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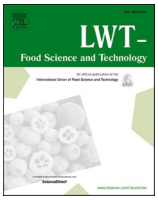

The effect of fishing season and storage conditions on the quality of European plaice (*Pleuronectes platessa*)

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ABSTRACT

The combined effect of fishing season (September/April) and storage conditions on the quality of European plaice (*Pleuronectes platessa*) was investigated. Investigated storage conditions were; fillets packaged in vacuum or a modified atmosphere (MA; 70% CO_2, 20% N_2, 10% O_2) and stored at 4 °C. As a control, whole fish on ice (0 °C) was used, representing the commercial standard. Plaice showed in general lower quality in April than September, demonstrated by a faster microbial evolution, higher content of biogenic amines, and higher rate of ATP degradation representing by K- and H-values. MA-fillets and whole fish on ice showed lower K- and H-values and biogenic amines content than fillets packaged in vacuum. VP-fillets had the lowest microbial quality as demonstrated by the shortest lag-phase of psychrotrophic aerobic plate count and aerobic bacteria, and the highest maximum specific growth rate of H_2S-producing bacteria. MA packaging significantly reduced microbial growth; however, MA-fillets showed the lowest water content and the highest drip loss and water holding capacity. No differences between groups were observed in colour intensity or hue angle at the storage end. Despite the significant seasonal variations, MA packaging stands out as the best solution to maintain the freshness of convenient retail plaice products.

1. Introduction

European plaice (*Pleuronectes platessa*) is one of the most widespread flatfish species in the North Sea (Madsen et al., 2013) and is a significant by-catch in many North-Western European fisheries (Bayse et al., 2016). The most significant catches are landed in the Netherlands, followed by Denmark and the United Kingdom (EUMOFA, 2016). The agreed quota in the North Sea and Skagerrak was 162,607 tons in 2021 (ICES, 2021), while the total landings of plaice in Norway were 794 tons (whole fish equivalent) (Directorate of Fisheries). Compared to the quota, the low percentage of caught plaice in Norway is due to its low commercial value. Although there is no official record, one part of the caught plaice is traded as a fresh whole fish on ice in the Norwegian fish market, and the rest is exported to Europe as fresh or frozen whole fish. The trend of consumers preferring convenient seafood products (Carlucci et al., 2015) represent a potential for value-added product development of plaice to increase its commercial use, domestic consumption, and exportable quantity.

Modified atmosphere-packaging (MAP) and vacuum-packaging (VP) combined with low temperature are used to prolong the shelf life of raw seafood, counteracting deteriorative effects during storage due to microbial and endogenous enzymatic activity (Bouletis et al., 2017). However, seafood's physicochemical and microbial quality can be affected differently by implementing these packaging technologies, as demonstrated in many studies (Esteves et al., 2021; Silbande et al., 2018). Moreover, it is well known that seasonal variation affects the quality of fresh fish (Cardoso et al., 2021; DurmuŞ et al., 2014; Grigorakis et al., 2003; Ntzimani et al., 2022; Papaharisis et al., 2019; Parlapani et al., 2021; Tzikas et al., 2007).

Plaice, like other seafood, is highly perishable, and the quality deteriorates fast due to enzymatic and microbial activity and oxidations (Gram & Huss, 1996). To our knowledge, there is no research on the physicochemical and microbial quality of plaice caught in Northern Europe. Moreover, literature on optimal packaging and storage conditions of plaice as well as seasonal quality variations, are limited. Therefore, the aim of this study was to investigate the combined effect of fishing season and storage conditions on microbial growth, metabolites, and physicochemical parameters during cold storage. Plaice was caught in September and April. Plaice fillets were packaged in either vacuum or modified atmosphere (70% CO_2, 20% N_2, 10% O_2) and stored at 4 °C.

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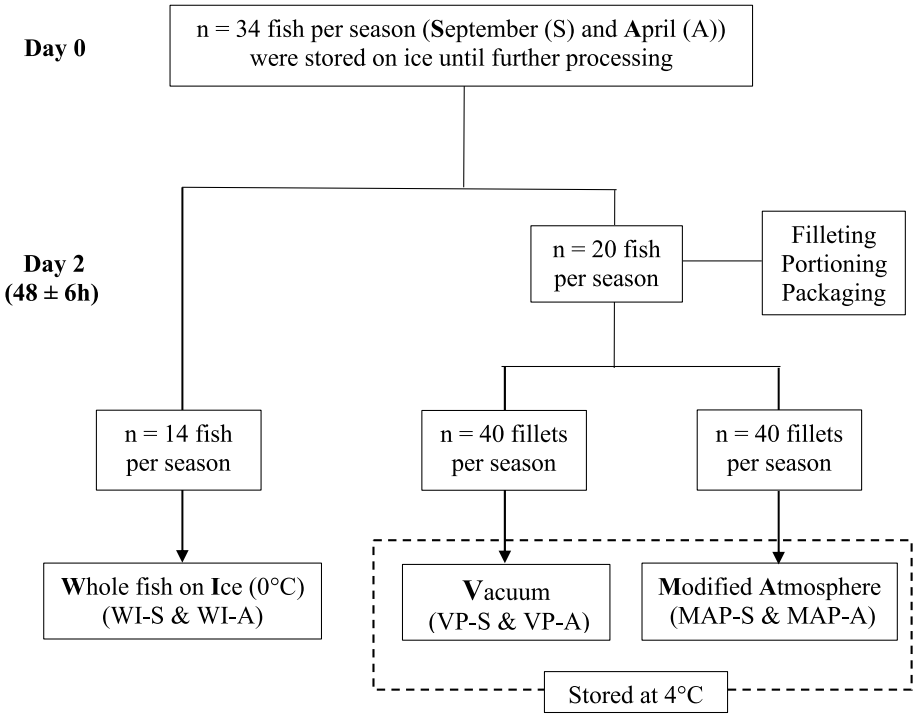

Fig. 1. Experimental overview. Thirty-four fish per season were stored on ice until further processing. On day 2 (48 ± 6 h), 14 fish per season were randomly selected, wrapped in plastic film, and stored as a whole fish on ice (WI–S and WI-A). The remaining fish (n = 20 per season) were filleted, deskinned, randomly distributed, and packaged in either vacuum (VP–S and VP-A) or modified atmosphere (70% CO_2, 20% N_2, 10% O_2) (MAP-S and MAP-A).

Whole fish stored on ice (0 °C) was selected as a commercial standard since it is the most predominant form of trading plaice in the Norwegian market. Increased knowledge of quality measures of plaice can increase the utilisation and commercial value through the production of high-quality, convenient retail plaice products.

2. Material and methods

2.1. Raw material and experimental design

Plaice used in the present study was caught in September 2020 and April 2021 by local fishermen using purse seine on the west coast of Norway (approximately 62.75°N, 6.51°S). The seawater temperature was 13 °C in September and 5.4 °C in April. The average weight of whole fish was 0.98 ± 0.31 kg in September and 0.93 ± 0.38 kg in April. The fresh-caught plaice (measured within 1 h after catch) had a pH value of 7.6 ± 0.1 in September (S) and 7.7 ± 0.2 in April (A). The fish (n = 34 per season) were instantly killed before being gutted, packaged in expanded polystyrene boxes with ice slurry, and transported within 12 h to the laboratory and stored until further processing.

A factorial design was set up to study seasonal variations and storage conditions on the physicochemical characteristics, microbial growth kinetic parameters, and autolytic and microbial deterioration of European plaice (Fig. 1). Plaice fillets were packaged in vacuum (VP–S and VP-A) and modified atmosphere (MAP-S and MAP-A) and stored at 4 °C. Whole fish on ice (WI–S and WI-A) was selected as a control group representing the commercial standard (0 °C).

