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Reluctance of farmed Atlantic salmon to feed in cold water revealed during automated hydroacoustic feeding control

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ABSTRACT

Waste feed remains a major issue in open sea-cage Atlantic salmon aquaculture. “Echofeeding” is an appetite-led feeding method that stops meals based on fish biomass detected by an echo sounder. The method reduced waste feed and upheld fish growth in a relatively vertically unstratified coastal farming environment. Here, we tested echofeeding at a commercially relevant scale over an 8-month period in a fjord environment with seasonal vertical temperature and salinity gradients. We compared fish behaviour and growth between echofed fish, fed at high intensity and near surface, and control fish, with feeding regulated by pellet detection without surface feeding restriction (conventional practice). Growth (SGR>1.81) and FCR (<0.87) were excellent and similar for three months after sea-transfer in August. However, a strong halocline in late November (<5°C surface water) led echofed fish to avoid surface feeding, resulting in underfeeding. Following the setting of a deeper depth interval for triggering feeding, the echofed fish fed more, and fed at similar levels to control fish when feeding intensity was reduced. Echofeeding underperformed in early spring as rising surface temperatures attracted salmon, making it difficult for the system to distinguish between feeding and routine behaviours. Both groups contracted salmonid alphavirus during winter, reducing appetite and promoting early harvest. Results highlight the need for echofeeding to take environmental changes into account. Further, as fish grew, a gradual decline in the echo signal measured during feeding suggests a method for refining meal termination threshold to minimize waste feed while maintaining good fish growth.

1. Introduction

Food waste in sea-cage aquaculture of Atlantic salmon (*Salmo salar*) is an enduring issue. Pellets that are uneaten by the farmed salmon fall outside of the cage into the wider marine environment. Feed loss from salmon farming has rarely, if ever, been estimated with robust methods, but what estimates exist range widely (e.g. 0.35 % - Black, 2008; 1.4 % - Dempster et al., 2009; 5 % - Kutti et al., 2007). Feed losses at these levels at a single farm feeding 1000 tons per year equate to 3.5–50 tons. This substantial economic loss to producers also has negative environmental consequences, as uneaten feed releases nutrient waste into surrounding ecosystems (Wang et al., 2012; Sardenne et al., 2020) and modifies the natural diets of wild organisms in the vicinity of farms (Fernandez-Jover et al., 2007; White et al., 2016). More effective feed control would reduce the financial and ecological impacts of waste feed in salmon farming.

Feed control is predominately carried out by visual assessment of feeding activity and pellet sinking depth in online streams from remotely controlled subsurface cameras. Several of the camera and feed technology suppliers have automatic image analysis algorithms to automate this process, and there are several published papers on this topic (e.g. Pinkiewicz et al., 2011; Skøien et al., 2014; Li et al., 2017; Måløy et al., 2019; Hu et al., 2021). However, solutions based on cameras suffer from difficulties from limited field of view, periods with unclear water, and

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variable lighting conditions (Li et al., 2020). Modern salmon farming cages are large and becoming larger through time (McIntosh et al., 2022), with average cage diameters exceeding 40 m in Norway. A single, horizontally facing camera that revolves in 360° to detect pellets falling below feeding fish, with a visual range of ~5 m, can cover just ~10 % of the total cage area of a 40 m diameter cage at a single depth. Further, to our knowledge, there are no estimates of feed loss rates using camera-based systems in salmon aquaculture. An alternative feeding control system uses sonar or echosounder technology to monitor fish behaviour in sea cages, which has been vital in research for understanding fish environmental preferences (e.g. Oppedal et al., 2011; Wright et al., 2015; Klebert et al., 2023) and feeding behaviour in salmon post-smolt farming (e.g. Juell et al., 1994; Fernö et al., 1995). Recent commercialization has paved way for increasing use of echosounder technology in daily farm and feeding management, as today used in ~5 % of Norwegian salmon sea cages (J. Myrland, pers. comm.).

Hydroacoustic feeding control, hereafter called echofeeding, uses echo sound to monitor fish biomass in a defined feeding area (Bjordal et al., 1993). As the fish become satiated and begin to leave the feeding area, the monitored biomass descends in the cage, enabling farmers to set a threshold level of biomass at a specific depth which autonomously terminates a meal. Folkedal et al. (2022) demonstrated that the method efficiently eliminates waste feed while achieving excellent growth in caged Atlantic salmon. However, their experimental testing was limited to a one-month period during summer with small fish (1 kg) and a one-month period during winter with large fish (5 kg) at a farming site with little vertical temperature stratification of the water column. Whether the method will work at more stratified sites with strong temperature differences with depth is uncertain.

While coastal farming sites often have some vertical stratification, fjord sites typically have strong gradients in temperature and salinity (Oppedal et al., 2011). This could create problems when using the upper 1-metre as the defined feeding area, as in Folkedal et al. (2022), when environmental conditions at the surface are not optimal for salmon. Salmon are repelled by brackish surface water that is colder than the underlying seawater (Johansson et al., 2007; Oppedal et al., 2011). These conditions, which can arise through abrupt changes in surface layers or during longer periods in winter when the fjord surface is cold, may create a trade-off between feeding and thermal avoidance that will affect feed intake during echofeeding. If this is the case, echofeeding settings, such as biomass-at-depth thresholds, must be adapted to changes in the environment. Moreover, Folkedal et al. (2022) showed that the biomass threshold level for continuation or finishing meals depends on fish size, and that periodic recalibration is required if echofeeding is used for periods longer than one month.

Salmon are efficient in adapting to feeding regimes, including the feeding intensity (pellet rate), number of daily meals, and when meals are delivered (Juell et al., 1994; Talbot et al., 1999; Folkedal et al., 2022; Lai et al., 2025). High feeding intensity is beneficial for reducing competition for pellets and provokes high feeding activity which gives a stronger signal for appetite assessment during feeding control, including echofeeding (Talbot et al., 1999; Folkedal et al., 2022), yet many farmers remain convinced that subordinate individuals will engage less in feeding which will widen the size distribution among the fish. Moreover, short intensive meals result in a deeper swimming depth day round compared with continuous feeding over the work hours (one long daily meal) (Fernö et al., 1995). This provides an intriguing mechanism towards lessening exposure to the infective copepodid stage of the ectoparasitic salmon lice (*Lepeophtheirus salmonis*), which resides mostly in the upper surface waters, as well as offering more time to swim at preferred depth (Oppedal et al., 2011).

