® 300 Portable Clinical Analyzer (I-stat, Abbott, Princeton, NY, U.S.A.). The analysers were used in conjunction with CG4 + disposable cartridges and analysed for lactate.

### 2.2. Rigor mortis and muscle pH

*Rigor mortis* was measured by the angle ( $0\text{--}90^\circ$ ) of the tail drop while placing half of the fish length outside a table. Rigor was measured at 0, 3, 6, 9, 12, 18 and 24 h *post mortem*.

In each fish the muscle pH was measured in white muscle tissue in the dorsal back anterior to the dorsal fin using a Mettler Toledo SevenGo pro™ pH meter (Mettler Toledo INC, N.Y., USA) equipped with Inlab puncture electrode. The pH meter was calibrated with pH 4.01, 7.00 and 10.01 buffers at  $20 \text{ }^\circ\text{C}$ .

### 2.3. Quality grading

All fillets were graded and given scores according to gaping (1–3), Blood content (1–3) and total visual appearance as shown in Fig. 1. Grading was carried out by 2 technicians, one scoring each fillet based on blood content and gaping and the other providing the score on the total visual appearance.

### 2.4. Color measurements

Fillet color was measured as Lightness ( $L^*$ ) redness ( $a^*$ ) and yellowness ( $b^*$ ) by image analysis DigiEye™ (VeriVide Ltd., Leicester, UK). Each fillet was placed into an illumination cabinet which ensures a uniform lighting, standard daylight (6400 K) and photographed with a Nikon D80 camera with a Nikkor lens. The color of the whole fillet, except the belly flaps was measured using DigiPix (VeriVide Ltd., Leicester, UK) color measurement software.

### 2.5. Texture analysis

For texture measurements a flat cylinder with a diameter of 5 mm was used for the test probe hardness (puncture test) with a TA-XT2®-Pro Texture Analyser (Stable Micro Systems, Surrey, UK) with a 10 kg load cell (Roth et al., 2008). The penetration depth for the probe was 80% of the fillet height and the speed was 1 mm/s. The texture profile was measured at 2 locations, 1 cm apart anterior to the dorsal fin. The breaking force was defined as the force required for the cylinder to penetrate the fillet surface.

### 2.6. Statistical analysis

To continuously test independent variables such as pH and blood lactate against time of crowding linear regression was used as the statistical model. Log transformation of both variables was carried out to obtain linearity and normal distribution of the residuals. Multiple regression was used to test pH against the two continuous and independent variables crowding and storage time. General linear model (GLM) was used to test categorical groups of stressed fish against pH using post mortem storage time as a covariate. Correlation analysis was used to test the correlation between pH and lactate measurements. The angle of rigor was turned into logit function (0–1) performing radians transformation and tested using log linear regression. For the quality analyses, factorial ANOVA was used for testing color against categorical variables such as stress and freezing, whilst for texture analysis ANCOVA was used, with fillet thickness as a covariate.

## 3. Results

By the time herring was crowded and ready for pumping the mean  $\pm$  SE lactate and muscle pH had reached  $2.0 \pm 0.31 \text{ mmol/L}$  and  $7.5 \pm 0.087$ , respectively. During crowding herring showed increased anaerobic muscle activity and hypoxia with a significant accumulation of lactate ( $P < 0.0005$ ,  $r = 0.81$ ; linear regression, Fig. 2a), followed by a drop in muscle pH ( $P < 0.005$ ,  $r = 0.72$ ; linear regression, Fig. 2b), peaking after 30 min with  $6.3 \pm 1.00 \text{ mmol/L}$  lactate, while pH varied

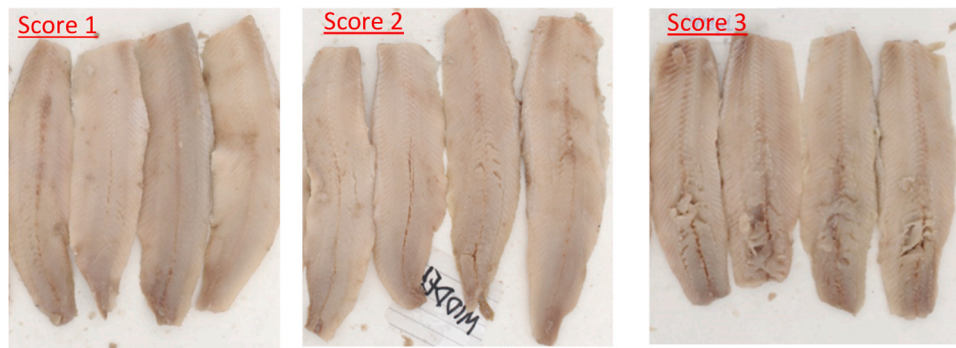


Fig. 1. Scoring (1–3) of Atlantic herring fillets based on appearance.