On day 2 (48 ± 6 h), 14 fishes per season (WI–S and WI-A) were randomly selected, wrapped in plastic film, and stored on ice. The rest of the fish (n = 20) were filleted. Due to the plaice's morphology, four fillets were obtained from each fish (upper loin, upper belly, bottom loin, bottom belly). The fillets were deskinned, randomly distributed, and packaged in either vacuum (VP–S and VP-A) or modified atmosphere (MAP-S and MAP-A).

2.2. Packaging

VP-S and VP-A were packaged in 20-μm polyamide (PA)/70-μm polyethylene (PE) bags (160 × 200 mm, oxygen transmission rate (OTR) 50 $cm^3/m^2 \times 24\ h \times bar$ at 23 °C, Star-Pack Productive, Boissy-l'Aillerie, France) with a Webomatic Supermax-C vacuum machine (Webomatic, Bochum, Germany). Air was evacuated to an end pressure of 10 mbar before sealing. MAP-S and MAP-A were placed in 230 mL semi-rigid crystalline polyethylene terephthalate (CPET) trays (C2125–1B, OTR 66–78 $cm^3 \times 25\ \mu m/m^2 \times 24\ h \times bar$ at 23 °C, Færch Plast, Holstebro, Denmark) with an absorbent underneath using a semi-automatic tray sealing packaging machine (TL250, Webomatic, Germany) to obtain a gas:product ratio of 1:2. The air was evacuated to an end pressure of 30 mbar before the trays were filled with the pre-set packaging gas mixtures before heat sealing of the top film (40-μm PE, ethylene vinyl alcohol (EVOH), PA and PET) (Topaz B-440 AF, OTR 2.5 $cm^3 \times 40\ \mu m/m^2 \times 24\ h \times atm$ at 23 °C, Plastopil, Almere, The Netherlands). CO_2, N_2 and O_2 (food grade quality) were mixed using a MAP Mix 9000 gas mixer (Dansensor, Ringsted, Denmark) to obtain a packaging atmosphere of 70% CO_2, 20% N_2 and 10% O_2. To ensure the correct settings, the gas composition was measured in six dummies (sealed packages without products) with an O_2 and CO_2 analyser (Checkmate 9900 analyser, Dansensor). A rubber septum (Nordic Supply, Skodje, Norway) was placed on the sealing foil before inserting the syringe for headspace gas collection to avoid the introduction of the surrounding atmosphere. The initial packaging gas composition (day 2) of the MAP-S fillets was CO_2 = 70.3 ± 0.4%, O_2 = 10.3 ± 0.1%, and N_2 = 19.4 ± 0.1%, and MAP-A fillets was CO_2 = 70.3 ± 0.3%, O_2 = 10.0 ± 0.1% and N_2 = 19.7 ± 0.5%. To control the packages' quality (MAP-S and MAP-A), the gas composition was also measured on day 4, 7, 9, 10, 14, 16, 17, and 20. The packaging gas composition analysis was performed in triplicates (n = 3) for each group at each sampling point.

2.3. Microbial analysis

Microbial analysis was performed in triplicates (n = 3) for each group on days 2, 4, 7, 10, 14, and 17 (VP) and days 2, 4, 7, 10, 14, 17, and 20 (WI and MAP). *Listeria monocytogenes* and Enterobacteriaceae were determined at day 2 and at the end of the storage trial (VP: 17th day; WI/MAP: 20th day). A 10-g sample of fish muscle was aseptically transferred to a sterile stomacher bag and diluted 1:10 with sterile peptone water (1.0 g bacteriological peptone (Lyngby, Oxoid, Oslo, Norway) and 8.5 g/L NaCl (AnalaR NORMAPUR® ACS)) and homogenised vigorously for 120 s in a Stomacher 400 Lab Blender (Seward Medical Ltd., UK). Appropriate serial dilutions were made in sterile peptone water and spread on or moulded in their respective agar plates.

Aerobic bacteria (APC) and H_2S-producing bacteria were quantified as total and black colonies, respectively, by pour plating on iron agar (Oxoid) supplemented with 0.04% L-cysteine (Sigma-Aldrich, Oslo, Norway). Plates were incubated at 22 °C for 72 h. Psychrotrophic aerobic plate count (PC) was quantified by spreading on Long and Hammer agar (LH) with 1% NaCl, in order to support the growth of the salt requiring *Photobacterium phosphoreum* (NMKL No. 184, 2006). Plates were incubated at 15 °C for six days. Lactic acid bacteria (LAB) were quantified by spreading on de Man, Rogosa and Sharp agar (MRS) (Oxoid) that was incubated under anaerobic conditions at 25 °C for five days. Enterobacteriaceae was quantified using violet-red-bile-glucose agar (VRBGA) (Oxoid) by pour plating and incubated at 37 °C for 24 h. *Pseudomonas* spp. was quantified on Pseudomonas agar base (CM0559, Oxoid) supplemented with Pseudomonas CFC selective supplement SR0103 (Oxoid) by spread plating and incubated aerobically at 25 °C for 48 h. *Brochothrix thermosphacta* was quantified using STAA agar base (CM0881) supplemented with STA selective supplement SR0162 (Oxoid) by spread plating and incubated aerobically at 22 °C for 48 h. Presumptive *Listeria monocytogenes* were quantified on Brilliance Listeria agar (Oxoid) supplemented with Brilliance Listeria Supplement (Oxoid). The plates were incubated at 37 °C and read after 24 and 48 h. Microbial counts were expressed as log CFU/g.

2.4. Metabolites analysis

Metabolite analysis samples were taken on days 2, 10, 17 (VP) and days 2, 10, 20 (WI and MAP) and kept at −80 °C until extraction and further analysis. All analyses were performed in triplicates (n = 3) for each group at each sampling point. Frozen samples were shredded using a kitchen grater, and approximately 2.0 g (exact weight listed) was homogenised with trichloroacetic acid (TCA, 6%, 10 mL) for 2 min with an Ultra Turrax T25 Basic (Janke & Kunkel IKA®-Labortechnik, Staufen, Germany). The sample solution was thereafter added 1.5 mL of potassium hydroxide (KOH, 1 M), shaken lightly, and centrifuged (12,000 rpm, 4 °C, 10 min) in a Kubota 1700 centrifuge (Kubota corporation, Tokyo, Japan) before the supernatant was filtered through a nylon filter (0.45 μm). One part of the supernatant was transferred to HPLC vials (Agilent, 862-09-16, 2 mL) for ATP-degradation products analysis, while another part was used for biogenic amines analysis. The degradation products of ATP were determined as described by Lerfall et al. (2018). The K-value and H-value were calculated by using the formulas (Hong et al., 2017); K-value (%) = [(HxR + Hx)/(ATP + ADP + AMP + IMP + HxR + Hx)] × 100, and H-value (%) = [Hx/(IMP + HxR + Hx)] × 100, where HxR is inosine, Hx is hypoxanthine, ATP is adenosine triphosphate, ADP is adenosine diphosphate, AMP is adenosine monophosphate, and IMP is inosine monophosphate.

The supernatant for biogenic amines analysis was neutralised by using potassium hydroxide (KOH, 1 M) and derived with benzyl-chloride (99%, Sigma-Aldrich, CAS: 98-88-4) according to Özogul et al. (2002). The reaction time was set to 20 min at room temperature. Benzyl-amines were thereafter extracted two times with diethyl ether. The upper organic layer was transferred to a glass tube and evaporated to dryness (N_2, 30 °C) before the residue was dissolved in a mixture of acetonitrile and water (90:10). The biogenic amines were quantified according to Lerfall et al. (2018).

