Aquacultural Engineering 91 (2020) 102124

Contents lists available at ScienceDirect

Aquacultural Engineering

journal homepage: www.elsevier.com/locate/aque

A closer look at closed cages: Growth and mortality rates during production of post-smolt Atlantic salmon in marine closed confinement systems

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ARTICLE INFO

Keywords:
CCS
Fish welfare
Growth rates
Mortality causes
Salmo salar

ABSTRACT

The most controversial environmental problems in commercial salmon farming are the negative effects of sea lice (*Lepeoptheirus salmonis*, *Caligus* spp.), the genetic introgression of farmed salmon in wild populations, nutrient waste load and the emission of potentially toxic waste to coastal waters. Moving production from sea cages to land-based facilities, offshore farming or marine closed containment systems (CCS) are suggested as possible ways to solve these problems. However, there are few published studies on production capacity and fish welfare in such systems. The main aim of this study was to describe growth rates, mortality rates and mortality causes in the commercial-scale production of Atlantic salmon (*Salmo salar*) post-smolts in CCS from sea transfer until the size of 1000 g. From October 2014 to May 2017, we recorded growth rates, feed use, mortality and mortality causes during 23 CCS production cycles, including 18 CCS periods with off-season smolt (S0) and 5 CCS periods with one-year smolt (S1). The mean (SD) growth rate, thermal growth coefficient (TGC), for all 23 CCS was 3.03 (0.34), with no difference between cages with S1 (n = 5) and cages with S0 (n = 1 8). Cumulative mortality three months after sea transfer (CM_{3mo}) was 2.6 %, while cumulated mortality throughout the total trial period (CM_{total}, mean number of days = 159) was 3.6 %. Both CM_{3mo} and CM_{total} were higher in S1 groups than in S0 groups. Mean (SD) feed conversion ratio in CCS with S0 (n = 18) was 1.11 (0.07). The two main mortality causes were 'Ulcers and fin rot' (S1 and S0) and 'Failed smolt' (S1), accounting for 36.1 % and 19.3 % of the total mortality, respectively. Water flow, oxygen saturation and other water quality parameters were within safe limits for fish health and welfare.

1. Introduction

In several countries, the rapid growth of salmon farming has been followed by sea lice infestations, an increase in medical interventions, and then to the development of drug-resistant sea lice (Helgesen and Marin, 2018). The emergence and rapid spread of drug-resistant lice have forced farms to abandon chemical treatments and to develop non-medicinal treatments or alternative farming strategies (Aaen et al., 2015; Overton et al., 2018; Helgesen and Jansen, 2019). Salmon lice (*Lepeophtheirus salmonis*) are considered a major threat to the survival and sustainability of wild salmon populations (Grefsrud et al., 2018). Treatment against sea lice comes at a high cost for the farmers (Costello, 2009; Norwegian Directorate of Fisheries, 2020) and chemical treatments could also have a significant impact on non-target marine organisms (Urbina et al., 2018). Negative effects on wild salmon populations caused by the spread of diseases and escaped fish (Naylor et al., 2005; Garseth et al., 2013), and the potentially negative effects of nutrient overloading in coastal areas (Braaten, 2007), are also important issues to solve.

The development and implementation of new farming technologies could mitigate these negative environmental impacts. In closed containment systems (CCS), intake water is pumped from deeper water layers, making it possible to avoid all infective salmon lice copepodites (Nilsen et al., 2017a). Fish escape from open cages, primarily because of broken nets, caused by rough weather conditions or operations such as treatments against salmon lice (Jackson et al., 2015; Anonymous, 2020). A cage design with tarpaulin bags surrounded by a security net should reduce the risk of escaped fish; this risk could potentially also be reduced by locating CCS at sheltered sea sites. In addition, with CCS it is possible to collect and reuse settleable particles from faeces and excess feed.

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https://doi.org/10.1016/j.aquaeng.2020.102124
Received 16 April 2020; Received in revised form 8 September 2020; Accepted 9 September 2020
Available online 15 September 2020

More detailed studies on growth, mortality and welfare of salmon in CCS are necessary to compare this technology with other farming systems. There is an expectation of high maximum densities in CCS, as a measure to reduce production costs. A maximum fish density of 80 kg/m^3 is suggested in the review by Thorarensen and Farrell (2011), while other studies indicate maximum density < 100 kg/m^3 (Sveen et al., 2018) or an optimal stocking density of 75 kg/m^3 (Calabrese, 2017). Fish density is also linked to the specific water consumption (SWC = L/kg/min) and both high density and low SWC are associated with a negative impact on fish health and welfare. Minimum SWC to remove CO_2 and other metabolites has been described as 0.06–0.12 L/kg/min (Forsberg, 1995a), 0.07–0.2 L/kg/min (Nilsen et al., 2017b), 0.2–0.3 L/kg/min (Thorarensen and Farrell, 2011) and 0.3 L/kg/min (Calabrese, 2017). Density $\geq$ 100 kg/m^3 and SWC $\leq$ 0.3 L/kg/min has a negative effect on wound healing in post-smolt salmon (Sveen et al., 2016). Water flow through CCS systems has an effect on water velocity and this also has an impact on fish growth and welfare. Optimum swimming velocity is suggested to be around 0.8–1.0 BL/s, salmon show signs of exhaustion with velocities $>$ 1.5 BL/s and there is a temperature-dependent critical swimming speed between 2.1 and 2.7 BL/s (Solstorm et al., 2015, 2016; Hvas et al., 2017). A moderate increase in water velocity increases growth rates for post-smolt Atlantic salmon (300–600 g) and for salmon towards harvest size (800–3000 g) (Nilsen et al., 2018), increased swimming activity in post-smolt also enhances the growth of skeletal musculature (Timmerhaus, pers.com.). In contrast to other studies, growth rates were reduced in a pilot study of a raceway CCS (Preline) compared to a reference group in open cages (Balseiro et al., 2018), but in the same study they observed a positive impact on muscle tissue with the recruitment of new skeletal muscle fibres and hypertrophy of heart muscle. Salinity and how the fish are acclimated to the new marine environment is also important. In RAS systems, a reduction of salinity to 12 ppt compared to 22 and 32 ppt improves the growth rates of post-smolt salmon and a swimming velocity of 1.0 BL/s compared to 0.3 BL/s also improves the growth rates across all salinities (Ytrestøyl et al., 2020). Karlsen et al. (2018) showed how skin thickness and mucus cell numbers increase with time after sea transfer, indicating an increased susceptibility to lesions and infectious agents during the first weeks of the post-smolt period. Moreover, the design and technology used in CCS is vital to understand and regulate water flow and water quality in these large units. Summerfelt et al. (2016) compared design, volumes, flow rates, feed load and other management parameters of large, land-based tanks with one pilot CCS, and computational fluid dynamics (CFD) studies have been published on different CCS systems (Gorle et al., 2018; Maximiano et al., 2018). After a period of increased interest in land-based salmon farming in Norway during the late 1980s and early 1990s, a number of studies were published describing ongrowing of post-smolt salmon in land-based, flow-through tanks supplied with oxygen-enriched seawater, with an emphasis on growth rates, feed utilisation and mortality (Forsberg, 1995a,b). In addition, a pilot study on the ongrowing of post-smolt salmon in closed, small tarpaulin-covered cages (CCS) was performed in South-western Norway (Skaar and Bodvin, 1993).