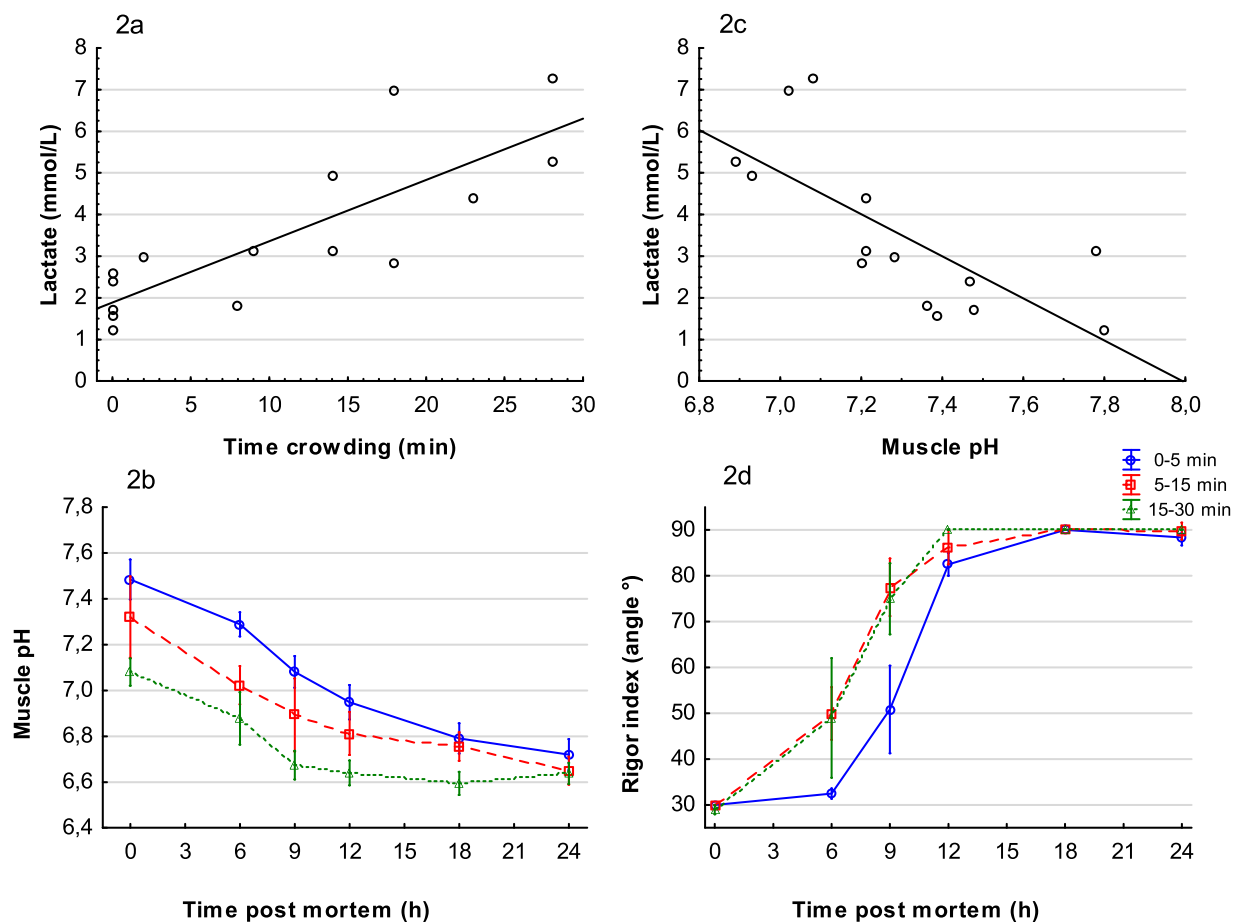


Fig. 2. Regression for blood lactate (2a), muscle pH (2b) and rigor measurement (2d) of Atlantic herring crowded for 0–30 min. For graphs on rigor and pH, the time of crowding was categorized into 0–5, 5–15 and 15–30 min. Fig. c is correlation matrix between blood lactate and muscle pH.

from  $7.1 \pm 0.14$  to  $7.23 \pm 0.34$  after 15 and 30 min of crowding. As shown in Fig. 2c, the muscle pH correlated with blood lactate ( $P < 0.005$ ,  $r = -0.72$ ; correlation analysis).

Multiple regression shows that muscle pH in Fig. 2b was dependent both on crowding duration and storage time ( $P < 0.0005$ ,  $r = 0.78$ ,  $F = 39$  and  $102$  receptively), whereas fish stressed for 5 min or more maintained a significant lower muscle pH the first 24 h ( $P < 0.0005$ ,  $F = 20$  and  $101$ , GLM) reaching an overall pH of  $6.7 \pm 0.13$  (mean  $\pm$  SD).

As shown in Fig. 2d fish sampled at the beginning of the pumping did not start onset of rigor mortis until 6 h post mortem, while all crowding beyond 5 min resulted in a significant accelerated onset of rigor mortis the first 18 h ( $P < 0.005$ , Wald chi 11.5: Log linear).