2.5. Physicochemical parameters

2.5.1. Muscle pH, drip loss, water holding capacity and water content

The muscle pH was measured on days 0, 2, 4, 7, 9, 10, 14, 16, 17, and 20 of the storage trial while samples for drip loss (DL), water content (WC), and water holding capacity (WHC) were taken on days 2, 9, and 16 of the storage trial. All analyses were performed in triplicates (n = 3) for each group at each sampling point, except for the drip loss of WI-S and WI-A where n = 7 for all sampling days. Muscle pH was measured using a portable pH meter (Hach HQ40d multi–Portable Meter, Hach, USA) equipped with a puncture pH electrode (Hach Intellical™ PHC108, Hach, CO, USA). DL was calculated gravimetrically as the percentage difference (%) of the weighed sample (g) to its initial weight (g) (initial average weight ± SD, WI-S: 810 ± 89.2; VP-S: 122.6 ± 15.9; MAP-S: 85.9 ± 1.3; WI-A: 694 ± 106.2; VP-A: 135.4 ± 22.9; MAP-A: 81.2 ± 1.5). WHC and WC was measured based on the low-speed centrifugation method of Skipnes et al. (2007). The muscle sample (~5 g) was punched with a metal cylinder (diameter 31 mm, height 6 mm) and transversally sliced into 2 pieces. Weighed top piece was placed in metal carriers (Part No. 4750, Hettich Lab Technology, Germany) and centrifuged (Rotina 420 R, Hettich Lab Technology, Germany) at 1800 rpm (15 min, 4 °C). The bottom piece was weighed and dried to analyse contents of dry matter, thereby WC, by drying at 105 °C for 16–18 h to constant weight.

2.5.2. Colour analysis

Colour was measured on days 2, 9, and 16 of the storage trial. Colorimetric analyses were performed in n = 34 (September) and n = 42 (April) replicates on day 2, and in triplicates (n = 3) for each group for the rest of the sampling days. The surface colour (CIE Lab) was measured on a DigiEye full system, VeriVide Ltd., Leicester, UK. The samples were placed in a standardised light-box (daylight, 6400 K) and photographed using a digital camera (Nikon D80, 35 mm lens, Nikon Corp., Japan). The software DigiPix (version 2.8) was used to calculate L*a*b* values from RGB values obtained from the fillet image where L* represents lightness, a* redness and b* yellowness (CIE, 1994). Chroma (C*) and hue angle (h*) was calculated by using the formulas; $C^* = (a^{*2} + b^{*2})^{1/2}$ and h* = arctan (b*/a*). Total colour difference (ΔE) was calculated based on CIE (1994).

2.5.3. Texture analysis

Texture analysis was performed on days 2 and 9. Texture was measured in n = 16 (September) and n = 21 (April) replicates on day 2, and in triplicates (n = 3) for each group on day 9. Instrumental textural analyses were performed on each sample using a Texture Analyser TA-XT plus (Stable Micro Systems Ltd, England) equipped with a 5-kg load cell and a flat-ended cylindrical probe (12.7 mm P/0.5). Force-time graphs were recorded and analysed by Texture Exponent light software for Windows (version 4.12, SMS). The breaking force was measured as the force (N) recorded when the breakage of the sample surface was observed. Textural measurement was performed with a constant speed of 2 mm/s.

2.6. Statistics and estimation of growth kinetics parameters

Statistical analyses were performed using an IBM SPSS statistics software (release 28, IBM Corporation, USA). Statistical analysis of microbial counts was done on log-transformed data. Log-transformed counts of PC, APC and H_2S-producing bacteria were fitted to the primary growth model of Baranyi and Roberts (1994) by applying the DMFit program available at www.combase.cc. Bacterial counts and estimated growth kinetics parameters are presented as mean values ± SE. All the other results are given as mean values ± SD. The data were analysed by a general linear model (GLM) with storage conditions and

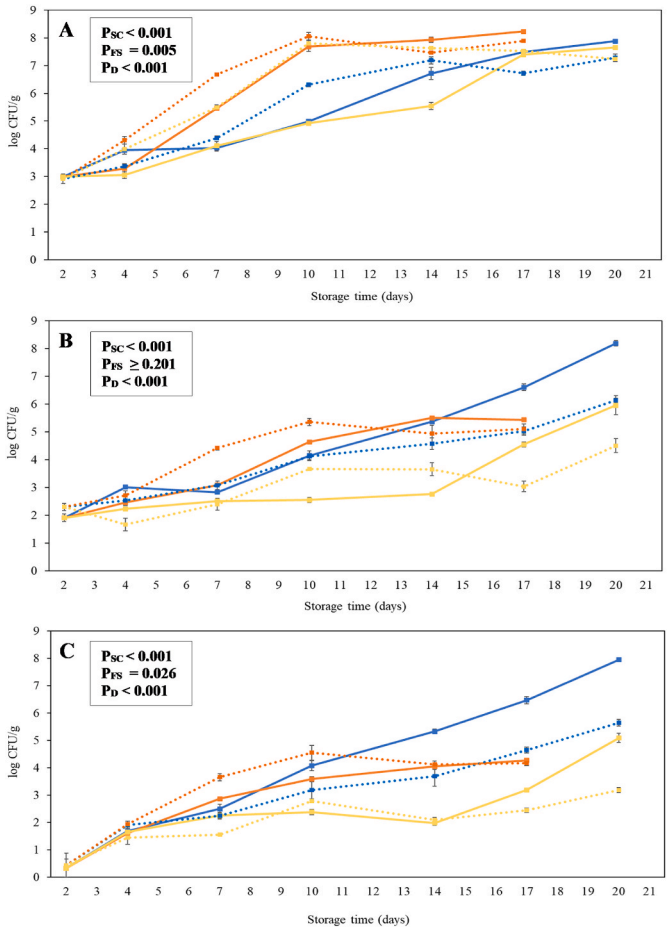

Fig. 2. Evolution of (**A**) psychrotrophic aerobic plate count (PC), (**B**) aerobic bacteria (APC) and (**C**) H_2S-producing bacteria in plaice caught at different seasons and stored at different storage conditions. Legends: Whole fish on ice-September (WI–S) (—■—); Vacuum packaged fillets-September (VP–S) (—●—); Modified atmosphere packaged fillets-September (MAP-S) (—▲—); Whole fish on ice-April (WI-A) (···■···); Vacuum packaged fillets-April (VP-A) (···●···); Modified atmosphere packaged fillets-April (MAP-A) (···▲···). Bars represent one standard error (n = 3). P_{SC}, P_{FS} and P_D are the significant levels (GLM) for the effects of storage conditions, fishing season and storage time, respectively.

season as fixed factors and storage time (days) as a covariate. Significant differences between experimental groups were analysed by one-way ANOVA combined with Tukey's pairwise comparison test. The significance level was set to 5% ($P < 0.05$). Pearson's correlation coefficient (r) was used to calculate the linearity dependence between variables X and Y.

3. Results & discussion

3.1. Seasonal variations in the quality of raw material

The reproductive season of plaice is usually from December to March in the North Sea (Hufnagl et al., 2013), indicating the plaice caught in September and April to be in a pre- and post-spawning condition, respectively. The initial pH of freshly caught plaice ranged between 7.6 and 7.7 at both seasons showing careful handling and good capturing routines (Morzel et al., 2003). No significant seasonal variations were found in the initial microbial loads of fillets. The initial microbial counts indicated high quality of the raw material and satisfactory hygiene conditions of the fishing vessel since the mean initial PC, APC and H_2S-producing bacteria counts were lower than 3 log CFU/g, 2.3 log CFU/g and 1 log CFU/g, respectively. Additionally, no *Pseudomonads* spp., *Brochothrix thermosphacta*, Enterobacteriaceae and *Listeria monocytogenes* were detected in the fresh plaice muscle in either season.

The plaice caught in September had significantly lower initial K-value and H-value (14.9% and 3.3%, respectively) compared to the April catch (26% and 6.9%, respectively). In the present study, K-values were in the range of 6–33% which have been previously reported in various flatfish species (Özogul et al., 2006, 2011). The initial WC, WHC and breaking force did not significantly differ between the seasons, while significant differences were found in the colorimetric characteristics of freshly caught fish. Fillets from the September catch were less translucence, more reddish, less yellowish, and had a lower colour intensity, and a hue angle closer to the orange side of the spectra compared to those from April.