However, to the best of our knowledge, there are still very few published studies on fish performance and rearing conditions in CCS in commercial-scale salmon farming. Therefore, the main aim of this paper was to describe growth rates, mortality rates and mortality causes during a pilot study of commercial-scale production of Atlantic salmon (*Salmo salar*) in CCS. In addition, we wanted to compare mortality data from CCS with the existing data from open cage studies.

2. Materials and methods

2.1. Sites and CCS technology

During the period from October 2014 to May 2017, two different sea sites (sites 1, 3) in the southern part of Nordland county, Norway, were used for a longitudinal survey of production of Atlantic salmon post-smolts in CCS (Fig. 1 and Supplementary data 1). In addition, two open cages (site 2) were monitored from October 2014 to May 2015.

In all CCS, the tarpaulin bags were filled with water pumped (5.5 kW, Xylem Norway AS) from 20 to 25 m depth (Nilsen et al., 2017a), and drained through one central outlet (Fig. 2). Sedimentable particles and dead fish were separated from the water flow in the outlet and pumped in separate tubes to the surface. The CCS were circular with open-ended inlets located at 1–1.5 m depth, creating a circular, primary horizontal current. Each cage was supplied with an external light mounted on the floating ring supporting the tarpaulin bags (LED 2 × 50W 230 V IP65, Etman Distribusjon AS, Egersund, Norway). An overview of site 3 is given in Fig. 3.

2.2. Fish and rearing conditions

The study monitored growth rates, mortality rates and mortality causes in commercial-scale production of Atlantic salmon (*Salmo salar*) post-smolts in CCS from sea transfer until final weight $\leq$ 1000 g. The Atlantic salmon smolt in the study population (Tables 1 and 2) were delivered as spring smolt (S1) or off-season smolt (S0) from three different hatcheries during three consecutive years; 2014, 2015 and 2016. Hatchery 1 delivered S0 in 2014, 2015 and 2016 to site 1 (CCS) and S0 in 2014 to site 2 (open cages). Hatcheries 2 and 3 delivered S1 and S0 to site 3 (CCS) in 2016. The period of sea transfer for spring smolt (S1) was from May 8 to June 1, for off-season smolt (S0) from October 16 to December 21. When cages are referred to by number, these are the chronological numbers assigned in Table 2. Cohorts were defined as groups of fish of the same genetic origin and generation, produced under similar conditions at one hatchery and delivered to the sea cages with an interval of less than 14 days (26 days in cohort 1). The number of cohorts was 9, with 1–4 cages per cohort.

The fish were of AquaGen or Salmobreed strain, and all were selected for IPNV resistance by use of quantitative trait loci (QTL) methods (Anonymous, 2013). Smoltification quality was measured before sea transfer with a combination of morphological evaluation and one or several of the following laboratory test procedures: determination of plasma chloride after 48 h exposure to seawater, measurement of levels of gill ATP-ase (Pharmaq analytic AS) or Smolt-Timer ® (Patogen AS). The smolt were transported to the sea sites in well boats and stocked directly in CCS. All fish were fed until satiation with commercial pelleted food (Skretting AS, Biomar AS), at sites 1 and 2 with automatic pneumatic feeding systems (AkvaGroup AS), and at site 3 with Betten feed automats.

The minimum specific water consumption (SWC), maximum feed load (FL) and density (kg/m^3) were calculated from reported water flow (m^3/min), feed use (kg/day), biomass (kg) in each cage and cage volume (2870−6000 m^3). Minimum values of SWC at site 1 were between 0.22 and 0.29 L/kg/min, at site 3 between 0.20 and 0.50 L/kg/min. The maximum feed load at site 1 was between 19 and 26 g/m^3, at site 3 between 11 and 30 g/m^3. Density at sea transfer in the CCS (both sites) ranged between 1.9 and 4.2 kg/m^3, with maximum densities at the end of the production period between 10 and 22.4 kg/m^3.

All farming operations were performed in a commercial or near-to-commercial setting, and with the same basic design of the closed tarpaulin bags, oxygenation systems and design of inlets and outlets. Oxygen to the CCS was supplied by a diffusor net (AkvaDesign AS); oxygen and temperature were logged at 10-minute intervals at 2 m depth (system: FDO 700 IQ SW, WTW/Xylem). Mean oxygen saturation was automatically regulated to 80–95 % in all CCS. Farming was performed with standard operational procedures applied regarding feed and feeding, transport and handling of live fish, health surveillance and humane treatment of individual fish during sea lice counts, weighing procedures or when culling fish. Permission from the Norwegian Research Authority was not required. Sea lice (*Lepeophtheirus salmonis* and *Caligus elongatus*) were monitored as described in Nilsen et al.