The results shown in Table 1, indicate that gaping score and blood content was significantly affected by freezing ( $P < 0.0005$ , Factorial ANOVA) and stress ( $P < 0.05$ , Factorial ANOVA). There was, however, an interaction on the blood content of stressed fish after freezing ( $P < 0.0005$ , Factorial ANOVA) as the blood is washed out in the brine in which it was frozen (Table 1).

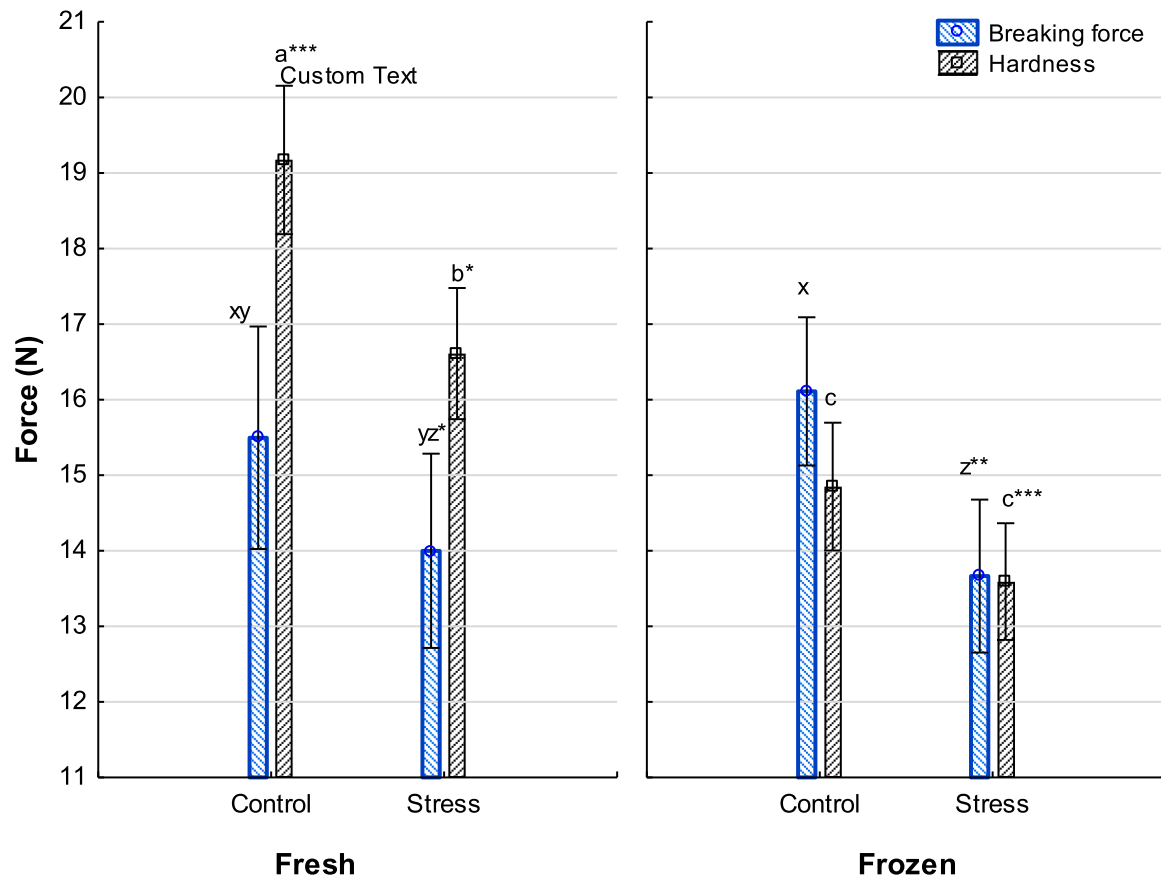
As shown in Fig. 3, the texture hardness was significantly dependent (ANCOVA) on fillet thickness ( $P < 0.0005$ ,  $F = 15$ ); stress ( $P < 0.0005$ ;  $F = 18$ ) and whether the fillets were fresh or had been frozen ( $P < 0.0005$ ,  $F = 32$ ). Similarly, the breaking force was also significantly dependent on thickness ( $P < 0.0005$ ,  $F = 15$ ); stress ( $P < 0.005$ ;  $F = 10$ ) and whether the fillets were fresh or frozen ( $P < 0.05$ ,  $F = 4$ ).

As shown in Table 2, freezing and thawing in brine made the fillet

**Table 1**  
Average (SE) gaping, blood and quality score of fillets from stressed or unstressed herring as fresh and frozen fillets.

Treatment		Gaping		Blood		Quality score		n
		Mean	SE	Mean	SE	Mean	SE	
Fresh	Control	1.04	0.04	0.40	0.13	1.08	0.06	25
	Stress	1.12	0.07	1.24	0.14	1.04	0.04	25
Frozen	Control	1.38	0.11	0.35	0.12	1.19	0.08	25
	Stress	1.75	0.14	0.29	0.09	2.00	0.09	25
Fresh vs Frozen		P < 0.005		P < 0.0005		P < 0.0005		
Control vs Stress		P < 0.05		P < 0.005		P < 0.0005		
Interaction		P > 0.14		P < 0.005		P < 0.0005		

In each column the statistical output from Factorial ANOVA.