In this study, we tested echofeeding at a commercially relevant scale over an 8-month period (August 2018 – May 2019) in a fjord environment to determine if a trade-off between cold surface water and appetite restricts feed intake and growth under echofeeding, and whether biomass threshold calibration levels align with growth rate and fish size. Intensive meals, as assumed best for echofeeding, were used, and were distributed throughout the day, taking advantage of automated feeding control. Control group cages followed a conventional feeding regime, providing feed throughout the workday with mild overfeeding. Feeding control in the control cages was conducted by a commercially available pellet detection system (SeaV) whose input was used for reducing feed and terminating meals. This method allows fish to consume pellets over a broader depth range than echofeeding, implying that it may be more robust to environmental changes in surface water. The design enabled a comparison of fish growth, including size distribution, and feed utilization between conventional and automated feeding practices during periods with cold surface water, such as in winter, and periods without, as in the autumn when the study commenced.

2. Material and methods

2.1. Location, experimental design and fish

The experiment was carried out at the Solheim Cage Environment Laboratory at the Matre research station (60°N) of the Institute of Marine Research (IMR), Norway. Six square sea-cages (12 × 12 m and 18 m depth; approximately 2000 m^3) were stocked with fish on the 8th of August 2018. Three cages were designated for echofeeding, and three cages for a control feeding regime, spatially distributed in two rows in a block-randomized design. The fish were produced as 0 + smolts at the Matre research station and were smoltified and given seawater in tanks on land on the 15th of May 2018 and kept on full strength seawater in tanks until transfer to sea cages. When pumped out of the wellboat used for transport from the land facility (transportation time ~30 minutes), the fish were automatically counted by an optical system. Continuous video from this was manually scrutinized for fish counts, showing an average underestimation of fish numbers of 2 ± 0.7 % (mean ± SE) by the automatic system. The manual count of fish was 6280, 2219, 6175, 6001, 6183, and 6144 for cages one to six respectively. To achieve similar numbers per cage, additional fish from the same batch were added to Cage 2 on August 15th to achieve a total of 6159. A sample of 100 fish per cage was taken to measure average fish length (cm), weight (g) and condition factor on the 15th August by capturing fish with a cast net, crowding and netting. Across all fish, mean fork length was 30.1 ± 2.6 cm (mean ± SD), weight was 292 ± 80 g, and condition factor was 1.05 ± 0.08. At the routine screening for fish disease early February, 7 out of 20 sampled fish tested positive for the salmonid alfavirus (SAV3), a disease which is well known to reduce fish appetite (McLoughlin and Graham, 2007).

2.2. Experimental protocol

The echofeeding group were fed from the first day of feeding (15th August) at a high feeding intensity of 250 g per ton per min (GTM), while the control group was fed at ~50 GTM, over the equivalent of five times longer meals. The echofeeding group was given three daily meals, initially at 08:00, 14:00 and 20:00. The control group was fed within work hours starting between 08:00 and 11:00 and until observed fish satiation was reached between 13:00 and 16:00. Feeding intensity was set to disperse the expected table ration over 6 h per day. Start of feeding for both groups, and the intervals between meals for echofeeding were adjusted according to change in daylight hours over the course of the study.

Over the initial week of feeding, the technical setup including echo sounder transducers (echofeeding group) and pellet detection cameras (control group) were tested and optimized. Appetite assessment and stop of feeding was then carried out by manual camera observation. After this, meal termination was automatically carried out by software for the echofeeding group, and manually for the control based on alarms of pellet detection (see details below).

Both the initial calibration of the echofeeding biomass threshold limit (continuation or stop of feeding) and periodic recalibration (according to expected reduction in threshold levels with fish growth) was carried out relative to when pellets sank to a depth of 5 m within meals as observed by camera in the feeding area. The per cage calibration value was set from concurrent and past two minutes total echo strength within the designated echofeeding feeding volume. Pellets were observed in video streams from one remotely controlled submerged camera per cage. This evaluation was carried out over the 3 daily meals over 3 days every 3–5 weeks during the experiment. The echofeeding observation volume was altered (deeper volume) according to changes in the water column environment if the fish failed to trigger feeding for a prolonged period under the given settings.

To account for potential effects of feeding regime on fish group vertical distribution during routine behaviour, the main volume of each cage was monitored by an upward facing transducer (43° opening angle, 50 kHz) positioned at 18 m depth (beneath the cage bottom) (Fig. 1).

Fish growth rate was determined from periodic sampling of fish from each cage by cast net (n = 200 fish per cage in October and January, and n = 100 fish in April and May).

2.3. Feed, feed distribution and feeding control

The fish were fed a standard commercial diet (Skretting Spirit, Skretting, Norway), with pellet size 3 mm until 20 august, 4.5 mm until 16 November, 7 mm until 11 January, followed by 9 mm until harvest.

For echofeeding cages, the pellets were distributed over a circular (Ø = 3 m) surface area in the cage center using automatic feeders (Betten Maskinstasjon AS, Norway) as controlled by PC software (CageEye 2.1.2. CageEye AS, Norway). Dependent on pellet amount, the pause between pellet batches/dispersion was 4–9 s, ensuring a nearly continuous presence of pellets in the main feeding volume during meals - an optimal condition for echofeeding input as feeding behaviour is maintained (Folkedal et al., 2022). For the control cages, a conventional pneumatic central feeding system was used (controlled by Fluctus vers. 7.0.0.4, Fluctus AS, Norway) where the pellets were spread over a surface area equivalent to the echofeeding cages. The pellets were dispersed in batches alternating between the cages, with ~1.5 minutes between each batch and about 4.5 min between each batch in the same cage. This batch feeding method provided fish with a noticeable pellet amount over ~3 seconds per dispersal, each triggering a short-term appetite response. The associated behavioural reaction and resulting pellet sinking depth reflect the conventional feeding control practice.

Echofeeding consists of a computer software program that via an echo sounder connected to a submerged upward-facing transducer monitors echo strength within a defined feeding area and converts the data to fish density or biomass in real-time (Fig. 1A). Based on pre-programmed echo intensity limits (fish biomass), the software decides whether to continue or stop feeding, as sea-caged salmon will descend and swim deeper within cages as they become satiated (see Folkedal et al., 2022 for details). Echofeeding is dependent on two main proxies: 1. the observation volume of feeding activity as determined by transducer settings and spatial positioning (echo beam volume) and depth limits set within software, and 2. the biomass threshold limit for feeding termination. Initially, the settings described for successful echofeeding in Folkedal et al. (2022) were used; a 200 kHz (14° opening angle) echo beam from a transducer positioned 8 m deep and directed upwards towards the center of pellet dispersion at the surface (Fig. 1A), where fish feeding activity between the surface and 1 m depth was used as the input whether to continue or terminate meals. After changing the cage nets the first week of March, the hose for the dead fish collector interfered with the echofeeding transducers, and from 14 March a shallower position was used (from 8 to 6 m) and a wider beam transducer setting (50 kHz, 44° opening angle) was used to compensate. A 3-min period was chosen for appetite testing (minimum duration of a meal), meal elongation (whenever biomass exceeded the echo intensity threshold within a meal), and for meal cessation (feeding stopped if the echo intensity persisted below the threshold).