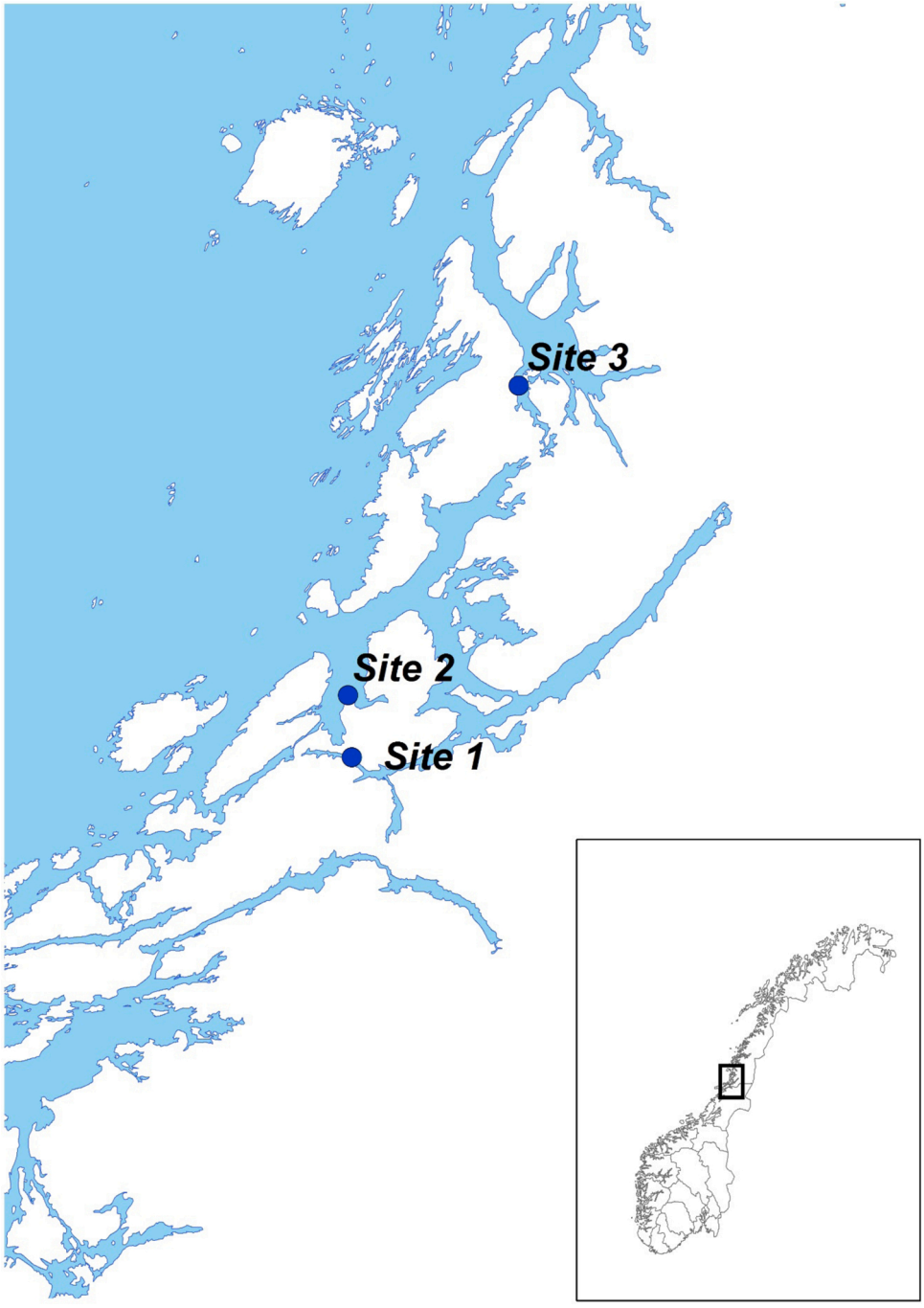

Fig. 1. Location of sea sites in Brønnøy and Bindal, Nordland county. Site 1: research site with CCS (2014-2017), site 2: commercial site with open cages (2015-2016), site 3: research site with CCS (2016-2017) (Illustration: A. Tarpai).

(2017a), following the Norwegian regulation on salmon lice in aquaculture (Norwegian Ministry of Trade and Fisheries, 2012). Water quality was measured between 12:00 and 16:00, at the time of day with assumed maximum impact of feed consumption and feeding activity on carbon dioxide (CO_2) production. More detailed methods for monitoring water quality, water velocity and sea lice are described in Supplementary data 2.

2.3. Growth and mortality rates

Start weight (W_0) was determined by the smolt documentation from the hatcheries, verified with weight controls during the time of sea transfer. End weight (W_1) was determined by weight samples (individual weight samples and bulk samples) compared to and validated with estimates of weight and number from well boats and output from the production database (FishTalk, AkvaGroup AS) (Supplementary data 3 and 4). Weekly data were collected from each cage: number of fish, stocking weight, feed use, water temperature, weekly mortality count and the number of fish assigned to each of the defined mortality causes. Dead fish were removed from the cages daily, with the use of lift-up systems (CCS) or dead fish haul (open cages). The dead fish were counted and categorised (Supplementary data 5) and n_1 was calculated by subtracting total mortality from n_0. Growth, mortality rates and feed conversion ratio in each cage were calculated from the total production data: number of fish in and out, mean weight at start and end, total feed consumption, total time period and mean temperature.

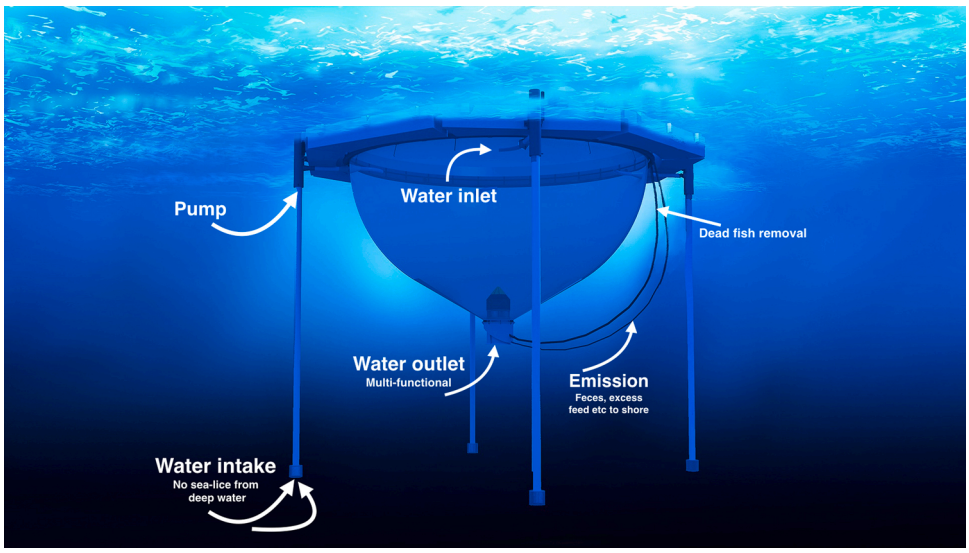

Fig. 2. Design of the CCS used at site 3, volume 6000 m^3. Water inlet at 25 m depth through a 25 mm filter. Effluents separated in three fractions: water, sludge and dead fish. A net (not shown) surrounded the cage and tubes to prevent escapees (Illustration: AkvaFuture As/Visual 360).

Fig. 3. Site 3 with 10 CCS, each with a volume of 6000 m^3 (Photo: AkvaFuture AS).

Table 1
Number of fish and cages with one-year smolt (S1) or off-season smolt (S0) in two open cages and 23 CCS at three different sea sites from October 2014 to May 2017.

	2014		2015		2016		SUM	
	fish	cages	fish	cages	fish	cages	fish	cages
Open cage S0	331,400	2	–	–	–	–	331,400	2
CCS S0	285,797	4	477,000	4	1,315,195	10	2,077,992	18
CCS S1	–	–	–	–	744,845	5	744,845	5
SUM	617,197	6	477,000	4	2,060,040	15	3,154,237	25

Size measurements of individual fish included weight (W) as round body weight in g (±1 g), length (L) as fork length (±0.5 cm), and condition factor: $CF = 100 \cdot (W/L^3)$.

Specific growth rate (SGR) was calculated as (Houde and Scheckter, 1981):

$$SGR = 100 \cdot (\ln(W_1) - \ln(W_0))/(t_1 - t_0)$$

where W_1 and W_0 are weights on days t_1 and t_0, respectively.

Thermal growth coefficient (TGC) was calculated as (Alanärä et al., 1994):

$$TGC = 1000 \cdot (W_1^{1/3} - W_0^{1/3})/(T \cdot t)$$

Table 2
Data from 23 CCS (sites 1, 3) and two open cages (site 2) from October 2014 to May 2017. Smolt 0 = S0, Smolt 1 = S1, H = hatchery, Co = Cohort group, n_0 and n_1 = number of fish at start and end, W_0 and W_1 = mean weight (g) at start and end, CM_{3mo} = cumulated mortality the first three months after sea transfer, CM_{total} = total cumulated mortality from start to end, t = days, T = mean water temperature (°C), Density = maximum density (kg/m^3), SGR = specific growth rate, TGC = thermal growth coefficient, FCR = feed conversion ratio.