**Fig. 3.** Hardness measured as newton (N) of fillets from control or stressed fish before and after freezing. Values provided is mean ± SE. Different asterisk (a,b,c) represent difference in hardness, while (x,y,z) for breaking force with significant difference of \* P < 0.05, \*\* P < 0.005, \*\*\* P < 0.0005.

**Table 2**  
Fillet colour (CIE L\*a\*b\*) measured in stressed and unstressed herring as fresh and frozen fillets.

Colour	Fresh				Frozen			
	Stress (n = 96)		Control (n = 100)		Stress (n = 100)		Control (n = 100)	
L*	53.2 <sup>a</sup>	6,3	53.3 <sup>a</sup>	5.6	62.2 <sup>b</sup>	7.2	61.2 <sup>b</sup>	6.3
a*	14.3 <sup>a</sup>	3,6	14.3 <sup>a</sup>	3.2	13.2 <sup>b</sup>	2.4	11.3 <sup>c</sup>	1.4
b*	9.6 <sup>a</sup>	2,9	10.5 <sup>a</sup>	2.7	12.9 <sup>b</sup>	2.9	14.8 <sup>c</sup>	2.9

In each row Different asterisk (a,b,c) represent a significant difference of P < 0.05 using Factorial ANOVA.

color significantly more white and less red (P < 0.05, Factorial ANOVA), than what was seen prior to freezing, and the frozen stressed fish were significantly more red (a\*) and less yellow (b\*) (P < 0.05, Factorial ANOVA), than the frozen and unstressed fish.

**4. Discussion**

In accordance with others (Anders et al., 2020, 2019a; Olsen et al., 2012; Tenningen et al., 2012), crowding densities within the purse seine resulted in anaerobic muscle activity followed by an increase of blood lactate (Fig. 2). The crowding densities and crowding duration within a catch may vary according to both the size of the catch and the size of purse seine itself (Tenningen et al., 2019). In order to pump the fish onboard the vessel, densities above 200 kg/m<sup>3</sup> is common both for fisheries and aquaculture industry (Erikson et al., 2016; Lerfall et al., 2015; Lockwood et al., 1983).

As demonstrated by Tenningen et al. (2012), crowding densities above 400 kg/m<sup>3</sup> resulted in drop of oxygen levels to below 50–60%, followed by hypoxia and accumulation of plasma lactate (4–8 mmol/L), all within 10 min. Comparing this against a commercial operation (Fig. 2) suggest conditions similar to Tenningen et al. (2012), although fish in this study were crowded up to 30 min



Commercial crowding conditions prior to pumping could result in 30–50% mortality (Tenningen et al., 2012) and plasma lactate levels up to 11 mmol/L have been reported in moribund herring (Olsen et al., 2012). In direct comparison to Atlantic herring, Atlantic mackerel is capable of fully exhausting itself during crowding reaching > 20 mmol/L of lactate (Anders et al., 2020). Crowding mackerel under similar conditions as the herring also resulted in higher lactate levels, approximately 11 mmol/L (Anders et al., 2020). Apparently, there are some specie differences as to how the animals respond to the crowding conditions and a hypoxic environment. One common response is an increase in primary and secondary stress responses that increases with the time of crowding (Anders et al., 2019a; Marcalo et al., 2006; Tenningen et al., 2012). Besides disrupting the animal's physiological homeostasis, the animal will also deplete its energy reserves over time causing lactate accumulation in the muscle and an early onset of *rigor mortis* (Sone et al., 2019).

Previous studies on mackerel show that the muscle pH at time of death will be as low as 6.5, where the muscle is in rigor already at time of death (Anders et al., 2020). Unlike mackerel, herring crowded for 30 min did not reach pH below 6.9 and maximum rigor until 9–12 h *post mortem* (Fig. 2). Most studies on both farmed and pelagic fish species show that completely exhausted animals will reach maximum rigor as early as 2 h *post mortem* (Anders et al., 2020, 2019b; Daskalova, 2019; Lerfall et al., 2015; Sone et al., 2019), indicating that the herring in this study was not particularly exhausted at time of death.

With respect to fillet quality it is well established that the pre mortem struggle can have negative effect on most fish species such as Atlantic cod (Erikson et al., 2011; Svalheim et al., 2020) as well as for pelagic species (Anders et al., 2020; Ando et al., 2001; Digre et al., 2016; Sone et al., 2019). Herring is no exception. As shown in Table 1 and Fig. 3, the stress associated with crowding resulted in more blood in the fillets, higher gaping scores, softer texture and lower quality grading scores. More recent studies on Atlantic cod under controlled conditions do show that the stress associated with crowding leads to distribution of blood to the muscle, thus increasing redness with time (Svalheim et al., 2020). Similarly, a vast pH drop can be related to the fact that the drop in muscle pH triggers autolysis and biochemical and physical degradation of the muscle (Ando et al., 2001; Bahuaud et al., 2010; Sato et al., 2002; Sone et al., 2019). Even more interesting is that the quality of the fish which is exposed to a prolonged period of stress deteriorates even further after freezing and thawing as compared to the control group. During freezing the formation of ice crystals within the muscle will cause damage to the muscle structure and cells (James et al., 2015; Li et al., 2018). Thawing is however also crucial point as one risks melting and re crystallization of water within the fillet while the temperature fluctuates. In this aspect the structure of the cells along with how the water migrate is of importance to avoid damage during freezing and thawing (Li et al., 2018). It can be assumed that an increased *post mortem* degradation is caused by stress and a subsequent loss of water and of water holding capacity (Anders et al., 2020) will enhance even further crystallization and migration during freezing and thawing.