Feed control in the control group was based on input from automatic pellet detection from camera observations (SeaV, FaroeSea, Faroe Islands). The upward facing pellet detection camera was positioned at 5 m depth in sea cages, and provided a warning signal (both in PC software and as mobile phone push notification) when detecting a pellet rate $\geq$ 0.2 pellets s^{-1} in its close vicinity (~1 m) (Fig. 1B). Based on two warnings within 8 minutes, the feeding rate within a meal was manually reduced by 50 %, and the meal was stopped when the same occurred at

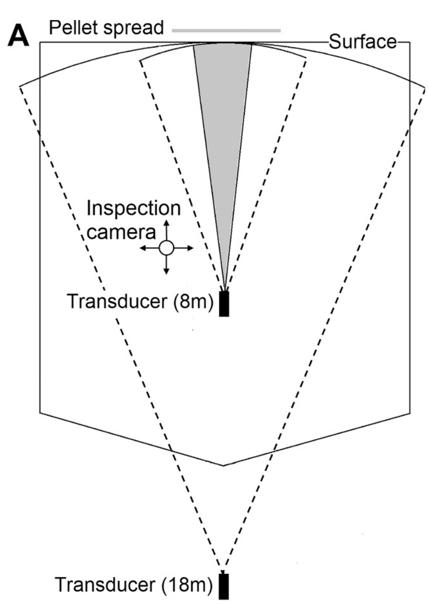

Fig. 1. A simplified schematic overview of the sea cages (12 × 12 and 14 m deep), respectively for echofeeding (panel A) and control (panel B). Position of echo sound transducer below cages and its echo beam of 50 kHz (43° opening angle, dashed lines) and pan and tilt inspection camera mounted to remote controlled winch and horizontal adjustment is indicated for both cage groups. Transducer positioned within echofeeding cages (panel A) is indicated with beam coverage of 50 kHz (dashed lines) and 200 kHz (14° opening angle, solid lines), and position of pellet detection camera is indicated for control cages (panel B). Area marked with grey in panel A indicate the smallest observation volume as predominately used for echofeeding, and area marked with grey in panel B indicate the pellet detection volume.

the 50 % rate.

2.4. Growth estimation and formulas

Daily growth was calculated by using the Skretting growth model (Skretting, 2012) based on manual samples for average size of the fish per cage and estimations based on amount fed.

Specific growth rate (SGR) day^{-1} was calculated as:

$$SGR = (\ln(W2) - \ln(W1)) * \frac{100}{t}$$

Where $W1$ is start and $W2$ is ending mean live body weights of the fish and t is the number of days between.

The thermal growth coefficient (TGC) was calculated with following formula (Iwama and Tautz, 1981):

$$W2^{0.33} = W1^{0.33} + \left(\frac{T}{1000}\right)t$$

Where T is the average temperature in °C (5 m depth).

Fulton's condition factor (K) was calculated with the following formula:

$$K = \left(\frac{W}{L^3}\right) \times 100$$

Where W is the mean live body weight (g), and L is the mean fork length (cm).

Feed conversion ratios (FCR) was calculated as economic FCR (eFCR) with the following formula:

$$\frac{Feed}{\Delta Biomass}$$

Where *Feed* is the total fed amount between time points of size sampling ($T1$ and $T2$), and *ΔBiomass* the estimated biomass increase based on $W1$ and $W2$ times number fish alive at $T1$ and $T2$. Biological FCR (bFCR) was calculated with the following formula:

$$\frac{Feed}{(BiomassT2 + Biomass\ morts) - BiomassT1}$$

Where *Biomass morts* is the estimated total biomass of mortalities.

2.5. Echo sounder configuration and fish vertical distribution in the cages

The fish vertical distribution and per depth density were observed continuously by a PC-based echo integration system (CageEye MK-4, software version 1.2.1., CageEye AS, Oslo, Norway) connected to the upward facing transducers both beneath (covering main cage volume) and within each cage (covering feeding volume for echofeeding). Echo intensity was integrated at 7 cm depth intervals with ping rate of one s^{-1} and data were stored as mean values per minute. Mean values of echo intensity per 12 s was used during the automatic online evaluation of feeding continuation in echofeeding. For practical convenience, depth intervals of 0.5 m were used for setting of depth intervals for echofeeding. Vertical fish distribution in the cages was calculated based on data from the transducer covering the main cage volume, where data was aggregated as 15 min mean values. From this the depth of maximum observed fish density (OFD_{max}, Oppedal et al., 2007) was calculated based on mean values per 0.5-m depth intervals.

2.6. Environmental variables

Water temperature, salinity and oxygen saturation were recorded daily outside the cages between the surface and 20 m depth by a profiling CTD connected to an automatic profiling buoy (APB5, SAIV AS, Norway). Oxygen levels were always > 80 % and are not shown in further detail. From September, the environment was vertically stratified by a surface pycnocline where salinity levels persistently were < 28 ppt and followed a sharp thermal gradient with colder water on top (Fig. 2). Regretfully, environmental data for periods during winter and spring is missing due to technical errors (Fig. 2).

2.7. Camera observations

Each sea-cage was monitored using a pan and tilt subsurface camera (Imenco Gemini, Imenco AS, Norway) connected to a winch and remote control (Imenco Insight, Imenco AS, Norway) that could move vertically within cages. Cameras were used for calibration of echofeeding, daily inspection of echofeeding, pellet detection functionality with focus on observing pellets below 5 m depth, and for general observation of fish physical condition, behaviour, mortalities and assessment of cage structures and environment.

2.8. Statistics

All statistical analyses were done with R software system Version 4.4.3 (The R Foundation for Statistical Computing, Vienna, Austria), and the level of significance was set to 0.05. Linear mixed-effects models (LME) were fitted to test the effect of treatment (control vs. echofeeding) on recorded fish weight, length and condition factor, respectively, using the lmer function in the lme4 package in R. Treatment and time (day), as well as their interaction, were included as fixed effects, and cage (nested within treatment) was included as a random effect to account for repeated measures and potential cage-level variation. Pairwise post-hoc comparison of treatments on each sampling day were carried out using estimated marginal means (EMMs) from the emmeans package, using Tukey-adjusted p-values to control for multiple comparisons. Model assumptions (normality and homoscedasticity of residuals) were visually inspected and regarded as acceptable. Cage level data of growth parameters, FCR, and periodic mean fed amount, swimming depth and mortality were tested using a Welsh two-sample t-test (paired comparison of periodic mortality). Echofeeding threshold relative to fish size was scrutinized by trend analysis. All data are presented as mean ± S.E. unless otherwise specified.