Cage	Site	Type	Smolt	H	Co	n_0	n_1	Start	End	W_0	W_1	CM_{3mo}	CM_{total}	t	T	Density	SGR	TGC	FCR
1	2	Open	0	1	1	164700	163317	24.10.2014	16.05.2015	96	617	0.3	0.8	204	6.9	3.0	0.91	2.80	1.03
2	2	Open	0	1	1	166700	165200	24.10.2014	16.05.2015	124	642	0.4	0.9	204	6.9	3.5	0.81	2.59	1.14
3	1	CCS	0	1	1	56366	55521	19.11.2014	06.05.2015	120	789	0.4	1.5	168	7.1	16.0	1.12	3.61	1.13
4	1	CCS	0	1	1	57014	56307	19.11.2014	06.05.2015	122	807	0.8	1.2	168	7.1	17.1	1.12	3.65	1.10
5	1	CCS	0	1	2	86895	85705	19.11.2014	05.05.2015	92	529	0.5	1.4	167	7.1	15.8	1.05	3.01	1.09
6	1	CCS	0	1	2	85522	84767	19.11.2014	05.05.2015	96	530	0.3	0.9	167	7.1	15.5	1.02	2.96	1.09
7	1	CCS	0	1	3	102000	99033	10.11.2015	11.04.2016	88	467	0.8	2.9	153	8.2	16.1	1.09	2.64	1.18
8	1	CCS	0	1	3	128000	125541	10.11.2015	11.04.2016	83	477	0.9	1.9	153	8.2	20.9	1.14	2.75	1.06
9	1	CCS	0	1	3	129000	126268	10.11.2015	11.04.2016	75	458	0.3	2.1	153	8.2	20.2	1.18	2.78	1.14
10	1	CCS	0	1	3	118000	112976	10.11.2015	11.04.2016	86	451	1.1	4.3	153	8.2	17.8	1.08	2.59	1.20
11	1	CCS	0	1	4	100500	99796	21.11.2016	04.04.2017	110	480	0.3	0.7	134	8.1	16.7	1.10	2.80	1.17
12	1	CCS	0	1	4	100600	99833	21.11.2016	04.04.2017	118	522	0.5	0.8	134	8.1	18.2	1.11	2.90	1.17
13	1	CCS	0	1	4	99900	98906	21.11.2016	04.04.2017	118	503	0.7	1.0	134	8.1	17.3	1.08	2.81	1.18
14	1	CCS	0	1	4	101700	100478	21.11.2016	04.04.2017	118	503	0.3	1.2	134	8.1	17.6	1.08	2.81	1.18
15	3	CCS	1	2	5	122853	115373	08.05.2016	20.09.2016	164	819	1.9	6.1	135	8.8	15.7	1.19	3.27	
16	3	CCS	1	2	5	150000	137420	09.05.2016	09.10.2016	103	681	8.2	8.4	153	9.4	15.6	1.23	2.86	
17	3	CCS	1	2	5	148545	138589	09.05.2016	08.10.2016	103	690	6.3	6.7	152	9.3	15.9	1.25	2.94	
18	3	CCS	1	2	5	180000	160356	21.05.2016	28.10.2016	74	660	10.6	10.9	160	9.9	17.6	1.37	2.85	
19	3	CCS	1	3	6	143447	139324	01.06.2016	04.11.2016	97	900	2.3	2.9	156	10.1	20.9	1.43	3.21	
20	3	CCS	0	3	7	190905	187058	16.10.2016	31.05.2017	60	717	1.3	2.0	227	7.7	22.4	1.09	2.88	1.02
21	3	CCS	0	3	7	109786	107524	16.10.2016	31.03.2017	125	1094	1.6	2.1	166	8.1	19.6	1.31	3.94	1.01
22	3	CCS	0	2	8	158000	151400	21.11.2016	26.05.2017	109	717	2.9	4.2	186	7.1	18.1	1.01	3.16	1.06
23	3	CCS	0	2	8	158040	151865	21.11.2016	25.05.2017	109	710	2.4	3.9	185	7.1	18.0	1.01	3.16	1.11
24	3	CCS	0	2	9	175282	168923	20.12.2016	25.05.2017	133	533	2.8	3.6	156	6.9	15.0	0.89	2.79	1.06
25	3	CCS	0	2	9	120482	117057	21.12.2016	24.05.2017	96	514	2.4	2.8	154	6.9	10.0	1.09	3.23	0.98

where T is temperature in °C and t is time in days. Both SGR and TGC were calculated at weekly intervals and for the total production period of each cage.

Specific feeding rate was calculated as:

$$SFR = (feed/biomass) \cdot 100$$

where feed is weekly mean kg feed/cage/day and biomass is average biomass/cage/day in the same week.

Feed conversion rate was calculated as:

$$FCR = \text{total feed use (kg)/total increase in biomass (kg)}$$

FCR was calculated for each cage and for the entire production cycles (sea transfer until end of study).

The number stocked in each cage (n_0) was given by the figures from the hatcheries, based on their records from vaccination, from which was subtracted the mortality between vaccination and sea transfer. For some cages the stocking numbers were rounded to the closest 1000. Cumulative mortality rates for the first three months after sea transfer (CM_{3mo}) and the total time period (CM_{total}) were calculated as the proportion of mortalities during the time period compared with n_0. Weekly mortality rates were reported as $(n_{week}/n_{risk}) \cdot 100$, where n_{week} = weekly mortality count and n_{risk} = number of fish at risk at the start of the week. The final numbers in each unit (n_1) were calculated by subtracting CM_{total} from n_0. Injured or weak fish were netted, killed and recorded as culled. Dead or killed fish were inspected and cause-specific mortality was assigned as described in Supplementary data 5. In the 2014 and 2016 generations at site 1, gills, kidneys and pseudobranchia (less frequent) were sampled from the hatchery before sea transfer and at two to three sampling points during the seawater period.

2.4. Statistical analysis

All production data were recorded daily at farm level and entered into the FishTalk database. From this database, data were exported as Microsoft ® Excel files. Data from each unit were aggregated with week as time unit: stocking weight (g), stocking number, stocking density (kg/m^3), total mortality count and cause-specific mortality count, feed use (kg) and temperature. Estimated weekly values of feeding rate (SFR) and growth rates (SGR and TGC) were calculated from number of days, mean weekly temperature, weight gain and feed use. The weekly data and the total production data were transferred from Excel to the IBM SPSS 25 statistical package (IBM Corporation, NY, US), quality controlled and checked for outliers and for missing data, and the data were described with tabular and graphical methods. The total production data were summarised for each cage unit; mean, SD, median, minimum and maximum values. These data were also explored with normality tests and box plots before SGR, TGC and mortality rates were analysed as outcome variables with smolt type (S0 and S1) as the predictor variable, using a Kruskal Wallis non-parametric test. The correlation between CM_{3mo} and CM_{total} was analysed with the use of Pearson correlation coefficient. For the weekly dataset, the relationships between SGR, TGC, weekly temperature and fish weight were evaluated with scatter plots and correlations analysed with use of Pearson correlation coefficient.

3. Results

3.1. Growth rates and FCR

Growth and mortality data from all 25 individual cages are reported in Tables 2 and 3. Comparing spring smolt (S1) and off-season smolt (S0), there were no significant differences in start weight (W_0) or end weight (W_1). SGR was higher in S1 ($p = 0.002$), but with higher water temperature during summer the mean TGC was identical in the two groups (both with TGC = 3.03). Differences of TGC between generations and sites are shown in Fig. 4, with lowest TGC in S0 at site 1 in the 2015 generations. The post-smolt salmon used an average of 159 days at 8.0 °C to grow from 104 to 633 g (Table 3), with a maximum density of 22.4 kg/m^3, a mean (SD) TGC of 3.03 (0.34). Mean (SD) FCR for the 18 CCS with S0 was 1.11 (0.07). Mean FCR from the five CCS with S1 was 0.94; we evaluated this as an unlikely positive outcome and FCR from these CCS was thus excluded.