Although capturing pelagic species will result in stress responses, the question rises as to what degree the welfare of the animal is compromised under commercial conditions? As demonstrated by Lockwood et al. (1983), the cumulative mortality of mackerel is a function of crowding densities and the duration of the crowding itself. The effect of crowding on the fish wellbeing is a sum of variables such as size of the catch, environmental conditions, choice of capturing methods and schooling behavior (Anders et al., 2019a; Breen et al., 2012; Marcalo et al., 2019; Sone et al., 2019; Tenningen et al., 2019, 2012). In this case the animal is captured for food and not slipped, meaning that crowding densities is going to remain high over longer periods of time, thus exposing the animal for higher risks for hypoxia. Based on the results shown in Fig. 2, the herring did express anaerobic muscle activity, but not sufficiently severe for the animals to deplete their energy reserves as rapidly as was seen in the case of mackerel (Anders et al., 2020). Besides

specie differences, one possible explanation could be related to the high pumping capacity of the modern vessels. Lockwood et al. (1983) reported the pumping capacity of the vessels to be approximately 100–150 tons/h with crowding densities around 1000 fish/m<sup>3</sup>. In contrast, this study used pumps with capacity around 800–1000 tons/h. A new study on a large slaughter vessel for Atlantic salmon (Chan et al., 2020), shows that a high pumping capacity combined with good crowding conditions, allows the vessel to keep salmon at lower densities, with minor effects on lactate levels (1.7 mmol/L) and pre rigor times (< 24 h) after 5 h of crowding and pumping. Although the biomass of fish handled in a cage or purse seine are very much similar, the responses in herring in this study was more severe (Fig. 2) as compared to salmonids (Chan et al., 2020) and also Atlantic cod (Svalheim et al., 2020). Considering that this study did consist of rather small schools of fish caught, questions arise as to how welfare is affected when the catches are 3 folds the largest catch of this study.

The commercial handling of pelagic species is quite different than that of farmed fish. Farmed fish are stunned unconscious and killed during slaughter (Lines and Spence, 2014; van de Vis et al., 2003). Methods for stunning pelagic species are however under investigation (Anders et al., 2019b; Nordgreen et al., 2008) and becoming adopted in a range of various types of fishing vessels (Erikson et al., 2016, 2021; Lambooij et al., 2013, 2012). This combined with results in this investigation provides some optimism for the future with respect to capturing herring and improving both its wellbeing and quality.

## 5. Conclusion

We conclude that herring respond with stress during crowding expressing anaerobic metabolism, increasing with increasing time. This does have consequences for the meat quality, leading to softer texture and more pronounced gaping of fresh fillets. Freezing and thawing accelerates the deterioration even further. Obtaining good welfare practices for handling and killing herring in the future will enhance more sustainable food in the future.

## Ethical considerations

Authorship was according to the Vancouver group (1979) <http://www.icmje-recommendations.pdf>. All animals used in this experiment was killed by percussive blow to the head prior to sampling and did not involve live animal experimentation.

## CRedit authorship contribution statement

Conceptualization, Torstein Skåra. Methodology, Bjørn Roth. Software, Bjørn Roth. Validation, Bjørn Roth and Torstein Skåra. Formal analysis, Bjørn Roth. Field Investigation, Bjørn Roth and Tor Evensen. Resources, Bjørn Roth and Torstein Skåra. Data curation, Bjørn Roth. Writing – original draft Preparation, Bjørn Roth. Writing – review & editing, Torstein Skåra. Visualization, Bjørn Roth. Supervision, Bjørn Roth. Project administration, Bjørn Roth and Torstein Skåra. Funding acquisition, FHF.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data Availability

Data is available on demand. Take contact with corresponding author.

## Acknowledgement

We would like to thank the crew on MS Birkeland, in particular Captain Alf Birkeland for organizing the catch and vessel according to our specifications. Also thanks to the rest of staff and project group at Nofima: Sveinung Birkeland, Bjørn Tore Rotabakk, Izumi Sone, Bente Husebø, Tor Evensen, Karin Tranøy, Laila Budal, Sigurd Øines, Leif Akse and Karsten Heia. This research was funded by Norwegian Seafood Research Fund (FHF), project no 900518.