3. Results

3.1. Fish growth, behaviour and fed amount

The overall linear mixed-effects models showed significant interaction between treatment × time for fish weight ($t = -7.44$, $p < 0.01$), length ($t = -7.03$, $p < 0.01$) and condition ($t = -8.22$, $p < 0.01$), indicating that the treatment effect on fish growth varied over time, with higher growth in the control than echofed fish. Random effects showed substantial cage-level variability in fish weight at the start of the study (SD=71 g, 27 % of the initial mean) and high residual variability (SD=442). Less cage variability was found for fish length (SD=0.80 cm, 2,7 % of the initial mean) and residual variability (SD=3.51 cm), and for condition factor (SD=0.02, 2.1 % of the initial mean) with moderate residual variability (SD=0.09). Post-hoc comparisons between the treatment groups per sampling time point are presented below.

3.1.1. Period 1 (P1): early autumn (August to October)

The environment was homogenous from the experimental start (mid-August) until mid-September when a colder and less saline surface layer was established (Fig. 2). Fish positioned themselves deeper and below the pycnocline during routine behaviour (non-feeding) and slight difference between night and daytime swimming depth was observed (Fig. 2A).

Both echofeeding and pellet detection were highly functional during this two-month period, where the initial echofeeding threshold was the highest used in the experiment (Fig. 3). The settings of the echofeeding

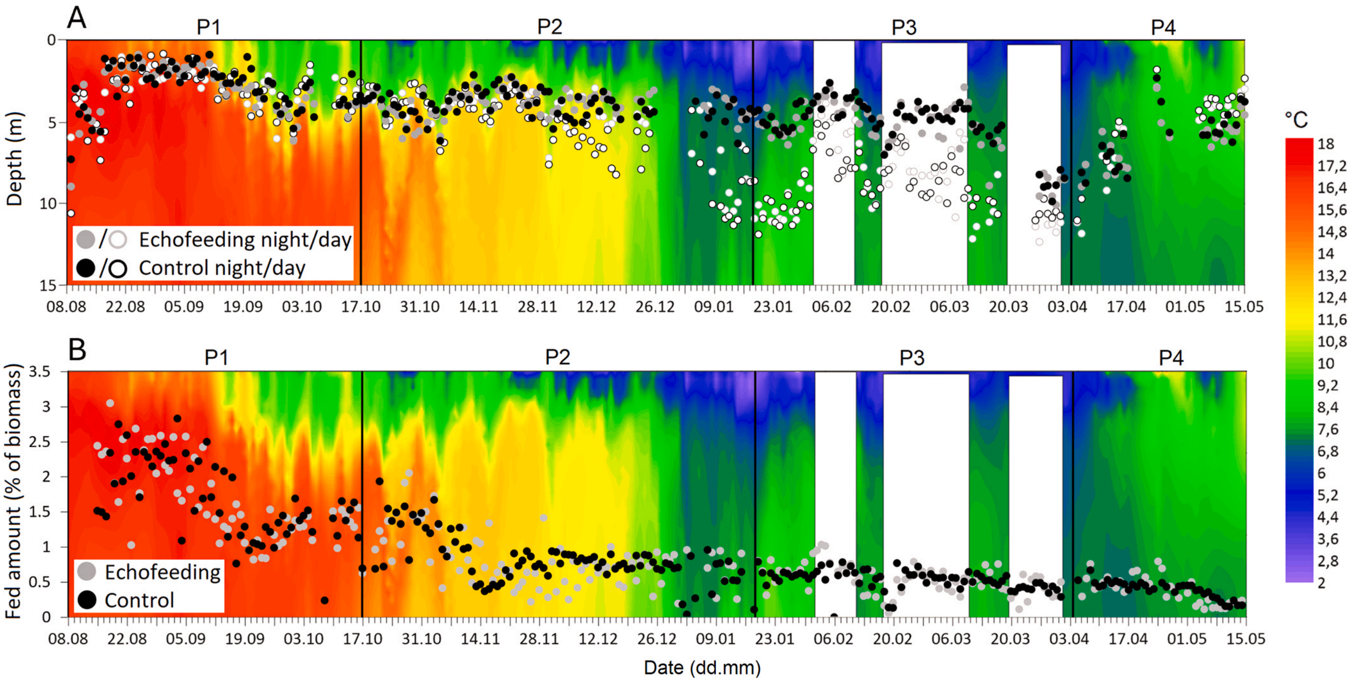

Fig. 2. Upper panel (A) shows the mean hourly swimming depth of maximum observed fish density as a mean for cages respectively with echofeeding and control feeding at night (0300–0400) and day (1100–1200), and the lower panel (B) the mean daily fed amount for the echofeeding and control cages, respectively. Background for each panel is an isoplot of the recorded water temperature from 0 to 15 m depth (missing data indicated with white). Experimental periods between fish size sampling are indicated with black vertical bars and numbers above panel A.

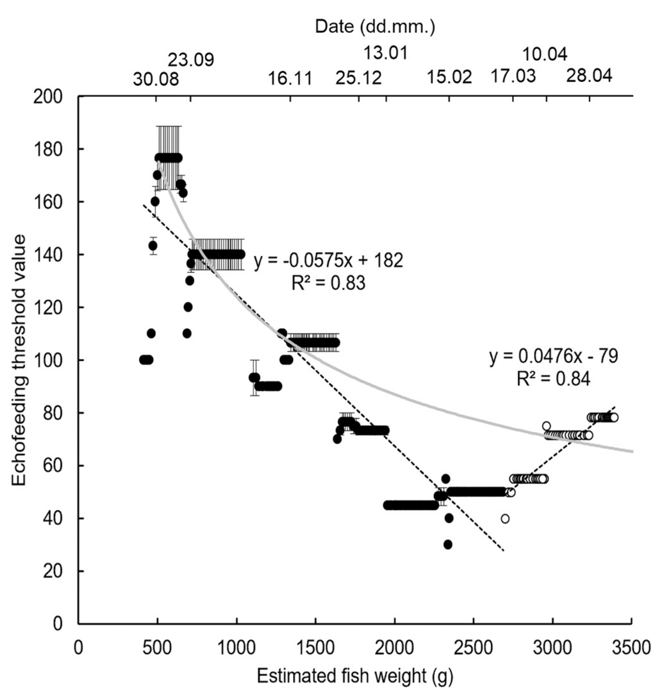

Fig. 3. Mean echofeeding threshold value (echo strength within depth volume used for autonomous feeding control) in three salmon sea cages vs. estimated daily fish weight (g). Filled symbols indicate values measured by 200 kHz transducers and open symbols 50 kHz transducers. Grey line indicates an extrapolated power function fitted over the three first mean calibration values were echofeeding was functional in avoiding waste feed and under steady state observation depth and volume settings ($y = 4219.9x^{-0.512}$, R^2=0.98).

system were recalibrated after three weeks and the feeding threshold value lowered (Fig. 3). For both threshold calibrations, mild waste feed was observed when echofeeding was effectuated, and thresholds were upregulated over 3–4 days (Fig. 3).