Table 1
Growth kinetic parameters (maximum specific growth rate (μ_{max}, day^{-1} ± SE), lag-phase duration (days) and maximum population density (Y_{max}, log CFU/g ± SE) in plaice caught at different seasons and stored at different storage conditions for psychrotrophic aerobic plate count (PC), aerobic bacteria (APC) and H_2S-producing bacteria.

Treatments	Lag-phase (days)	μ_{max} (day^{-1})	Y_{max} (log CFU/g)	R^2	SE
PC					
WI-S	3.25 ± 0.17^{a}	0.38 ± 0.04^{d}	7.88 ± 0.12^{bc}	0.97	0.31
VP-S	2.08 ± 0.18^{b}	0.92 ± 0.09^{a}	8.08 ± 0.10^{ab}	0.99	0.35
MAP-S	2.17 ± 0.31^{b}	0.32 ± 0.02^{d}	8.24 ± 0.12^{a}	0.96	0.35
WI-A	2.50 ± 0.22^{b}	0.61 ± 0.04^{c}	7.07 ± 0.04^{e}	0.98	0.26
VP-A	0.17 ± 0.10^{d}	0.86 ± 0.03^{ab}	7.63 ± 0.05^{cd}	0.98	0.31
MAP-A	1.12 ± 0.10^{c}	0.69 ± 0.02^{bc}	7.55 ± 0.03^{d}	0.97	0.32
*P-value**	*< 0.001*	*< 0.001*	*< 0.001*		
APC					
WI-S	3.89 ± 0.74^{b}	0.40 ± 0.03	NA^{x}	0.97	0.37
VP-S	2.47 ± 0.55^{c}	0.47 ± 0.03	5.49 ± 0.08^{b}	0.98	0.19
MAP-S	11.10 ± 0.36^{a}	0.55 ± 0.07	6.05 ± 0.39^{a}	0.95	0.33
WI-A	1.93 ± 0.66^{cd}	0.35 ± 0.08	NA^{x}	0.95	0.29
VP-A	1.53 ± 0.33^{d}	0.63 ± 0.05	5.14 ± 0.16^{b}	0.94	0.32
MAP-A	3.12 ± 1.29^{b}	0.41 ± 0.07	3.74 ± 0.20^{c}	0.74	0.55
*P-value**	*< 0.001*	*0.385*	*< 0.001*		
H_2S-producing bacteria					
WI-S	ND	0.41 ± 0.04^{bc}	NA^{l}	0.98	0.34
VP-S	ND	0.48 ± 0.07^{b}	4.07 ± 0.35^{a}	0.95	0.32
MAP-S	ND	0.37 ± 0.06^{cd}	NA^{l}	0.74	0.72
WI-A	ND	0.26 ± 0.02^{d}	NA^{l}	0.91	0.51
VP-A	ND	0.79 ± 0.08^{a}	4.25 ± 0.31^{a}	0.94	0.39
MAP-A	ND	0.27 ± 0.06^{d}	2.62 ± 0.35^{b}	0.71	0.50
*P-value**		*< 0.001*	*< 0.001*		

R^2, coefficient of determination; SE, standard error of fit to the model; $NA^{x,l}$, not analysed due to no asymptote, linear model, respectively; ND, not detected.
Whole fish on ice-September (WI–S); Vacuum packaged fillets-September (VP–S); Modified atmosphere packaged fillets-September (MAP-S); Whole fish on ice-April (WI-A); Vacuum packaged fillets-April (VP-A); Modified atmosphere packaged fillets-April (MAP-A).
*Anova was applied to detect differences in lag-phase, maximum specific growth rate (μ_{max}) and maximum population density (Y_{max}); where significant differences were detected ($P < 0.05$), a Tukey's pairwise comparison test was applied.
[a–e]Different superscript letters within each column and each parameter indicate significant differences ($P < 0.05$) between treatments.

3.2. Storage quality

3.2.1. Microbial evolution

The evolution of microbial counts and growth kinetics as a function of storage conditions, storage time and fishing season are presented in Fig. 2 and Table 1. The storage conditions and storage time significantly affected the microbial evolution of PC, APC, H_2S-producing bacteria, LAB, and *Pseudomonas* spp. ($P < 0.001$). The fishing season significantly affected the PC, H_2S-producing bacteria, and LAB counts ($P < 0.027$), whereas APC ($P \geq 0.201$) and *Pseudomonas* spp. ($P \geq 0.428$) were not affected.

The WI-S was the only treatment that surpassed the upper acceptable APC limit of 7 log CFU/g for marine species suitable for human consumption (ICMSF, 1986) on the last day of the storage trial. However, in the present study, higher PC than APC counts were found at all sampling points, and all groups reached PC counts higher than 7 log CFU/g at the end of storage (Fig. 2A and B). The high PC loads can be attributed to the high prevalence *Photobacterium* spp., as *Photobacterium* spp. are a common psychrotrophic spoilage organism in marine cold-water fish species (Dalgaard et al., 1993). *Photobacterium* spp. counts higher than 7 log CFU/g indicate microbial spoilage and sensory rejection of seafood (Dalgaard et al., 1997; Kuuliala et al., 2018). Based on the PC counts, the storage trials of the VP-groups were terminated earlier than the others (17 days vs 20 days). In general, PC counts might be a better indicator for microbiological spoilage in marine cold-water fish species than APC.

The shortest lag-phase and the highest μ_{max} of PC (Table 1) were observed for VP-groups in both seasons, reaching Y_{max} (7–8 log CFU/g) on the 10th day (Fig. 2A). The μ_{max} of PC in VP-S was 2.9–2.4 times higher than for MAP-S and WI-S, respectively. However, a lower effect on the PC growth rate was seen for the April samples. Randell et al. (1999) and Hansen et al. (2009) have also reported faster evolution of PC counts in VP compared to MAP salmon. The presence of CO_2 in the MAP-groups resulted in significantly lower μ_{max} of PC than observed for VP-groups and was almost comparable to WI-groups. Devlieghere and Debevere (2000) stated the linear relationship between the concentration of dissolved CO_2 in the food matrix and the μ_{max} of Gram-negative bacteria, including *P. phosphoreum*. However, the psychrotrophic *P. phosphoreum* is regarded as CO_2-tolerant as high *P. phosphoreum* counts ($>10^7$ log CFU/g) have been found in CO_2 equilibrum between 38 and 50% (Dalgaard et al., 1993, 1997; Kuuliala et al., 2018). The significantly longer lag-phase in WI-groups was expected due to lower storage temperature (0 °C vs 4 °C) and whole fish deteriorate slower than the fish fillets (Paleologos et al., 2004).

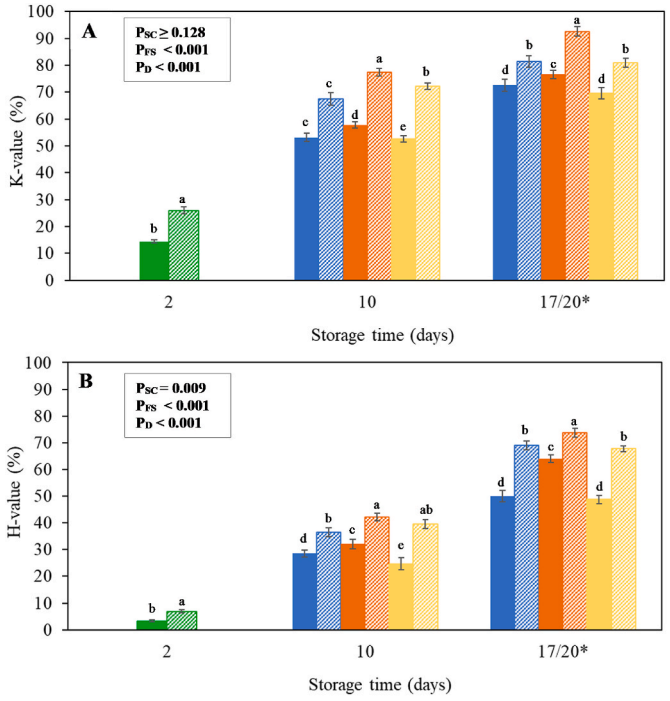

Fig. 3. K-value and H-value evolution in plaice caught at different seasons and stored at different storage conditions. Legends: Freshly caught fish-September (■); Freshly caught fish-April (▨); Whole fish on ice-September (WI–S) (■); Vacuum packaged fillets-September (VP–S) (■); Modified atmosphere packaged fillets-September (MAP-S) (■); Whole fish on ice-April (WI-A) (▨); Vacuum packaged fillets-April (VP-A) (▨); Modified atmosphere packaged fillets-April (MAP-A) (▨). [a–e]Different letters within each storage time (days) indicate significant differences ($P < 0.05$) between treatments. Bars represent one standard deviation ($n = 3$). P_{SC}, P_{FS} and P_D are the significant levels (GLM) for the effects of storage conditions, fishing season and storage time, respectively. *Comparison of K-value and H-value at the end of storage (17 days for VP-groups while 20 days for WI and MAP-groups).