## References

- Addis, P., Corrias, S., Garau, C., Secci, M., 2013. Physiologic responses to stress and changes in Atlantic Bluefin Tuna (*T. thynnus*) meat color during trap fisheries capture and processing in Sardinia (W. Mediterranean). *J. Aquat. Food Prod. Technol.* 22 (3), 298–309. <https://doi.org/10.1080/10498850.2011.647596>.
- Anders, N., Howarth, K., Totland, B., Handegard, N.O., Tenningen, M., Breen, M., 2019a. Effects on individual level behaviour in mackerel (*Scomber scombrus*) of sub-lethal capture related stressors: crowding and hypoxia. *PLoS One* 14 (3), 0213709. <https://doi.org/10.1371/journal.pone.0213709>.
- Anders, N., Roth, B., Grimsbo, E., Breen, M., 2019b. Assessing the effectiveness of an electrical stunning and chilling protocol for the slaughter of Atlantic mackerel (*Scomber scombrus*). *PLoS One* 14 (9), 0222122. <https://doi.org/10.1371/journal.pone.0222122>.
- Anders, N., Eide, I., Lerfall, J., Roth, B., Breen, M., 2020. Physiological and flesh quality consequences of pre-mortem crowding stress in Atlantic mackerel (*Scomber scombrus*). *PLoS One* 15 (2), 0228454. <https://doi.org/10.1371/journal.pone.0228454>.
- Ando, M., Joka, M., Mochizuki, S., Satoh, K.I., Tsukamasa, Y., Makinodan, Y., 2001. Influence of death struggle on the structural changes in chub mackerel muscle during chilled storage. *Fish. Sci.* 67 (4), 744–751. <https://doi.org/10.1046/j.1444-2906.2001.00315.x>.
- Bahuaud, D., Morkore, T., Ostbye, T.K., Veiseth-Kent, E., Thomassen, M.S., Ofstad, R., 2010. Muscle structure responses and lysosomal cathepsins B and L in farmed Atlantic salmon (*Salmo salar* L.) pre- and post-rigor fillets exposed to short and long-term crowding stress. *Food Chem.* 118 (3), 602–615. <https://doi.org/10.1016/j.foodchem.2009.05.028>.
- Breen, M., Isaksen, B., Ona, E., A.O, P., Pedersen, G., Saltskår, J., Vold, A., 2012. A review of possible mitigation measures for reducing mortality caused by slipping from purse-seine fisheries, Paper presented at the ICES CM 2012.
- Bronnmann, J., Bittmann, T., 2019. Asymmetric adjustment of retail cod and herring prices in Germany: a NARDL approach. *Mar. Policy* 106, 103513. <https://doi.org/10.1016/j.marpol.2019.103513>.
- Chan, S.S., Roth, B., Skare, M., Herner, M., Jessen, F., Lovdal, T., Lerfall, J., 2020. Effect of chilling technologies on water holding properties and other quality parameters throughout the whole value chain: from whole fish to cold-smoked fillets of Atlantic salmon (*Salmo salar*). *Aquaculture* 526, 735381. <https://doi.org/10.1016/j.aquaculture.2020.735381>.
- Crawford, L., Irwin, E.J., Spinelli, J., Brown, W.D., 1970. Premortem stress and postmortem biochemical changes in Skipjack Tuna and their relation to quality of the canned product. *J. Food Sci.* 35 (6), 849–851. <https://doi.org/10.1111/j.1365-2621.1970.tb02010.x> (849–8).
- Dang, H.T.T., Gudjonsdottir, M., Ren, D.D., Karlsdottir, M.G., Minh, V.N., Tomasson, T., Arason, S., 2018. Effects of pre and post-rigor freezing and temperature stress during frozen storage on physicochemical stability of Atlantic herring (*Clupea harengus*) muscle. *J. Food Process. Preserv.* 42 (9), e13754. <https://doi.org/10.1111/jfpp.13754>.
- Daskalova, A., 2019. Farmed fish welfare: stress, post-mortem muscle metabolism, and stress-related meat quality changes. *Int. Aquat. Res.* 11 (2), 113–124. <https://doi.org/10.1007/s40071-019-0230-0>.
- Digre, H., Tveit, G.M., Solvang-Garten, T., Eilertsen, A., Aursand, I.G., 2016. Pumping of mackerel (*Scomber scombrus*) onboard purse seiners, the effect on mortality, catch damage and fillet quality. *Fish. Res.* 176, 65–75. <https://doi.org/10.1016/j.fishres.2015.12.011>.
- Erikson, U., Digre, H., Misimi, E., 2011. Effects of perimortem stress on Farmed Atlantic Cod product quality: a baseline study. *J. Food Sci.* 76 (4), S251–S261. <https://doi.org/10.1111/j.1750-3841.2011.02141.x>.
- Erikson, U., Gansel, L., Frank, K., Svendsen, E., Digre, H., 2016. Crowding of Atlantic salmon in net-pen before slaughter. *Aquaculture* 465, 395–400. <https://doi.org/10.1016/j.aquaculture.2016.09.018>.