At the experiments start in mid-August the fish designated for echofeeding were statistically similar in weight (estimate of control - echofeeding=-36.4, SE=67.8, z = -0.54, p = 0.59) length (-1.18, 0.705, z = -1.68, p = 0.09) and condition factor (-0.01, 0.02, z = -0.71, p = 0.48) to the control fish (Table 1). Until size sampling in mid-October the mean fed amount in both groups was 1.66 % of biomass day^{-1} with between cage variation of ± 0.005 and 0.025 for echofeeding and the control, respectively. In mid-October, the between group similarity in size parameters persisted for weight (-75.7, 63, z = -1.21, p = 0.23), length (-1.11, 0.68, z = -1.64, p = 0.10) and condition factor (-0.01, 0.02, z = -0.43, p = 0.67). The SGR was slightly, but not statistically significant, higher in the control group (t = 2.04, df=3,96, p = 0.11), and similar for bFCR (t = 1.28, df=2.3, p = 0.31) and the same TGC was calculated for both groups (Table 1).

3.1.2. P2: late autumn to winter (October to January)

From October the water below the pycnocline got progressively colder while the above temperature dropped abruptly below 5°C from the 22 of November, followed by fluctuations throughout the year before a deeper cold-water layer was established (Fig. 2).

The echofeeding recalibration at the start of Period 2 was ~20 % down from the last calibration level with a ~30 % fish size increase in between, and as for previous calibration an increase in threshold over the first days was required due to mild pellet wastage (Fig. 3). The mean daily fed amount since the size sampling in mid-October and until the abruptly colder surface on 22 November was similar between the echofeeding (1.08 ± 0.07 %) and the control group (1.02 ± 0.08 %) (t = 1.49, df=3.25, p = 0.23). The following next 3 weeks the mean daily fed amount was drastically reduced and more variable between days for echofeeding vs. the control (0.59 ± 0.06 vs. 0.82 ± 0.02 %) (t = 8.5, df=3.17, p < 0.01). For the same periods, the mean temperature difference between 0 and 1 m and daytime swimming depth of the echofeeding fish increased from 3.16 ± 0.27–5.4 ± 0.34 °C. Further, while the control followed the descending temperature gradient from 5 December, the echofeeding group maintained a swimming depth closer

Table 1
Fish size parameters of weight, body length and condition factor (K) from periodic samples per cage (n = 100 for August, April and May, and 200 fish for October and January) per treatment group (mean ± SE), and periodic mortality (% of initial number), estimated SGR (percent growth day $^{-1}$), economic FCR, biological FCR and TGC.

Date	Treatment	Weight (g)	Length (cm)	K	Mortality (%)	SGR	eFCR	bFCR	TGC
15.08.2018	*Echofeeding*	*299 ± 11*	*30.5 ± 0.30*	*1.04 ± 0.005*	-	-	-	-	-
	Control	*264 ± 12*	*29.3 ± 0.64*	*1.03 ± 0.016*	-	-	-	-	-
17.10.2018	*Echofeeding*	*950 ± 35*	*41.9 ± 0.45*	*1.28 ± 0.016*	*1.26 ± 0.15*	*1.81 ± 0.02*	*0.88 ± 0.02*	*0.87 ± 0.02*	*3.68 ± 0.06*
	Control	*874 ± 40*	*40.8 ± 0.75*	*1.27 ± 0.010*	*1.01 ± 0.43*	*1.87 ± 0.02*	*0.85 ± 0.01*	*0.84 ± 0.01*	*3.68 ± 0.07*
17.01.2019	*Echofeeding*	*2007 ± 50*	*52.8 ± 0.40*	*1.35 ± 0.010*	*0.21 ± 0.01*	*0.82 ± 0.01*	*0.89 ± 0.01*	*0.88 ± 0.01*	*2.93 ± 0.03*
	Control	*2120 ± 73*	*53.0 ± 0.52*	*1.40 ± 0.013*	*0.21 ± 0.02*	*0.97 ± 0.03*	*0.86 ± 0.01*	*0.85 ± 0.02*	*3.45 ± 0.08*
04.04.2019	*Echofeeding*	*2912 ± 106*	*60.8 ± 0.59*	*1.27 ± 0.021*	*0.33 ± 0.02*	*0.48 ± 0.02*	*1.00 ± 0.06*	*0.99 ± 0.06*	*2.89 ± 0.12*
	Control	*3098 ± 52*	*61.5 ± 0.48*	*1.31 ± 0.007*	*0.27 ± 0.05*	*0.49 ± 0.02*	*1.03 ± 0.05*	*1.02 ± 0.10*	*2.93 ± 0.12*
20.05.2019	*Echofeeding*	*2997 ± 49*	*64.1 ± 0.32*	*1.12 ± 0.006*	*0.44 ± 0.18*	*0.06 ± 0.09*	*2.61 ± 1.96*	*2.74 ± 1.81*	-
	Control	*3204 ± 84*	*64.6 ± 0.42*	*1.16 ± 0.008*	*0.49 ± 0.25*	*0.07 ± 0.09*	*2.33 ± 1.84*	*2.53 ± 1.62*	-

to the pycnocline (Fig. 2A). The mean daytime swimming depth between the 5 and 18 of December was 4.2 ± 0.3 vs. 6.6 ± 0.6 m ($t = 3.5$, df=3.04, $p < 0.05$) for the echofeeding and control respectively, and the corresponding mean temperature 0.5 °C higher for the control ($t = 3.5$, df=2.55, $p = 0.05$).

Given the apparent reluctance of the salmon to feed in the cold surface, the Echofeeding observation volume was changed from 0 to 1–1–2 m depth starting with calibration of the biomass threshold from the 12 of December, which was set ~30 % lower than the previous value after an estimated ~23 % fish size increase since last calibration (Fig. 3). Under the new setting for echofeeding and until a technical problem hampered feeding on 1 January and the subsequent 5 days, the echofeeding fish closed in on the control with a mean daily fed amount of 0.68 ± 0.02 vs. 0.75 ± 0.02 % ($t = 2.75$, df=3.38, $p = 0.06$). The pellet detection for the control worked throughout the decreasing temperature and shifting conditions of the pycnocline.