Table 3
Summarised production data from 23 CCS, October 2014 to May 2017. Start weight (W_0), end weight (W_1), number of days, temperature in °C, maximum density in kg/m^3, specific growth rate (SGR), thermal growth coefficient (TGC) and feed conversion ratio (FCR). Data are grouped for CCS with S0 (n = 18), CCS with S1 (n = 5) and all CCS (n = 23), except for FCR, where CCS with S1 were excluded and all data came from 18 CCS with S0.

	Smolt	Mean	SD	Median	Min	Max
W_0 (g)	S0	103	20	109	60	133
	S1	108	33	103	74	164
	ALL	104	23	103	60	164
W_1 (g)	S0	600	171	526	451	1094
	S1	750	105	690	660	990
	ALL	633	169	533	451	1094
Days	S0	161	23	155	134	227
	S1	151	10	153	135	160
	ALL	159	21	154	134	227
T (°C)	S0	7.6	0.6	7.9	6.9	8.2
	S1	9.5	0.5	9.4	8.8	10.1
	ALL	8.0	1.0	8.1	6.9	10.1
Density (kg/m^3)	S0	17.4	2.7	17.5	10.0	22.4
	S1	17.1	2.3	15.9	15.6	20.9
	ALL	17.3	2.5	17.3	10.0	22.4
SGR	S0	1.09	0.08	1.09	0.89	1.31
	S1	1.29	0.10	1.25	1.19	1.43
	ALL	1.13	0.12	1.10	0.89	1.43
TGC	S0	3.03	0.37	2.89	2.59	3.94
	S1	3.03	0.20	2.94	2.85	3.27
	ALL	3.03	0.34	2.90	2.59	3.94
FCR[a]	S0	1.11	0.07	1.11	0.98	1.20

[a] FCR from 5 CCS with S1 were excluded.

Weekly data on growth, temperature, specific feeding rate (SFR %), TGC and mortality rate (%) are reported in Table 4. SFR increased with increasing water temperature (Pearson coefficient = 0.556, $p < 0.001$) and decreased with increasing fish weight (Pearson coefficient = −0.459, $p < 0.001$). For TGC the correlation was reversed; TGC decreased with increasing water temperature (Pearson coefficient = −0.138, $p = 0.001$) and decreased with increased weight (Pearson coefficient = 0.256, $p < 0.001$). At the same time, TGC was positively correlated to SFR (Pearson coefficient = 0.443, $p < 0.001$). The growth

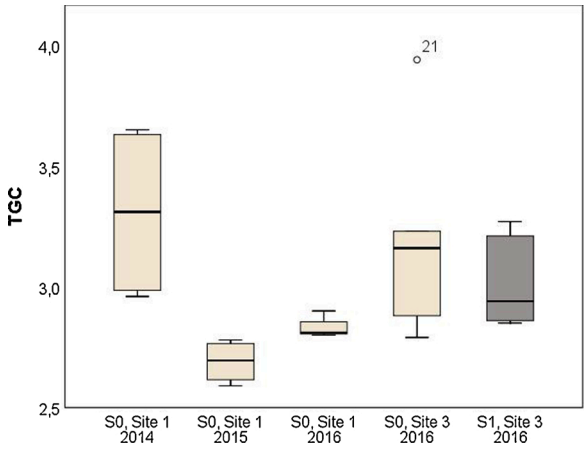

Fig. 4. Distribution of TGC-values from 23 CCS, October 2014 to May 2017. Off-season smolt (S0) at site 1 in 2014 (n = 4), 2015 (n = 4) and 2016 (n = 4), off-season smolt (S0) at site 3 in 2016 (n = 6) and spring smolt (S1, dark grey) at site 3 in 2016 (n = 5).

Table 4
Weekly production data from 23 CCS, October 2014 to May 2017. Temperature (°C), specific feeding rate (SFR %), thermal growth coefficient (TGC) and weekly mortality rate (%). Weeks = number of weekly registrations. Reported as mean, standard deviation (SD), median, minimum and maximum values. Data are grouped for CCS with S0 (n = 18), CCS with S1 (n = 5) and all CCS (n = 23).

	Smolt	Weeks	Mean	SD	Median	Min	Max
Temperature (°C)	S0	432	7.6	1.3	7.2	5.8	12.7
	S1	113	9.6	2.4	8.3	7.0	13.1
	ALL	545	8.0	1.8	7.4	5.8	13.1
SFR (%)	S0	393	1.19	0.35	1.17	0.37	2.14
	S1	99	1.24	0.34	1.28	0.41	1.87
	ALL	492	1.20	0.35	1.18	0.37	2.14
TGC	S0	387	3.09	0.77	3.19	0.59	5.28
	S1	92	2.89	0.86	2.92	0.85	5.21
	ALL	479	3.04	0.79	3.13	0.59	5.28
Mortality rate (%)	S0	430	0.09	0.10	0.06	0.00	0.61
	S1	113	0.32	0.70	0.04	0.00	5.33
	ALL	543	0.14	0.34	0.05	0.00	5.33

(IB weight) and the weekly mortality rates are plotted for three of the cohorts in Supplementary data 6. Weekly specific feeding rates (SFR) and water temperatures were plotted against week after sea transfer in Supplementary data 7. All weekly data are also reported in the Supplementary dataset, weekly data.

3.2. Mortality rates and mortality causes

Both CM_{3mo} ($p = 0.006$) and CM_{total} ($p = 0.003$) were higher in CCS with one-year smolt (S1) than in CCS with off-season smolt (S0), with a peak in S1 mortality the first four weeks after sea transfer, but with higher mortality in S1 cages during most of the production cycle (Fig. 5). CM_{3mo} for all salmon in CCS was 2.6 % and CM_{total} (159 days) was 3.6 % (shown in the 'Total mortality' column in Table 5). Mortality was not evenly distributed over time or between cages. More than 72 % of mortality occurred during the first three months after sea transfer (representing 57 % of the total trial period), mortality the first three months and total accumulated mortality were closely correlated (Pearson coef. = 0.933, $p < 0.001$). Looking at the average mortality across cages, median levels were lower than the means, especially for the first three months. This was caused by a skewed mortality pattern, with high mortality in few of the cages. The 5 cages with highest mortality (mean CM_{total} = 7.3 %) represented 53.2 % of the total mortality while the 5 cages with lowest mortality rates (mean CM_{total} = 0.91 %) represented only 4.3 %. In Table 5, mortality rates at cage level (columns under 'Cages') are summarised as mean, SE, median, minimum and maximum values. CM_{total} in the 23 CCS ranged between 0.7 and 10.9 %, with median 2.1 % and interquartile range (IQR) of 1.2–4.2 %. The mean values of cumulated mortality at cage level were close to the total CM_{3mo} and CM_{total}.