- Erikson, U., Grimsbo, L., Digre, H., 2021. Establishing a method for electrical immobilization of whitefish on board fishing vessels. *J. Aquat. Food Prod. Technol.* 30, 694–705. <https://doi.org/10.1080/10498850.2021.1931606>.
- Felberg, H.S., Slizyte, R., Mozuraityte, R., Dahle, S.W., Olsen, R.L., Martinez, I., 2009. Proteolytic activities of ventral muscle and intestinal content of North Sea herring (*Clupea harengus*) with full and emptied stomachs. *Food Chem.* 116 (1), 40–46. <https://doi.org/10.1016/j.foodchem.2009.02.001>.
- Felberg, H.S., Hagen, L., Slupphaug, G., Batista, I., Nunes, M.L., Olsen, R.L., Martinez, I., 2010. Partial characterisation of gelatinolytic activities in herring (*Clupea harengus*) and sardine (*Sardina pilchardus*) possibly involved in post-mortem autolysis of ventral muscle. *Food Chem.* 119 (2), 675–683. <https://doi.org/10.1016/j.foodchem.2009.07.012>.
- Hamre, K., Lie, O., Sandnes, K., 2003. Seasonal development of nutrient composition, lipid oxidation and colour of fillets from Norwegian spring-spawning herring (*Clupea harengus* L.). *Food Chem.* 82 (3), 441–446. [https://doi.org/10.1016/s0308-8146\(03\)00069-4](https://doi.org/10.1016/s0308-8146(03)00069-4).
- Hattula, T., Luoma, T., Kostianen, R., Poutanen, J., Kallio, M., Suuronen, P., 1995. Effects of catching method on different quality parameters of Baltic herring (*Clupea harengus* L.). *Fish. Res.* 23 (3–4), 209–221. [https://doi.org/10.1016/0165-7836\(94\)00358-4](https://doi.org/10.1016/0165-7836(94)00358-4).
- Hyldig, G., Jørgensen, B.M., Undeland, I., Olsen, R.E., Jonsson, A., Nielsen, H.H., 2012. Sensory properties of frozen herring (*Clupea harengus*) from different catch seasons and locations. *J. Food Sci.* 77 (9), S288–S293. <https://doi.org/10.1111/j.1750-3841.2012.02838.x>.
- James, C., Purnell, G., James, S.J., 2015. A review of novel and innovative food freezing technologies. *Food Bioprocess Technol.* 8 (8), 1616–1634. <https://doi.org/10.1007/s11947-015-1542-8>.
- Jensen, K.N., Jørgensen, B.M., Nielsen, H.H., Nielsen, J., 2005. Water distribution and mobility in herring muscle in relation to lipid content, season, fishing ground and biological parameters. *J. Sci. Food Agric.* 85 (8), 1259–1267. <https://doi.org/10.1002/jsfa.2112>.
- Lambooij, B., Digre, H., Erikson, U., Reimert, H., Burggraaf, D., van de Vis, H., 2013. Evaluation of electrical stunning of Atlantic Cod (*Gadus morhua*) and Turbot (*Psetta maxima*) in seawater. *J. Aquat. Food Prod. Technol.* 22 (4), 371–379. <https://doi.org/10.1080/10498850.2011.654047>.
- Lambooij, E., Digre, H., Reimert, H.G.M., Aursand, I.G., Grimsbo, L., van de Vis, J.W., 2012. Effects of on-board storage and electrical stunning of wild cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) on brain and heart activity. *Fish. Res.* 127, 1–8. <https://doi.org/10.1016/j.fishres.2012.04.004>.
- Lerfall, J., Roth, B., Skare, E.F., Henriksen, A., Betten, T., Dziatkowiak-Stefaniak, M.A., Rotabakk, B.T., 2015. Pre-mortem stress and the subsequent effect on flesh quality of pre-rigor filleted Atlantic salmon (*Salmo salar* L.) during ice storage. *Food Chem.* 175, 157–165. <https://doi.org/10.1016/j.foodchem.2014.11.111>.
- Li, D.M., Zhu, Z.W., Sun, D.W., 2018. Effects of freezing on cell structure of fresh cellular food materials: a review. *Trends Food Sci. Technol.* 75, 46–55. <https://doi.org/10.1016/j.tifs.2018.02.019>.
- Lines, J.A., Spence, J., 2014. Humane harvesting and slaughter of farmed fish. *Rev. Sci. Tech. Off. Int. Des. Epizoot.* 33 (1), 255–264. <https://doi.org/10.20506/rst.33.1.2284>.
- Lockwood, S.J., Pawsom, M.G., Eaton, D.R., 1983. The effects of crowding on mackerel (*Scomber scombrus* L.) - physical condition and mortality. *Fish. Res.* 2, 129–147.
- Losada, V., Barros-Velazquez, J., Aubourg, S.P., 2007. Rancidity development in frozen pelagic fish: Influence of slurry ice as preliminary chilling treatment. *Lwt Food Sci. Technol.* 40 (6), 991–999. <https://doi.org/10.1016/j.lwt.2006.05.011>.