The period of lower fed amount negatively affected the SGR ($t = 3.19$, df=5.12, $p < 0.05$) and TGC ($t = 6.06$, df=2.65, $p < 0.05$) of the echofeeding group compared to the control which maintained excellent growth (Table 1). The FCR was maintained at a good level in both groups, yet slightly but not significantly better in the control ($t = 1.60$, df=3.99, $p = 0.18$) (Table 1). Fish weight in mid-January was close to significantly higher in the control than echofeeding fish (112, 62.7, $z = 1.79$, $p = 0.07$) while condition factor was significantly higher (0.05, 0.02, $z = 2.92$, $p < 0.01$). Body length remained statistically similar between the two groups (0.22, 0.68, $z = 0.33$, $p = 0.74$) (Table 1).

3.1.3. P3: winter to early spring (January to April)

The cold surface layer persisted during this period, and the fish persisted to utilize the higher water temperature area lower in the cage at daytime and swam close to the pycnocline at night (Fig. 2A).

Following the recent improvement by lowering the echofeeding observation volume, as well as colder water in the full depth profile (Fig. 2A), we decided to lower the feeding intensity to a level previously found successful for large fish during winter (Folkedal et al., 2022). Starting 15 January, feeding intensity was reduced by 50 % to 125 g per ton per minute. Biomass thresholds were again calibrated and were ~40 % lower than the previous and the volume for observation was altered to 1.5–3 m depth in line with the deeper pycnocline (Figs. 2 and 3). After observing recurring waste feed for echofeeding the first week of February, the echofeeding thresholds were increased by 10 % (Fig. 3). Depth of the echofeeding observation volume was again changed on 18 March, to 0–2 m depth as the fish fed shallower in line with temperature increase at surface (Fig. 2).

Pellet detection remained functional, but vulnerable at days when water current drifted pellets outside its observation volume, and periods when the detection camera spatially overlapped with the fish school. Human assessment from standard cage camera video was used for meal determination under such circumstances.

Since the last size sampling mid-January, the average fed amount until 4 April was 0.55 ± 0.02 for the echofeeding cages and 0.53 ± 0.01 % for the controls. The SGR, FCR and TGC was statistically similar between the groups and the difference in fish size persisted for weight (183, 67, $z = 2.73$, $p < 0.01$) and condition factor (0.08, 0.02, $z = 4.27$, $p < 0.0001$), while body length persisted to be similar (0.72, 0.70, $z = 1.03$, $p = 0.30$).

3.1.4. P4: spring until experimental termination

During April the pycnocline moved gradually shallower and disappeared, and the fish positioned themselves accordingly (Fig. 2A). From April 21 and until the 30th the surface contained the warmest available water and echofeeding became problematic as the fish were residing the echofeeding observation volume also when not feeding (Fig. 2A), and little increase in echo strength was recorded in response to feeding. Manual feeding control was therefore required for this period. From the start of May with cooler surface water, echofeeding was again functional while fish appetite dropped severely for both echofeeding and the control (Fig. 2B). During the same period the fish showed an opposite diurnal pattern compared to previous periods with a deeper swimming depth at night than daytime (Fig. 2A). The fed amount for the period was very similar between echofeeding and the control cages (0.40 ± 0.04 vs. 0.40 ± 0.03) ($t = 0.03$, df=3.17, $p = 0.97$).

Obduction at size sampling (n = 10 fish per cage) in mid-May revealed clinical signs (dark liver) of SAV in all fish, and it was decided to discontinue feeding and harvest the fish. The sample from both Cage 3 (control) and 4 (echofeeding) showed lower weight than previously recorded. All over, the control persisted to have the highest weight (177, 74, $z = 2.40$, $p < 0.05$) and condition factor (0.04, 0.02, $z = 2.16$, $p < 0.05$) while the fish length (0.31, 0.74, $z = 0.42$, $p = 0.67$) was like the echofeeding fish (Table 1). There was a strong drop in condition factor from the previous size sampling 6 weeks earlier, and growth parameters were overall very poor (Table 1).

3.2. Fish mortality

Mortality rates were not different between the treatment groups for any period and the overall accumulated mortality of 2.8 ± 0.4 and 2.3 ± 0.4 for the echofeeding and control cages respectively was also statistically similar ($t = 0.98$, df=3.99, $p = 0.38$) (Table 1). The highest mortality was registered over the first two months of the experiment, where 50 ± 0.06 % of the periodic mortality was registered within 14 days after transfer to the sea cages (Table 1). The sickness inflicted by PD had no apparent strong effect on mortality, whereas the mortality during the last half of Period 4 accounted for 77 % of the mortality within this period ($t = 3.15$, df=5, $p < 0.05$, paired *t*-test), signalling an increase.

3.3. Individual size variation

The difference in feeding control and feeding intensity, including periodic underfeeding caused by maintaining challenging settings for echofeeding, did not have apparent effects on the between individual variation for any of the recorded size parameters, as measured by the coefficient of variation on length, weight and condition factor (Table 2).

3.4. Echofeeding threshold

Comparing the thresholds used for the 200 kHz transducer, a linear negative trend with increasing fish size is the most evident (F-stat=961, df=193, R^2=0.83, $p < 0.001$), while a positive linear trend was found during the spring when using the 50 kHz transducer (F-stat=327, df=61, R^2=0.84, $p < 0.001$) (Fig. 3). By isolating the first three mean calibration values as found functional to avoid waste feed under steady echofeeding setting and in the estimated fish size span 511–1342 g, a power function ($y = 4219.9x^{-0.512}$, R^2=0.98) shows the best fit, and indicates that the linear model including all data, and under various depth and volume setting will underestimate the threshold for both small (<~750 g) and larger fish (>~1500 g).

4. Discussion

We tested hydroacoustic feeding control (echofeeding) in salmon cages within a fjord farming environment that varied in time and space. The echofeeding system fed the salmon automatically after calibration within a stable environment. Re-calibration and depth area interval adjustment changes were needed when vertical gradients in water temperature changed the vertical behaviour of fish and when fish size increased. Challenges in echofeeding functionality were seasonally dependent, linked to fish avoiding the cold surface during late autumn and winter, and crowded in warm surface waters during spring. These challenges both relate to the temperature preferences of the salmon, illustrating a need for dynamic "parameterization" of the threshold settings based on the fluctuating environment in fjords and corresponding shifts in salmon behaviour to fully utilize echofeeding as an automatic feeding system.