H$_2$S-producing bacteria constitute one of the most relevant specific spoilage organisms in aerobically stored and vacuum packaged marine fish (Skjerdal et al., 2004). The absence of lag-phase confirms that H_2S-producing bacteria proliferated quickly ($P < 0.001$) and were dominant among the APC (Table 1, Fig. 2C). The proliferation of APC and H_2S-producing bacteria in WI-groups was slower than in VP-groups until the middle of the storage trial but WI-groups had the highest APC and H_2S-producing bacteria loads compared to VP and MAP-groups at the end of storage. A possible explanation for the slower growth in WI-groups at the first days of storage is the lower storage temperature (0 °C) due to the use of ice. However, Zotta et al. (2019) have reported the absence of H_2S-producing bacteria in thawed plaice fillets stored at 0 °C in air. Also, Baixas-Nogueras et al. (2007) have found lower counts of H_2S-producing bacteria in frozen-thawed than unfrozen Mediterranean hake stored on ice for 15 days. The possible sensitivity of H_2S-producing bacteria to freezing and thawing could explain the higher H_2S-producing bacteria in our study than thawed plaice. Moreover, Zotta et al. (2019) found higher μ_{max} and load of APC compared to our study.

The presence of CO_2 significantly extended the lag-phase of APC and reduced the μ_{max} of H_2S-producing bacteria, resulting in significantly lower APC and H_2S-producing bacteria counts in MAP-groups than in all other treatments. The bacteriostatic effect of CO_2 on APC have also been stated in other studies (Masniyom et al., 2002; Rodrigues et al., 2016). Although initial CO_2 headspace concentrations and gas:product ratio higher than 50% and 0.5, respectively, inhibit the growth of the H_2S-producing *Shewanella putrefaciens* (Lerfall et al., 2018), several studies have shown no complete inhibition of H_2S-producing bacteria in high initial CO_2 concentrations (Dalgaard et al., 1993; Hovda et al., 2007; Stamatis & Arkoudelos, 2007). Despite, *P. phosphoreum* is not commonly recognised as H_2S-producing bacteria (Dalgaard, 1995), its potential contribution to H_2S production would need to be further investigated.

The MAP-groups had the lowest *Pseudomonas* spp. counts ($P < 0.05$), while the WI-A and WI-S had the highest numbers of 5.6 ± 0.1 and 6.4 ± 0.1 log CFU/g, respectively, on the last day of the storage. Chilled marine cold-water fish stored aerobically are primarily spoiled by *Shewanella* and secondarily *Pseudomonas* species (Gram, 2009). Our study is in accordance with these results since *Pseudomonas* spp. followed the population of H_2S-producing bacteria at WI-S and WI-A treatments. *Pseudomonas* spp. are known to be CO_2-sensitive (Devlieghere & Debevere, 2000).

The VP and MAP-groups had the highest and lowest LAB concentrations ($P < 0.05$), respectively. Similar results have been reported in saithe fillets (Lerfall et al., 2018) and farmed Atlantic cod fillets (Hansen et al., 2007) packaged in vacuum and CO_2 equilibrium concentrations above 40%. Despite high CO_2 headspace concentration of MAP favouring LAB's growth (Devlieghere & Debevere, 2000), a delay in the proliferation of LAB has also been found at initial CO_2 headspace concentration higher than 40% (Kostaki et al., 2009; Sørensen et al., 2020; Yesudhason et al., 2014).

Table 2
Average content (mg/100g ± SD) (n = 3) of the biogenic amines cadaverine, tryptamine, spermidine and spermine in plaice caught at different seasons and stored at different storage conditions.

		Treatments						
Amine	**Day**	**WI-S**	**VP-S**	**MAP-S**	**WI-A**	**VP-A**	**MAP-A**	*P-value***
Cadaverine	2	0.09 ± 0.02^{C}	0.09 ± 0.02^{C}	0.09 ± 0.02^{C}	0.1 ± 0.03^{C}	0.1 ± 0.03^{C}	0.1 ± 0.03^{C}	*0.904*
	10	1.90 ± 0.22^{Bc}	2.32 ± 0.15^{Bc}	1.8 ± 0.3^{Bc}	2.45 ± 0.36^{Bbc}	4.30 ± 0.15^{Ba}	3.02 ± 0.37^{Bb}	*< 0.001*
	17/20*	4.53 ± 0.28^{Ab}	6.73 ± 0.5^{Aa}	3.7 ± 0.52^{Ac}	5.23 ± 0.10^{Ab}	7.34 ± 0.31^{Aa}	4.99 ± 0.19^{Ab}	*< 0.001*
	*P-value***	*< 0.001*	*< 0.001*	*< 0.001*	*< 0.001*	*< 0.001*	*< 0.001*	
Tryptamine	2	ND	ND	ND	ND	ND	ND	
	10	0.12 ± 0.02^{Bc}	0.17 ± 0.02^{Ba}	0.13 ± 0.01^{Bbc}	0.16 ± 0.01^{Bab}	0.15 ± 0.01^{Bab}	0.13 ± 0.03^{Bab}	*0.01*
	17/20*	0.26 ± 0.01^{A}	0.27 ± 0.03^{A}	0.26 ± 0.04^{A}	0.24 ± 0.04^{A}	0.26 ± 0.01^{A}	0.24 ± 0.04^{A}	*0.825*
	*P-value***	*< 0.001*	*< 0.001*	*< 0.001*	*< 0.001*	*< 0.001*	*< 0.001*	
Spermidine	2	0.06 ± 0.01^{C}	0.06 ± 0.01^{C}	0.06 ± 0.01^{C}	0.07 ± 0.01^{C}	0.07 ± 0.01^{C}	0.07 ± 0.01^{C}	*0.533*
	10	0.42 ± 0.02^{Bd}	0.63 ± 0.01^{Bb}	0.37 ± 0.02^{Bd}	0.50 ± 0.06^{Bc}	0.75 ± 0.01^{Ba}	0.53 ± 0.03^{Bc}	*< 0.001*
	17/20*	0.89 ± 0.05^{Acd}	1.03 ± 0.05^{Aab}	0.86 ± 0.04^{Ad}	1.01 ± 0.02^{Ab}	1.12 ± 0.06^{Aa}	0.97 ± 0.04^{Abc}	*< 0.001*
	*P-value***	*< 0.001*	*< 0.001*	*< 0.001*	*< 0.001*	*< 0.001*	*< 0.001*	
Spermine	2	0.04 ± 0.01^{C}	0.04 ± 0.01^{C}	0.04 ± 0.01^{C}	0.04 ± 0.01^{C}	0.04 ± 0.01^{C}	0.04 ± 0.01^{C}	*1.000*
	10	0.26 ± 0.01^{Bc}	0.36 ± 0.03^{Ba}	0.23 ± 0.05^{Bc}	0.24 ± 0.01^{Bc}	0.34 ± 0.04^{Bab}	0.28 ± 0.03^{Bbc}	*0.002*
	17/20*	0.57 ± 0.01^{Acd}	0.62 ± 0.01^{Abc}	0.55 ± 0.02^{Ad}	0.63 ± 0.02^{Aab}	0.67 ± 0.03^{Aa}	0.64 ± 0.04^{Aab}	*< 0.001*
	*P-value***	*< 0.001*	*< 0.001*	*< 0.001*	*< 0.001*	*< 0.001*	*< 0.001*	