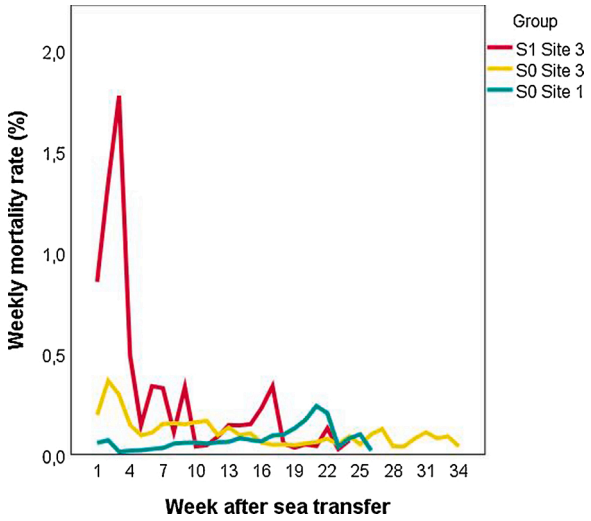

Fig. 5. Weekly mortality rates plotted against weeks after sea transfer, split into three groups: spring smolt (S1) at site 3 (red), off-season smolt (S0) at site 3 (yellow) and off-season smolt (S0) at site 1 (green). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

The most frequent mortality category in all cages was 'Ulcers and fin rot' (36.1 %), and this was observed in all 25 cages (23 CCS and two open cages). 'Failed smolt' was the second most frequent diagnosis (19.3 %), but observed only in the CCS with S1, where undersized fish, precocious males, parr and fish with a more diffuse yellow discolouring were frequently observed during autopsies. The category 'Other' (27.4 %) represented fish with no diagnosis or diagnoses with low prevalence. The relative proportion of undiagnosed fish often increased during periods with moderate to low mortality, while during periods with higher mortality most fish were assigned to one or two specific mortality categories. The proportion of dead fish that were too decomposed to specify was 7.2 %. In the cages with problems with 'Failed smolt', 'Ulcers and fin rot' was also an important cause of death, and 'Culling' was necessary to meet husbandry standards of fish welfare. Plots of weekly mortality rates are shown in Fig. 5 and in Supplementary data 6. Cumulated mortality assigned to mortality categories in S1 and S0 groups is shown in Fig. 6 and summarised in Supplementary data 8. Data from the present study are compared to data from open cages (Aunsmo et al., 2008) in Table 6.

The majority of bacteriological examinations of ulcers and fin lesions showed a broad variety of pathogens and possible pathogens, dominated by *Aliivibrio wodanis*, other unidentified *Aliivibrio* species and *Moritella viscosa*. *Tenacibaculum* sp. did not appear to be of importance for the skin and fin lesions observed in this study. *Aliivibrio* species and *Moritella viscosa* were isolated from ulcers/fin lesions, kidneys and other organs, and we also received positive PCR tests of *Moritella viscosa* (PCR protocols for *A. wodanis* were not developed) from head kidney samples from fish with clinical signs of infection.

3.3. Histology of gills and kidneys

In the 2014 generation (site 1, cages no. 3-6 and site 2, cages no. 1, 2), 56 % of the fish from the hatchery had mild to severe nephrocalcinosis (Smart et al., 1979). At sea transfer of the 2016 year class (site 1, cages no. 7–10), 27 % of the smolt at the hatchery had mild kidney lesions compatible with nephrocalcinosis. Only a few individuals with mild signs of nephrocalcinosis were found during the seawater period, indicating no further development of kidney lesions and perhaps even an improvement at sea. All gills were normal from smolt sampled at sea transfer. After the seawater period from October 2014 to April 2015 and from October 2016 to April 2017, all gills from post-smolt in open cages (2015) and CCS (2015 and 2017) had mild to moderate proliferative lesions. This coincided with a spring rise in plankton concentrations and increased turbidity in the seawater, a common feature of April at this latitude. Farm personnel also observed periods with reduced appetite, especially in the open cages in April 2015. Lesions caused by the myxosporidian parasite *Parvicapsula pseudobranchicola* were present in a few of the pseudobranchia from fish in open cages in 2015. In gills from CCS in April 2017 we also identified lesions involving costia (*Ichthyobodo necator*) and epitheliocysis-like inclusions (suspected *ca. Branchiomonas cysticola*).

3.4. Other observations

The oxygen saturation in the ocean outside the cages ranged from 80.7 to 130.9 %. Inside the CCS, mean oxygen saturation was 81–86 %, with lowest measured DO% > 71 %. Inside CCS, measured pH ranged between 7.5 and 8.1 at site 1 and between 6.8 and 8.4 at site 3. Median and maximum concentrations of CO_2 in open cages and in seawater

Table 5
Cumulated mortality 3 months after sea transfer (CM_{3mo}) and after completed production of post-smolt (CM_{total}) from 23 CCS. Upper: CM_{3mo}, lower: CM_{total}. For the first two columns (Total mortality) the population is the total number of fish (S0, S1 and total), for the other columns the population is cages.

					CM_{3mo}				
		Total mortality				Cages			
Cage type	Smolt	n_0	%	n	Mean	SE	Median	Min	Max
CCS	S0	2,077,992	1.3	18	1.1	0.2	0.8	0.3	2.9
CCS	S1	744,845	6.2	5	5.9	1.7	3.3	1.9	10.6
CCS	Total	2,822,837	2.6	23	2.2	0.6	1.1	0.3	10.6
					CM_{total}				
		Total mortality				Cages			
Cage type	Smolt	n_0	%	n	Mean	SE	Median	Min	Max
CCS	S0	2,077,992	2.4	18	2.1	0.3	2	0.7	4.3
CCS	S1	744,845	7.2	5	7	1.3	6.7	2.9	10.9
CCS	Total	2,822,837	3.6	23	3.2	0.6	2.1	0.7	10.9

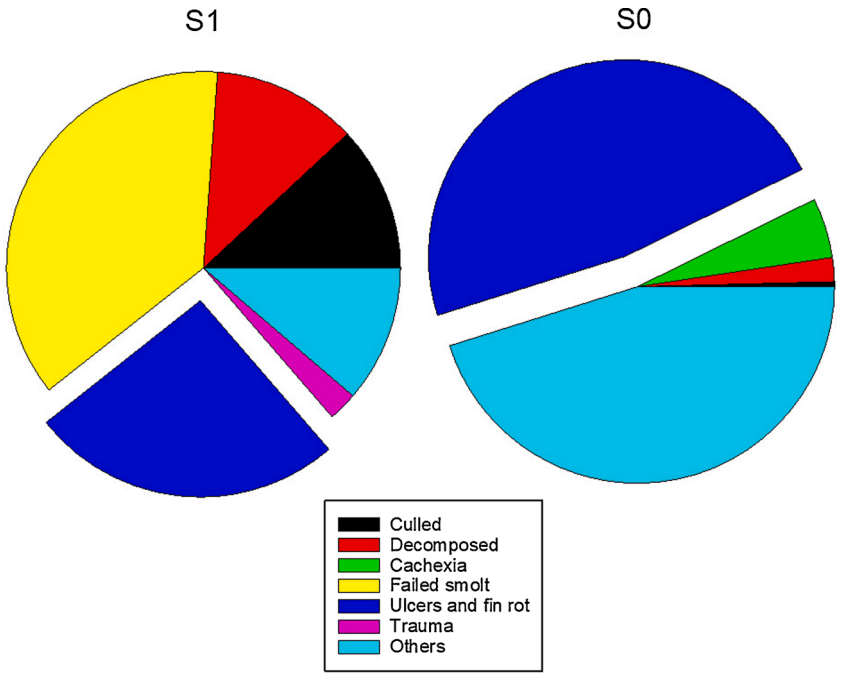

Fig. 6. Cause-specific mortality recorded in CCS, October 2014 to May 2017. Left panel: spring smolt (S1, n = 5), right panel: off-season smolt (S0, n = 18). (For interpretation of the colour codes, the reader is referred to the web version of this article).