4.1. Fish growth and mortality

Mean fish size, as estimated from a sample of 100 fish per cage, showed high between cage variation from the first sampling, suggesting that fish were unevenly distributed over cages by the wellboat. While representative sampling from sea cages is inherently difficult (Nilsson and Folkedal., 2019), the calculated cage level FCR between the 4 first samplings were close to table expectations, indicating a low degree of sampling bias. For the last sample, when salmonid alphavirus was physiologically apparent in all tested fish, a negative weight development was recorded for two cages over the final six weeks, without difference in fed amount to other cages, signalling the last sampling was unreliable.

The estimated SGR, TGC and FCR for both treatment group during Period 1 was excellent (Skretting, 2012; Aunsmo et al., 2014), demonstrating that echofeeding using the very same setting as described in Folkedal et al. (2022) is applicable to small and newly sea-cage transferred salmon under relatively stable environmental conditions. The control maintained excellent growth figures and FCR until the last experimental period, suggesting the pellet detection technology and method was efficient for fish growth while minimizing waste feed. During Period 2 (October to January), the mild underfeeding of the echofeeding group (-6 % less fed compared with the control over the full period) negatively affected SGR and gain in condition factor compared to the control group fish. The estimated FCR was not significantly affected, indicating that feed utilization may be normal during mild underfeeding. Neither periodic underfeeding or the between group difference in feeding intensity and temporal distribution of daily meals affected fish size distribution, suggesting that social hierarchies are not a strong factor in groups of caged salmon (Juell, 1995). Fish did not appear to compensate for underfeeding after echofeeding parameters were changed at the end of Period 2 and the start of Period 3. Atlantic salmon have a strong ability to compensate for lost growth after restricted feed intake (Thorpe et al., 1990; Johnsen et al., 2013; Hvas et al., 2022; Lai et al., 2025). Here, a lack of compensation might be due to insufficient echofeeding settings or be influenced by the concurrent onset of SAV. A deep learning model (EchoBERT; Måløy, 2020) was fitted to whole cage echo data from the current experiment, and picked up a change in fish behaviour from mid-February. This coincided with the onset of SAV infection in fish, although appetite as indicated by calculated TGC remained good. The well-known negative effect of SAV on salmon appetite (McVicar, 1987; McLoughlin and Graham, 2007) was, however, highly apparent from May.

The current production performance can be regarded as successful from sea transfer in August until May. The fish were not treated for salmon lice or other parasites, which induce stress and physical damage and are major drivers of poor appetite and mortalities (Overton et al., 2019). Although production was prematurely terminated due to SAV, the accumulated mortality of 2.5 % was low and far below average for farms in the production area, which for the 2018 generation was 21 % (Grefsrud et al., 2023). The highest mortality rate occurred during the initial two weeks, which accords with benchmarks of industry mortality data (Soares et al., 2011; Stien et al., 2018).

4.2. Sea cage environment and feeding control

Our results revealed that echofeeding is sensitive to environmental changes in the surface water layer as fish avoid colder temperatures. Under the strong pycnocline conditions present from mid-September, and where surface temperature fluctuated between 6.2 and 12.8 °C until 21 November, no systematic difference in fed amount for the echofeeding fish vs. the control fish was obvious. The fed amount for echofeeding dropped dramatically when surface temperature dropped below 5 °C on 22 November, while no dramatic change of the temperature at the preferred swimming depth of fish occurred. It is, however, difficult from the present data to conclude whether the reluctance of salmon to enter the surface layer was due to the increased temperature difference between deeper and surface waters or cold (<5 °C) water *per se*. Regardless of the mechanism, the results suggest salmon chose to feed less when presented with a trade-off between feeding and entering a cold surface layer. Moreover, after weeks of reduced feed intake, the echofed fish were less efficient than the control fish in following vertical

Table 2
Mean coefficient of variance in fish samples from echofeeding and control cage groups (± SE) for body length, weight and condition factor over the five sampling points of the experiment.

Date	Length (cm)		Weight (g)		Condition factor	
	Echofeeding	Control	Echofeeding	Control	Echofeeding	Control
15.08.2018	0.071 ± 0.003	0.081 ± 0.016	0.233 ± 0.017	0.267 ± 0.047	0.067 ± 0.007	0.078 ± 0.015
17.10.2018	0.057 ± 0.005	0.065 ± 0.008	0.178 ± 0.009	0.205 ± 0.020	0.059 ± 0.005	0.055 ± 0.003
17.01.2019	0.059 ± 0.001	0.060 ± 0.004	0.188 ± 0.005	0.195 ± 0.010	0.057 ± 0.003	0.062 ± 0.002
04.04.2019	0.067 ± 0.003	0.059 ± 0.006	0.230 ± 0.017	0.198 ± 0.018	0.090 ± 0.001	0.087 ± 0.001
20.05.2019	0.071 ± 0.007	0.069 ± 0.003	0.257 ± 0.031	0.273 ± 0.010	0.086 ± 0.006	0.089 ± 0.005

temperature gradients, indicating that surface attraction in hungry salmon did partly overrule their thermal preferences. Caged salmon vertical behaviour is largely determined by their environmental preferences to temperature and light. Trade-offs exist that affect the spatial decisions of salmon, as occurs when food attraction to the surface can be overridden by surface light avoidance (Fernö et al., 1995; Oppedal et al., 2011; Folkedal et al., 2022). Our result revealing a trade-off between surface temperature and hunger level add to knowledge of these situations.

Cage size, depth and volume used in this experiment were small by commercial standards (see McIntosh et al., 2022). Accordingly, a rather shallow echofeeding observation volume was used, which amplified fish exposure to the highly variable water conditions at the surface. When the echofeeding method is applied at commercial scale, and thus deeper cages with more fish, a deeper observation volume would presumably be required and be more robust towards environmental changes.

Our study used traditional pellet dispersion at the water surface, as predominately used in commercial salmon farming. Water based feeding systems are, however, becoming more available and popular for several reasons including submerged feed dispersion. For at least the winter half year of the present study, submerged feed dispersion to 3 m depth, and correspondingly a deeper observation volume for echofeeding, would likely have alleviated negative environmental effects on echofeeding functionality.

4.3. Feeding intensity

The higher feeding intensity in the echofeeding group did not result in lower fed amount or growth rate over the autumn, and it did not affect fish size variability at any time point. Pragmatically, we reduced feeding intensity from 250 to 125 g per ton fish per minute in mid-January to account for any possible effect of declining water temperature or increased biomass on the capability of fish to efficiently consume pellets. This coincided with an increase in pellet size from 7 to 9 mm, which represents a ~52 % reduction in the number of pellets for the same quantity of feed. The echofeeding fish caught up to the control fish in fed amount after this, but did not compensate for previous lost growth. Atlantic salmon standard and active metabolic rate and scope for activity scales positively with acclimated temperature (Hvas et al., 2017), but little is known about thermal effects of voluntary activity levels under natural behaviours such as feeding activity. Dedicated studies are required to establish knowledge of salmon feeding efficiency relative to acclimated temperature to better set thresholds for feeding intensities.