Whole fish on ice-September (WI–S); Vacuum packaged fillets-September (VP–S); Modified atmosphere packaged fillets-September (MAP-S); Whole fish on ice-April (WI-A); Vacuum packaged fillets-April (VP-A); Modified atmosphere packaged fillets-April (MAP-A).
*Comparison of the biogenic amines content at the end of storage (17 days for VP−groups while 20 days for WI and MAP-groups)
**Anova was applied to detect differences in biogenic amines content; where significant differences were detected ($P < 0.05$), a Tukey's pairwise comparison test was applied.
$^{a-d}$Different superscript letters within each row and each parameter indicate significant differences ($P < 0.05$) between treatments.
$^{A-C}$Different superscript letters within each column and each parameter indicate significant differences ($P < 0.05$) throughout the storage time.
ND, not detected.

The fishing season significantly affected the PC evolution ($P = 0.005$). The PC counts were significantly higher in the April than September-groups until the middle of storage due to the higher μ_{max} and shorter lag-phase (Table 1, Fig. 2A). The seawater temperature was lower in April (5.4 °C vs 13 °C, respectively). Therefore, higher growth rates and shorter lag-phases were expected as the microbiota of fresh fish coming from colder water suffers a less intensive thermal shock when the fish is stored at low temperatures (Grigorakis et al., 2003).

Similarly, the lag-phase of APC was shorter in April than for September-groups, resulting in lower APC counts until the middle of the storage trial (Fig. 2B). On the other hand, no lag-phase was detected for H_2S-producing bacteria in either of the seasons. While no significant difference was found in either APC or H_2S-producing bacteria counts of VP-groups at the end of the storage trial, the APC and H_2S-producing bacteria counts were significantly higher in WI-S and MAP-S compared to the WI-A and MAP-A (Fig. 2B and C). The higher μ_{max} following these groups confirms the higher APC and H_2S-producing bacteria counts observed in WI-S and MAP-S samples. The apparent faster microbial deterioration of April-groups agrees with the results of other studies (DurmuŞ et al., 2014; Ntzimani et al., 2022; Papaharisis et al., 2019) which stated that the lower seawater temperatures at catching led to higher microbial deterioration.

No seasonal variations in the *Pseudomonas* spp. proliferation were found. The LAB concentration ranged between 2.4 and 3.2 log CFU/g in fillets from fish captured in September during the storage trial. Moreover, their counts remained significantly higher than those observed in April throughout storage. Dalgaard et al. (1993) also stated low levels of LAB populations (<4 log CFU/g) during VP and MAP storage of cod fillets.

Brochothrix thermosphacta was analysed at all sampling points but not detected in any sample. Potentially harmful bacteria, such as Enterobacteriaceae and *Listeria monocytogenes*, were analysed but not detected.

3.2.2. Metabolites

K-value and H-value as a function of storage conditions, storage time and fishing season are presented in Fig. 3. The storage conditions significantly affected the samples H-value ($P = 0.009$) but not the K-value ($P \geq 0.128$). Both measures were affected by season and storage time ($P < 0.001$). The VP-groups had significantly higher K and H-values in both seasons due to the significantly lower IMP and HxR content and higher Hx content in these groups (data not shown). The results indicate a similar delay in autolytic and microbial degradation of nucleotides for storage of plaice fillet in MAP (70% CO_2, 20% N_2, 10% O_2) at 4 °C as for the WI-groups (0 °C).

The K- and H-value observed in fillets from plaice caught in September remained significantly lower than April's catch through the entire storage period, indicating the comparative higher quality of plaice caught in September. Grigorakis et al. (2003) also reported higher K-values in winter than summer caught seabream after the middle of storage when microbial counts were significantly increased. A correlation ($P < 0.001$) was found between PC, APC, H_2S-producing bacteria and *Pseudomonas* spp. and the H-value ($r = 0.92, 0.84, 0.84, 0.68$, respectively), indicating increased microbial counts in April-groups have contributed to higher nucleotides' degradation.

Previous studies of various flatfish species reported a K-value above 70% at sensory rejection (Rodríguez et al., 2006; Özogul et al., 2006, 2011). The April treatments had already surpassed (VP-A and MAP-A) or was close (WI-A) to the above-mentioned sensory rejection limit in the middle of storage trial (Fig. 3A) when the PC counts were also quite high (>6.3 log CFU/g) (Fig. 2A). However, the VP-S had also high PC counts (7.2 ± 0.2 log CFU/g) on day 10, but its K-value was 58%.

The content of biogenic amines as a function of storage conditions, storage time and fishing season are given in Table 2. The storage time had a significant effect on the content of biogenic amines ($P < 0.001$). Tryptamine was the only biogenic amine that was not affected by the

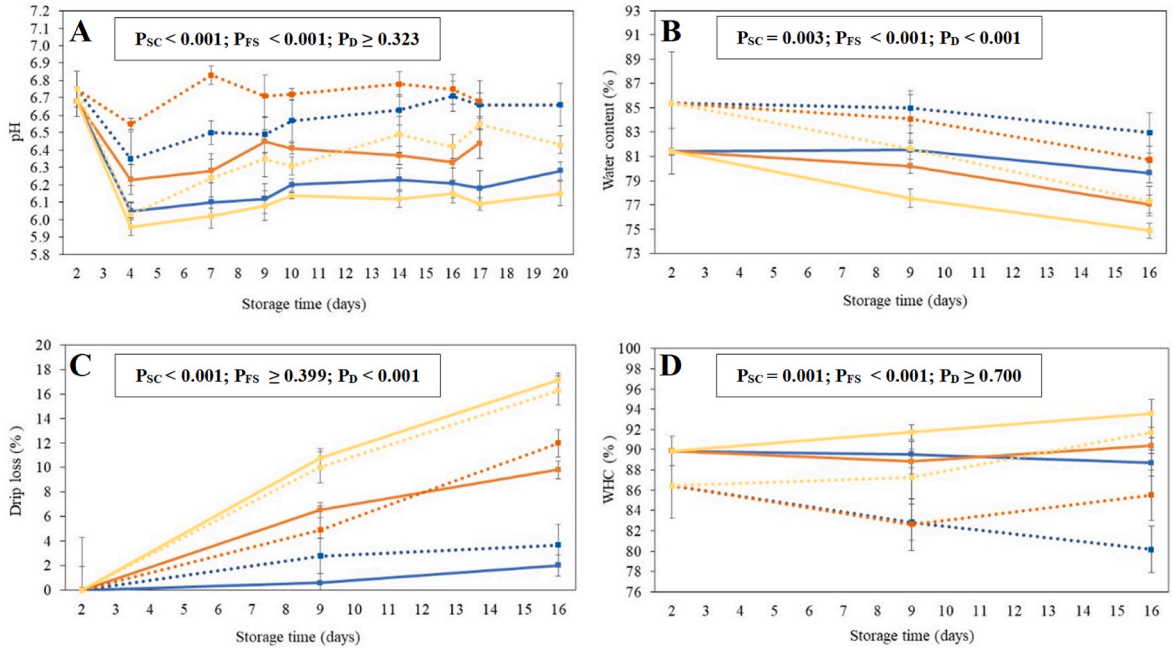

Fig. 4. Evolution of (**A**) muscle pH, (**B**) water content (WC) (%), (**C**) drip loss (DL) (%) and (**D**) water holding capacity (WHC) (%) in plaice caught at different seasons and stored at different storage conditions. Legends: Whole fish on ice-September (WI–S) (—■—); Vacuum packaged fillets-September (VP–S) (—■—); Modified atmosphere packaged fillets-September (MAP-S) (—■—); Whole fish on ice-April (WI-A) (···■···); Vacuum packaged fillets-April (VP-A) (···■···); Modified atmosphere packaged fillets-April (MAP-A) (···■···). Bars represent one standard deviation (n = 3, except for the DL of WI-S and WI-A where n = 7). P_{SC}, P_{FS} and P_D are the significant levels (GLM) for the effects of storage conditions, fishing season and storage time, respectively.

storage conditions and fishing season (P ≥ 0.226 and 0.670, respectively). Cadaverine became the dominant amines in all treatments during the storage trial, however lower than sensory rejection limit of 9.1 mg/100g (Vallé et al., 2020).