Table 6
Comparison of weight at sea transfer (g), CM_{3mo} and mortality causes in the present trial and a study of 20 open cages with S0 Atlantic salmon and national reference data from 667 open cages stocked with S0, all from the 2006 year class (Aunsmo et al., 2008). Data from all 23 CCS with both S1 and S0 in our study are also shown.

		CCS S0+S1	CCS S0	Open cage S0	National data 2006
Number of fish (millions)		2.8	2.1	2.7	71.1
Number of sites		2	2	10	114
Number of cages (mean no. fish/cage)		23 (122,700)	18 (115,400)	20 (139,700)	667 (103,100)
Species		A. salmon	A. salmon	A. salmon	A. salmon and R. trout
Sea transfer period		08.05–21.12	16.10–21.12	28.8–26.11	1.8 - 31.12
Mean (SD) weight at sea transfer (g)		104 (23)	103 (19)	81 (25.8)	109.7 (43.2)[a]
CM_{3mo} (%)		2.6	1.3	2.1	3.7
CM_{total} (%) (159 days)		3.6	2.4	n	n
Mortality causes (% of total mort.)	Cachexia	2.4	4.9	3.7	n
	Failed smolt	19.3	0	7.4	n
	Ulcers and fin rot	36.1	47.5	50.9	n
	Trauma	1.3	0	7.3	n
	Others	40.9	47.6	30.7	n

[a] Mean weight one month after sea transfer.

outside the cages were ≤ 1 mg/L and 2 mg/L, respectively. Inside CCS at site 1, median and maximum concentration of CO_2 was 2 mg/L and 4 mg/L, respectively. At site 3, median concentration of CO2 was 4 mg/L, but the variation here was larger with a maximum concentration of 20 mg/L. Total ammonia nitrogen (TAN) values from CCS were 0.3 to 0.5 mg/L. With salinity of 32.0 ppt, alkalinity between 2.2 and 2.3 mM and pH ≥ 7.4, this corresponds with levels of toxic ammonia (NH_3) of less than 0.004 mg/L (Fivelstad et al., 1995). Levels of total suspended solids (TSS) ranged between < 8 and 169 mg/L, fluctuating with the observed TSS levels in the seawater around the cages. More detailed water quality data are shown in Supplementary data 9 and 10. All sea lice counts in CCS showed zero salmon lice. Adult *Caligus elongatus* were identified sporadically, and at a low prevalence (mean number of *C. elongatus* per fish between 0 and 0.1).

4. Discussion

4.1. Growth rates, feeding rates and feed conversion ratio

Based on the review from Thorarensen and Farrell (2011), a TGC between 2.7 and 3.0 should be anticipated in CCS, with values > 3.0 in more long-term studies. In a study of production of Atlantic salmon one-year smolt (S1) in a raceway CCS (Balseiro et al., 2018) both TGC and condition factor (CF) were highest in the open cages 4 months after sea transfer, with TGC around 3.1 and CF = 1.20 in the open cage and TGC around 2.8 and CF = 1.12 in the raceway CCS. The growth data reported by Skaar and Bodvin (1993) from a trial of post-smolt Atlantic salmon between 60 and 700 g showed a TGC in CCS of approximately 3.5, compared to the moderate growth rate of 2.1 in the open reference cages. The results from our study support the review of Thorarensen and Farrell (2011) and point towards the possibility of achieving higher growth rates with the optimisation of technology and farming methods. In comparison to open cages, fish growth in CCS could be boosted by higher and more stabilised water velocities (Johansson et al., 2014; Solstorm et al., 2015, 2016; Nilsen et al., 2018) and CCS production of S0 post-smolts could get the possible benefit of access to deep water with higher temperatures during winter. The specific growth rate declines with fish size and increases with water temperature within the temperature optimum of the species (Brett and Groves, 1979). A seasonal variation of TGC between 1.24 and 4.95 has been reported from studies of Atlantic salmon in open cages (Mørkøre and Rørvik, 2001), and our weekly data showed approximately the same range of TGC values. There were too few cage observations and too many other confounding variables in this study to test the true impact of seasonal variations. Nevertheless, seasonal variations and the impact of photoperiod could be important determinants for growth rate in CCS, and should be further investigated.

Evaluation of growth rates relies on precise and comparable weight estimates and it is a challenge to collect these data in field surveys. Notably, the estimates of end weight (W_1) in our study are systematically less reliable than W_0, and this represents an important source of error when calculating growth rates. We used TGC to compare growth rates of post-smolt across different production cycles with variable temperature profiles and temperature sums. TGC is a growth model validated for use in fish between 100 and 3000 g and for water temperatures between 4 and 14 °C (Alanärä et al., 2001); and these conditions were met in our study. Our study was performed at neighbouring sea sites, but with studies across different latitudes a growth model incorporating the effect of day length, such as the Ewos Growth Index (EGI), would have been appropriate (Aunsmo et al., 2014). As weighing procedures represent a possible negative impact on fish welfare, the use of biomass frames or methods based on picture analysis of the swimming fish should be the standard procedure in future research and in supervision of commercial production.

The feed conversion ratios (FCR) were calculated from total feed distributed and total increase in biomass. This does not account for possible loss of excess feed; thus the calculated values are probably higher than if actual feed consumption of the fish could be used. This is common when using the data of FCR from commercial farming to benchmark feed quality and feeding methods. FCR declines with increasing temperature, thus it also declines with increased SGR. At the same time, FCR increases with fish size (Brett and Groves, 1979). In this study, the moderate FCR values from 18 CCS with S0 correspond to the good growth rates with TGC around 3.0 and to the fact that the study was performed with salmon between 100 and 1000 g. The moderate FCR values also indicate efficient feeding systems with moderate loss of feed. However, the inaccuracies of the data material do not allow for detailed analysis of any group differences.

4.2. Mortality rates and mortality causes

Our study covered one specific CCS project and it would be useful to compare these results with data from other CCS projects with different technologies, different site specifications and with fish of different origin. However, there are, so far, fewer comparable datasets published from such CCS projects. In the first published study of CCS (Skaar and Bodvin, 1993), total cumulated mortality (CM_{total}) over a period of 5 months after sea transfer was lower in CCS (1.3 %) than in the open cage (3.6 %). This situation was partly explained by three bath treatments with organophosphates against salmon lice in the open cage during the trial period. In a study of S1 smolt (Balseiro et al., 2018), CM_{total} was similar in the CCS raceway system (1.3 %) and the open cage (1.0 %) after a trial period of 4 months. The annual mortality data from Norwegian salmon farming from the years 2014–2017 ranged between 14.2 and 16.2 % (Hjeltnes et al., 2019), corresponding to an average monthly mortality rate around 1.3 %. The median CM_{3mo} and CM_{total} for S0 in our study was between the median and the 75-percentile of the national 2014–2015 data reported by Svåsand et al. (2017), while the data from S1 in our study showed a median mortality above the 75-percentile from the national data. Cumulated mortality three months after sea transfer in CCS was equal to or lower than in a study of open cages (Aunsmo et al., 2008) and the national reference data from S0 in 2006 (Table 4). In our study, 72 % of the total mortality was recorded during the first three months (57 % of the total time period). Historically, mortalities have also been highest during the first months after sea transfer and low towards the time for harvest, but for the 2014 and 2015 generations this trend was reversed, with increasing mortality rates towards harvest size (Svåsand et al., 2017). Our study covered only fish size to 1000 g, and there is a need for more studies on performance and mortality in CCS, also with larger fish. Ulcers and fin rot represented around 50 % of the total mortality after three months (91 days) in the open cages (Aunsmo et al., 2008), this is similar to our data (although our scores were counted from CM_{total}, 159 days). Both our study and Aunsmo et al. (2008) showed a moderate prevalence of smolt quality problems, cachexia and physical trauma and a larger bulk of 'Other' causes of mortality. To some extent, the problems with smolt quality in our study were also observed during the smolt quality assessments, however with few possibilities to intervene and remove these fish before sea transfer or to exclude these groups altogether. Some of the mortality in S0 groups classified as 'Other' during the period in seawater could have been caused by gill lesions. However, the accuracy of the cause-specific mortality records performed by trained professionals in Aunsmo et al. (2008) was probably higher than in the present paper where we had to rely more on farm data.