- Marçalo, A., Mateus, L., Correia, J.H.D., Serra, P., Fryer, R., Stratoudakis, Y., 2006. Sardine (*Sardina pilchardus*) stress reactions to purse seine fishing. *Mar. Biol.* 149 (6), 1509–1518. <https://doi.org/10.1007/s00227-006-0277-5>.
- Marçalo, A., Breen, M., Tenningen, M., Onandia, I., Arregi, L., Gonçalves, J.M.S., 2019. Mitigating slipping-related mortality from purse seine fisheries for small pelagic fish: case studies from European Atlantic waters. In: Uhlmann, S., Ulrich, C., Kennelly, S. (Eds.), *The European Landing Obligation*, 1st ed. Springer, Cham, pp. 297–318.
- Nordgreen, A.H., Slinde, E., Møller, D., Roth, B., 2008. Effect of various electric field strengths and current durations on stunning and spinal injuries of Atlantic herring. *J. Aquat. Anim. Health* 20 (2), 110–115. <https://doi.org/10.1577/h07-010.1>.
- Olsen, R.E., Oppedal, F., Tenningen, M., Vold, A., 2012. Physiological response and mortality caused by scale loss in Atlantic herring. *Fish. Res.* 129, 21–27. <https://doi.org/10.1016/j.fishres.2012.06.007>.
- Olsen, S.H., Tobiassen, T., Akse, L., Evensen, T.H., Midling, K.O., 2013. Capture induced stress and live storage of Atlantic cod (*Gadus morhua*) caught by trawl: consequences for the flesh quality. *Fish. Res.* 147, 446–453. <https://doi.org/10.1016/j.fishres.2013.03.009>.
- Roth, B., Øines, S., Rotabakk, B.T., Birkeland, S., 2008. Using electricity as a tool in quality studies of Atlantic salmon. *Eur. Food Res. Technol.* 227 (2), 571–577. <https://doi.org/10.1007/s00217-007-0758-x>.
- Sato, K., Uratsui, S., Sato, M., Mochizuki, S., Shigemura, Y., Ando, M., 2002. Effect of slaughter method on degradation of intramuscular type V collagen during short-term chilled storage of chub mackerel *Scomber japonicus*. *J. Food Biochem.* 26 (5), 415–429. <https://doi.org/10.1111/j.1745-4514.2002.tb00763.x>.
- Sone, I., Skara, T., Olsen, S.H., 2019. Factors influencing post-mortem quality, safety and storage stability of mackerel species: a review. *Eur. Food Res. Technol.* 245 (4), 775–791. <https://doi.org/10.1007/s00217-018-3222-1>.
- SSB, 2021. Fisheries (terminated in Statistics Norway). Retrieved from (<https://www.ssb.no/en/fiskeri>).
- Suuronen, P., Erickson, D.L., Orrensalo, A., 1996. Mortality of herring escaping from pelagic trawl codends. *Fish. Res.* 25 (3–4), 305–321. [https://doi.org/10.1016/0165-7836\(95\)00446-7](https://doi.org/10.1016/0165-7836(95)00446-7).
- Svalheim, R.A., Aas-Hansen, O., Heia, K., Karlsson-Drangsholt, A., Olsen, S.H., Johnsen, H.K., 2020. Simulated trawling: Exhaustive swimming followed by extreme crowding as contributing reasons to variable fillet quality in trawl-caught Atlantic cod (*Gadus morhua*). *PLoS One* 15 (6), 0234059. <https://doi.org/10.1371/journal.pone.0234059>.
- Tenningen, M., Vold, A., Olsen, R.E., 2012. The response of herring to high crowding densities in purse-seines: survival and stress reaction. *ICES J. Mar. Sci.* 69 (8), 1523–1531. <https://doi.org/10.1093/icesjms/fss114>.
- Tenningen, M., Pobitzer, A., Handegard, N.O., de Jong, K., 2019. Estimating purse seine volume during capture: implications for fish densities and survival of released unwanted catches. *ICES J. Mar. Sci.* 76 (7), 2481–2488. <https://doi.org/10.1093/icesjms/fsz119>.

- van de Vis, H., Kestin, S., Robb, D., Oehlenschläger, J., Lambooi, B., Munkner, W., Nesvadba, P., 2003. Is humane slaughter of fish possible for industry? *Aquac. Res.* 34 (3), 211–220. <https://doi.org/10.1046/j.1365-2109.2003.00804.x>.
- Veliyulin, E., Felberg, H.S., Digre, H., Martinez, I., 2007. Non-destructive nuclear magnetic resonance image study of belly bursting in herring (*Clupea harengus*). *Food Chem.* 101 (4), 1545–1551. <https://doi.org/10.1016/j.foodchem.2006.04.007>.
- Zimmermann, F., Heino, M., 2013. Is size-dependent pricing prevalent in fisheries? The case of Norwegian demersal and pelagic fisheries. *ICES J. Mar. Sci.* 70 (7), 1389–1395. <https://doi.org/10.1093/icesjms/fst121>.