In general, VP-groups had the highest content of cadaverine, spermidine and spermine followed by WI and MAP-groups. A correlation (P < 0.001) was found between cadaverine, spermidine, spermine, and PC (r = 0.87, 0.92 and 0.87, respectively) as well as APC (r = 0.80, 0.86 and 0.86, respectively). A similar strong correlation between biogenic amines and PC or APC has been found in other seafood (Hu et al., 2012). The observed inhibitory effect of CO_2 on biogenic amine production agrees with other studies (Rodrigues et al., 2016; Özogul et al., 2002). The April catch had significantly higher average biogenic amines content than the September catch at the end of storage which could be attributed to the different patterns in the microbial evolution of PC and APC. Given that the formation rate and the final concentration of biogenic amines is considered a chemical indicator of seafood quality and decomposition (Laly et al., 2017; Prester, 2011; Ruiz-Capillas & Herrero, 2019), September catch seems to maintain better quality than April.

3.2.3. *Physicochemical quality deterioration*

3.2.3.1. *Muscle pH, drip loss, water content and water holding capacity.*

Changes in muscle pH, WC, WHC, and DL of plaice as a function of storage conditions, storage time and fishing season are illustrated in Fig. 4. No significant effect of storage time was found on muscle pH (P ≥ 0.323) and WHC (P ≥ 0.700). The DL was the only parameter that was not affected by the fishing season (P ≥ 0.399), while the storage conditions significantly affected muscle pH, WC, WHC, and DL (P < 0.004).

Several studies have reported no seasonal variations in muscle pH (Grigorakis et al., 2003; Tzikas et al., 2007). Contrastingly, in the present study, the muscle pH was significantly affected by season (P < 0.001). The pH of postmortem muscle depends on the glycogen content, and fish accumulate higher amounts of glycogen during the pre-spawning period (Kumari & Ahsan, 2011) and mature plaice hardly fed during the spawning period (Rijnsdorp, 1989). The muscle pH significantly decreased up to day 4 in all groups and remained significantly lower for September-groups (Fig. 4A) due to the possible production of higher amounts of lactic acid during anaerobic glycolysis. A correlation analysis was performed including the time interval from the recording of the lowest muscle pH in all groups (day 4) to the end of the storage trial. From this analysis, a significant correlation was found between the muscle pH and either fishing season (r = 0.68, P < 0.001) or microbial counts (r = 0.49 (PC), 0.35 (APC), 0.27 (H_2S-producing bacteria), P < 0.006). The possible accumulation of higher amounts of alkaline compounds due to higher microbial spoilage could contribute to higher pH in April-groups through the storage time which advocates the lower quality of April-groups. Moreover, the lower pH in September-groups could partially be attributed to higher LAB counts. MAP-groups had the lowest pH at all sampling points in either of the seasons (P < 0.05), due to the dissolution of CO_2 in the aqueous phase of the muscle tissue (Kostaki et al., 2009; Lerfall et al., 2018; Masniyom et al., 2002).

A linear increase in DL and a subsequent decrease in the WC was observed in all treatments as the storage days increased (Fig. 4B and C). The WC of VP and MAP-groups was significantly reduced during the storage. The MAP-groups had the highest DL and the lowest WC in all sampling points at both seasons, followed by VP and WI-groups. Moreover, a significant correlation was found between the WC and DL (r = −0.63, P < 0.001). Increased DL in MAP-groups compared to VP-groups has also been reported by Dalgaard et al. (1993) and Randell et al. (1999). The differences in pH between VP and MAP-groups as well as the significant correlation between the muscle pH and either DL (r = −0.49, P < 0.001) or WC (r = 0.64, P < 0.001) indicates that the capacity of fish proteins to hold water is reduced at lower pH. Although higher DL was expected in September-groups due to lower pH, no seasonal variation was found. The increased proteolytic activity caused by higher bacterial counts in April-groups could induce a faster muscle protein degradation as visualised with highest DL of April samples (Olsson et al., 2003). Moreover, April-groups have lower protein levels (Kendler et al., 2023) which probably creates a less strong protein matrix that, combined with

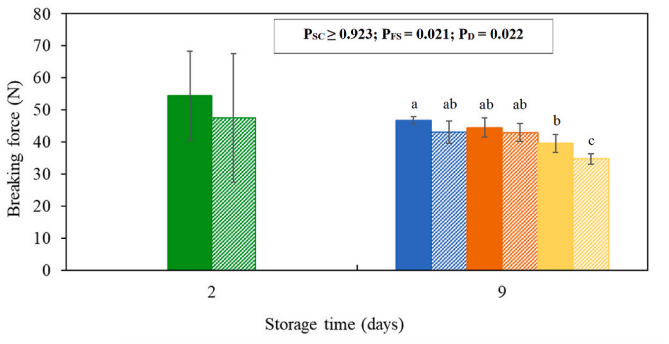

Fig. 5. Breaking force (N) changes in plaice caught at different seasons and stored at different storage conditions. Legends: Freshly caught fish-September (■); Freshly caught fish-April (▨); Whole fish on ice-September (WI–S) (■); Vacuum packaged fillets-September (VP–S) (■); Modified atmosphere packaged fillets-September (MAP-S) (■); Whole fish on ice-April (WI-A) (▨); Vacuum packaged fillets-April (VP-A) (▨); Modified atmosphere packaged fillets-April (MAP-A) (▨). $^{a–c}$Different letters within each storage time (days) indicate significant differences ($P < 0.05$) between treatments. Bars represent one standard deviation (n = 3, except for day 2 where n = 16 (September) and n = 21 (April)). P_{SC}, P_{FS} and P_D are the significant levels (GLM) for the effects of storage conditions, fishing season and storage time, respectively.

higher water concentrations, can lead to similar DL as the September-groups.

Independent of season, the WHC of WI-groups was continuously decreasing throughout the storage. However, increased WHC was observed in VP and MAP-groups on day 16 compared to day 2 of storage trial. These increased measures can be attributed to the "leaking-out" effect according to which the reduced WC can cause an increase in WHC during storage since the DL removes a large amount of free water. Similar observations have been reported in Atlantic cod (Herland et al., 2010) and halibut (Olsson et al., 2003). The WHC on the last sampling day of April-groups was significantly lower than those observed in September. As WHC is an important quality parameter (Chan et al., 2021), the higher ability of September-groups' muscle to retain water might indicate a better fish quality. Moreover, an inverse relationship between WHC and WC ($r = -0.47$, $P = 0.001$) was found.

3.2.3.2. Texture and colour parameters. The textural and colorimetric properties of plaice as a function of storage conditions, storage time, and fishing season are shown in Fig. 5 and Table 3. The breaking force ($P = 0.022$) as well as the L*, h*, and ΔE ($P < 0.001$) were significantly affected by the storage time. The ΔE was the only parameter that was not affected by the fishing season ($P \geq 0.760$), while the storage conditions did significantly affect the L* and ΔE ($P = 0.041$ and <0.001, respectively).

The observed decrease in the surface breaking force implies that the fillet structure tenderised during storage. The post-mortem softening could be associated with the degradation of myofibrillar proteins and the weakening of connective tissue due to the activity of autolytic enzymes (e.g. collagenase, ATPase) (Viji et al., 2015).