The mortality rate is an important welfare indicator, as well as an economically important parameter for the salmon producer. High mortality indicates low welfare for the fish that die, but also the survivors might have experienced a period of discomfort, loss of appetite or pain. Because most of the mortality appears with an epidemic pattern (few cages, high mortality, one or two identifiable major causes of death), measures must be taken to better identify and prevent the underlying causes of disease. The main cause of mortality, as measured in

terms of proportion of total mortality or as the diagnosis affecting most cages, was 'Ulcers', comprising skin ulcers and fin rot. This is a common cause of disease and mortality in Norwegian salmon farms (Hjeltnes et al., 2019). The manifestation of ulcers and fin lesions during rearing in seawater cages was diverse, both "classical winter ulcer" lesions (Hjeltnes et al., 2019) and pathologies characterised by superficial skin lesions and more severe fin lesions (fin rot). Tenacibaculosis ("untypical winter ulcer") was not a common observation in our study. Isolation of *Aliivibrio* species and *Moritella viscosa* from kidney and other internal organs, together with positive PCR tests for *Moritella viscosa* in kidney tissue, also indicated systemic infections, at least in the most severe cases. Pathological lesions observed in necropsies and histological samples supported this. It is important to remember that the retention time of the water and the self-cleaning capacity of CCS are two technological variables with high impact on a broad range of water quality parameters, including microbiology. The diversity of pathology and clinical appearance reflects the variation of pathogens involved, and the complex interaction between fish, pathogens and the environment. The microbiological balance in the water and the interaction between cage technology, fish and pathogens in the rearing environment continues to be an important issue for health and welfare of farmed Atlantic salmon, also with the use of CCS cages.

Mortality in the five S1 cages at site 3 was high, with failed smolt quality as the most important mortality cause. Lesions and stress during sea transfer could induce mortality and reduced performance (Handeland et al., 1996; Iversen et al., 2005), but this was not recorded as a significant problem in any of the groups in this study. High prevalence of nephrocalcinosis at the date of sea transfer was observed in the two generations of S0 groups where kidney histology was investigated (site 1, 2014 and 2016, site 2, 2014). This indicated suboptimal water quality in the hatchery, with a possible exposure to CO_2 levels above the recommended maximum levels of 10–15 mg/L (Fivelstad et al., 1995, 2003; Thorarensen and Farrell, 2011; Mota et al., 2019). After oxygen depletion, the accumulation of CO_2 is considered the next limiting water quality parameter in such flow-through systems, in hatcheries as well as in CCS, and nephrocalcinosis has been reported as a problem in many Norwegian hatcheries (Gu and Olsen, 2019). Exposure to high levels of CO_2 could also lead to other physiological adaptations, to reduced growth rates in the initial seawater period (Martens et al., 2006), and possibly also to increased mortality. The impact of the rearing environment in hatcheries on fish health and welfare at sea transfer and during the first period in seawater should be investigated more thoroughly. In our study, after sea transfer to CCS or open cages with median levels of $CO_2 \leq 2$ mg/L, the kidney lesions seemed to disappear during the seawater period without any significant mortality in these cages at site 1 and site 2. Throughout the study period, concentrations of CO_2 were usually ≤ 10 mg/L, and on a few occasions > 15 mg/L. The production intensity was higher at site 3 than at site 1, with a lower minimum SWC and higher maximum feed load and density, and at site 3 the maximum levels of CO_2 were also highest (20 mg/L).

The observed oxygen concentrations in CCS were considered to be within safe limits for the welfare and growth performance of Atlantic salmon post-smolt (Bergheim et al., 2006; Remen et al., 2013, 2016), but it is important to emphasise the need for accurate monitoring and regulation of oxygen, especially at high temperatures and high production intensities. Future studies of oxygen consumption in CCS with a focus on diurnal variations, the impact of temperature, fish size, feeding rates and possible stressful events (fluctuations in rearing environment, crowding, etc.) would be of interest to optimise oxygenation use and oxygenation systems in CCS.

Gill pathology developed during the seawater period both in 2014/2015 and 2016/2017. Harmful algal blooms have been shown to cause gill lesions characterised by swelling and pyknosis of lamellar epithelium, congestion of branchial vessels and increased mucus production is in farmed salmonids (Rodger et al., 2010). The epithelial irritation observed on gills during April and May in this study could also be caused by high phytoplankton concentrations, but more specific pathology caused by specific gill pathogens could also be a contributing factor. Inside CCS, increased levels of TSS could contribute to gill irritation, skin lesions and elevated plasma cortisol (Schumann and Brinker, 2020), however we had too few observations and too high variation in TSS levels, both outside and inside CCS, to evaluate the impact of particles on fish health or performance. The influence of gill lesions on growth and mortality is this study is uncertain. More in-depth studies of algal blooms, gill health and gill pathology in commercial salmon farming systems should be performed.

5. Conclusions

Production of post-smolt Atlantic salmon in closed containment systems (CCS) showed good growth rates, low feed conversion rates and low to moderate mortality rates. Mortalities caused by 'Ulcers and fin rot' (various bacterial infections) and 'Failed smolt' were the two most important specific mortality causes and fish welfare issues in CCS. It was possible to maintain water flow, oxygen saturation and water quality within safe limits for fish health and welfare. With production of off-season smolt in CCS, access to warmer water during the coldest season (October to April) could contribute to improved growth rates and fish welfare. With the use of deep water (25 m) in CCS, it was also possible to effectively prevent infestation with salmon lice (*L. salmonis*).

Transparency document

The Transparency document associated with this article can be found in the online version.

Declaration of Competing Interest

The authors report no declarations of interest.

Acknowledgements

The authors thank the staff at AkvaFuture AS and Sinkaberg Hansen AS for all their help and contributions. Special thanks are extended to Anders Næss, Trond Otto Johnsen, Glenn Ovesen, Alexander Ormøy and Benny Fjelldalselv (AkvaFuture AS), Signar Berg Hansen, Bent Brevik, Børre Skjevelnes and Kari Lervik (Sinkaberg Hansen AS). We also owe our gratitude to Dr. Henning Sørum (NMBU) and his staff for the microbiological analysis and valuable discussions and to Jinni Gu and Stephanie Wüstner (Norwegian Veterinary Institute) for histopathological examination of kidney and gill samples. This study was supported by Innovation Norway (2011/102413, 2012/110747, 2013/112006), the Norwegian Research Council (Project no. 269013), AkvaFuture AS and by the Norwegian Veterinary Institute.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.aquaeng.2020.102124.

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