The fish fillets became less translucent, less reddish, and retained a slightly more yellowish colour throughout the storage time. No significant changes were found in the colour intensity, C* ($P \geq 0.203$), while the significant increase in h* value indicates that the fish muscle gradually leaned from orange-yellowish on day 2, to be more green-yellowish on day 16.

The MAP-groups were observed to be the least translucent, followed by VP and WI-groups ($P < 0.05$) while no significant difference was found in the C* and h* on the last day of analysis. The correlation between L* and both DL and WC ($r = 0.68$ and -0.46, respectively, $P < 0.001$) confirms that larger water deposits on fish surfaces could cause increased lightness (Duun & Rustad, 2008). Moreover, the dissolution of CO_2 in the fish muscle of MAP-groups caused the denaturation of sarcoplasmic proteins and increased flesh's lightness (Ruff et al., 2002). Poli et al. (2006) did also report higher lightness in European sea bass MAP-fillets compared to whole fish on ice at the end of storage.

According to C* and h*, the effect of the fishing season seemed to

Table 3
Changes in lightness (L*), chroma (C*), hue angle (h*) and total colour difference (ΔE) (mean ± SD) (n = 3, except for day 2 where n = 34 (September) and n = 42 (April)) in plaice caught at different seasons and stored at different storage conditions.

		Treatments						
	Day	**WI-S**	**VP-S**	**MAP-S**	**WI-A**	**VP-A**	**MAP-A**	*P-value**
L*	2	65.9 ± 3.5^{a}	65.9 ± 3.5^{Ba}	65.9 ± 3.5^{Ca}	59.7 ± 4.7^{Bb}	59.7 ± 4.7^{Bb}	59.7 ± 4.7^{Cb}	*< 0.001*
	9	65.6 ± 3.5^{c}	75.9 ± 1.0^{Aab}	81.0 ± 1.6^{Ba}	66.5 ± 4.5^{ABc}	69.8 ± 0.7^{Abc}	73.9 ± 3.5^{Bb}	*< 0.001*
	16	69.9 ± 1.6^{c}	78.9 ± 1.8^{Ab}	87.21 ± 0.8^{Aa}	70.7 ± 2.5^{Ac}	73.9 ± 2.2^{Ac}	80.8 ± 2.1^{Ab}	*< 0.001*
	*P-value**	*0.158*	*< 0.001*	*< 0.001*	*< 0.001*	*< 0.001*	*< 0.001*	
C*	2	11.8 ± 1.3^{Bb}	11.8 ± 1.3^{Bb}	11.8 ± 1.3^{Bb}	15.2 ± 2.2^{Aa}	15.2 ± 2.2^{Aa}	15.2 ± 2.2^{Aa}	*< 0.001*
	9	12.1 ± 1.4^{AB}	12.2 ± 1.4^{B}	13.7 ± 1.7^{AB}	12.6 ± 1.3^{B}	13.2 ± 2.0^{B}	12.3 ± 1.1^{B}	*0.763*
	16	14.2 ± 0.8^{A}	15.9 ± 1.9^{A}	15.7 ± 1.4^{A}	13.6 ± 1.6^{B}	13.9 ± 1.0^{B}	14.3 ± 1.6^{A}	*0.308*
	*P-value**	*0.017*	*< 0.001*	*< 0.001*	*0.040*	*0.226*	*0.011*	
h*	2	56.1 ± 4.9^{Cb}	56.1 ± 4.9^{Bb}	56.1 ± 4.9^{Bb}	73.2 ± 6.1^{Ca}	73.2 ± 6.1^{Ba}	73.2 ± 6.1^{Ca}	*< 0.001*
	9	85.4 ± 6.7^{Bb}	106.0 ± 8.8^{Aa}	102.9 ± 1.1^{Aa}	102.4 ± 8.5^{Ba}	114.6 ± 5.5^{Aa}	118.5 ± 0.5^{Ba}	*< 0.001*
	16	111.9 ± 4.3^{A}	117.2 ± 7.1^{A}	120.0 ± 19.5^{A}	123.3 ± 7.0^{A}	123.9 ± 5.6^{A}	125.5 ± 2.8^{A}	*0.518*
	*P-value**	*< 0.001*	*< 0.001*	*< 0.001*	*< 0.001*	*< 0.001*	*< 0.001*	
ΔE	2	0.0 ± 0.0^{C}	0.0 ± 0.0^{C}	0.0 ± 0.0^{C}	0.0 ± 0.0^{C}	0.0 ± 0.0^{C}	0.0 ± 0.0^{C}	
	9	5.4 ± 1.7^{Bc}	10.1 ± 1.3^{Bab}	11.5 ± 0.2^{Ba}	7.2 ± 1.4^{Bbc}	9.6 ± 0.9^{Bab}	11.4 ± 1.1^{Ba}	*< 0.001*
	16	10.6 ± 0.4^{Ad}	13.8 ± 1.4^{Abc}	16.4 ± 2.2^{Aa}	11.4 ± 0.5^{Ad}	12.4 ± 0.5^{Acd}	14.9 ± 0.3^{Aab}	*< 0.001*
	*P-value**	*< 0.001*	*< 0.001*	*< 0.001*	*< 0.001*	*< 0.001*	*< 0.001*	

Whole fish on ice-September (WI–S); Vacuum packaged fillets-September (VP–S); Modified atmosphere packaged fillets-September (MAP-S); Whole fish on ice-April (WI-A); Vacuum packaged fillets-April (VP-A); Modified atmosphere packaged fillets-April (MAP-A).
*Anova was applied to detect differences in colour parameters; where significant differences were detected ($P < 0.05$), a Tukey's pairwise comparison test was applied.
$^{a–d}$Different superscript letters within each row and each parameter indicate significant differences ($P < 0.05$) between treatments.
$^{A–C}$Different superscript letters within each column and each parameter indicate significant differences ($P < 0.05$) throughout the storage time.

weaken as the muscle aged since no significant differences were found between treatments on day 16 (Table 3). Roth et al. (2009) stated a negative correlation between the L* value and muscle pH, which agrees with our observations ($r = -0.56$, $P < 0.001$).

The MAP-groups had the highest total colour difference (ΔE) followed by VP and WI-groups. On the other hand, no significant seasonal variations were found according to ΔE. Although no correlation was observed between ΔE and C* ($r = 0.04$, $P \geq 0.541$), a strong correlation was found between ΔE and L* ($r = 0.66$, $P < 0.001$), indicating changes in L* to be the parameter of highest significance to ΔE observed. However, the final colour perception could be assumed similar in all treatments on the last day of analysis as no significant difference was found in the C* and h* on day 16.

4. Conclusion

The fishing season, storage conditions and storage time were found to affect the quality of European plaice. The observed seasonal variations in the metabolites, microbial and physicochemical parameters lead us to the conclusion that the overall quality is lower of plaice caught in April than September. Moreover, this study shows that MAP (70% CO_2, 20% N_2, 10% O_2) combined with cold storage (4 °C) resulted in comparable quality as the whole fish on ice (0 °C). However, the production of MAP-fillets has a comparative advantage over the whole fish on ice in terms of convenient use and easier transport. Given that the quality measures showed a satisfactory quality of plaice, increasing utilisation and commercial value could be achieved through the production of modified atmosphere-packaged plaice fillets. Nevertheless, future research is needed to investigate how seasonal variations in the initial microbiome affects microbial spoilage of plaice. This knowledge can contribute to the extent of the shelf life of plaice and in the production of high-quality, convenient retail plaice products.

CRediT authorship contribution statement

Dionysios Tsoukalas: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing. **Sophie Kendler:** Investigation, Conceptualization. **Jørgen Lerfall:** Conceptualization, Methodology, Supervision, Writing – review & editing. **Anita Nordeng Jakobsen:** Conceptualization, Methodology, Supervision, Writing – review & editing, Project administration.

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 will be made available on request.

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