4.4. Echofeeding settings

We demonstrated that calibration of the echofeeding biomass threshold to fish size is needed, and that the routine behaviour of fish can interfere with echofeeding functionality. While fish density is evidently the main proxy for echofeeding within and between meals, several factors affect echo strength over different time scales. Within meals, level of competition for pellets may affect fish body tilt angle, which affects echo strength (Nakken and Olsen, 1977; Juell and Fosseidengen, 1995) and the degree of body tilt angle is observed higher in small (<1 kg) compared to larger salmon during feeding (Kannelønning, 2021). During early spring, when fish showed routine behaviour close to the surface, high levels of surface feeding activity was visually observed, without an apparent increase in recorded echo strength. We speculate that although fish density seemingly increased during feeding, increased fish body tilt angle dampened the signal. Over time and with fish growth, the number of individual Atlantic salmon per feeding volume as well as their echo strength is found to linearly decrease, while fish biomass increases despite fewer individuals per volume (Kannelønning, 2021; essentially, the fish density in terms of weight provides less echo as fish grow). The present linear function of echo threshold reduction using 200 kHz and between ~500 and ~2500 g fish size, which includes variation in depth of echofeeding observation volume and feeding intensity, is evidently not explanatory for echo thresholds in larger fish (Fig. 3). Less linear decay was reported by Kannelønning (2021), where fish growth from ~650 to ~2500 g gave a 46 % decrease in mean individual echo strength for fish engaged in high feeding activity. Correspondingly for the same size span, 50 % reduction is calculated by the present power function based on calibration values under steady state echofeeding settings between ~500 and ~1350 g (Fig. 3). We suggest this model as a plausible guideline towards automatic echofeeding calibration based on fish growth estimates, instead of using challenging threshold settings based on pellet sinking depth. Under the new wider echo beam settings from mid-March in the trial, as driven by practical implications, the threshold was increased at the start and end of April. Other factors than fish growth was most likely influential for this, including rising surface temperature which future models may need to account for.

We used a depth of 5 m for pellet observation, which may have been too deep as the fish were accustomed to feed near the surface, and thereby not sensitive enough to prevent waste feed from occurring. In practice, the current thresholds were set in stepwise increments until camera observations confirmed no waste.

4.5. Pellet detection

The automatic pellet detection system (SeaV) used effectively assisted feed control for the control group, where the current description is experience based rather than a rigid test of system functionality. Although not systematically accounted for, daily visual inspection of video streams from both pellet and cage camera confirmed that detection alarms were consistently precise in reflecting its preprogrammed threshold of pellet rate. In terms of reflecting fish appetite, the consistent depth position of the pellet detection camera should in line with the depth terms set for echofeeding aid in conditioning the salmon to where food is available (Folkedal et al., 2022), where pellet detection at 5 m depth was sufficient to allow for efficient food consumption by the fish, regardless of water temperature profile. The control fish feeding activity and vertical response to the batches of feed was typically short term as they were served over seconds with minutes in between. Echofeeding was different in this regard, with both feed and fish feeding activity continuous during meals. Batch feeding may thereby minimize fish exposure to thermal gradients. The current setup of pellet detection was vulnerable to spatial change in pellet dispersion or drift relative to camera detection volume, as occurred with feed pipe movement during stormy weather or strong water currents. Moreover, for periods when the detection camera spatially overlapped with the fish school during the winter and spring, human assessment from the standard cage camera was used to ensure appetite assessment. Use of the camera manufacturers "wings" which transports the lightweight camera according to pellet drift is efficient in high current environments but was not applied here. Feed pipe dislocation and fish severely blocking the camera view occurred in the current setup of moderate cage size, which both limited pellet detection area and volume without fish in the middle of the donut shaped fish school, which periodically was skewed due to net deformations. Overall, the pellet detection system and deployment represent a highly promising tool suitable for more detailed testing and input to automatic feeding control.

4.6. Future perspectives

Echofeeding as explained by Folkedal et al. (2022) and first introduced by Bjordal et al. (1993), has yet to be implemented in modern full-scale salmon farming. Technically and methodologically, the setup in full scale should remain relatively simple and intuitive. Scaling up will primarily require suspending the transducer from the feeder to maintain alignment with the sinking pellets. A larger biomass of fish can undoubtedly increase acoustic shadowing effects, potentially restricting the input to the echofeeding system. Transducer depth will be a key factor in minimizing shadowing and prevent negative effects of pellet drift with water current. Using a depth of 8 m, as in the present study, may still result in a comparable amount of biomass within the echo beam in commercial-scale cages. Nevertheless, if shadowing occurs only at echo levels well above the feeding continuation or stop threshold, it should not interfere with the functionality of echofeeding. Alternative transducer setups - such as positioning the transducer at the surface and directing it downward or combining input from multiple transducers - could also be considered. Long-term echofeeding tests at sites with little vertical temperature stratification, implying stable conditions for echofeeding (Folkedal et al., 2022), could improve understanding of echo thresholds during fish growth, and also clarify whether fish routine behaviour near surface in the summer half-year masks appetite responses.

From our experience, the biggest barrier to the commercial adoption of echofeeding or pellet detection is human reluctance to rely on fixed day-to-day settings. In other words, there is hesitance to trust that fish will consistently respond to feed within a defined volume. That said, the pellet detection method tested in this study is already in use on most salmon farms in the Faroe Islands. This suggests that the broader transition toward automated feeding control in other farming nations may depend more on cultural factors than on technical limitations.

5. Conclusion

Autonomous feeding control via echofeeding is possible in vertically stratified farming environments, as typical for fjords, but requires adjustment of spatial observation volume according to the environmental preferences of salmon. Feeding control based on pellet detection below surface gradients is robust to environmental changes. The present study thus demonstrates large potential for autonomous feed control for caged salmon post-smolt. Within fish groups, the individual size variation was not affected by feeding intensity and time of day for feed distribution, including a period of underfeeding in the echofeeding group, suggesting that social hierarchies are not significant in groups of caged salmon. The biomass threshold used as input for echofeeding needed to be adjusted as the fish grew. This adjustment could be automated using the model input suggested in this study. The high growth rates and low FCR recorded suggest that use of simple and consistent proxies for measuring appetite are highly promising toward future autonomous feeding control in Atlantic salmon post-smolt production.

CRediT authorship contribution statement

Ole Folkedal: Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Georgia Macaulay:** Writing – original draft, Validation, Investigation. **Jan Erik Fosseidengen:** Methodology, Investigation, Conceptualization. **Frode Oppedal:** Writing – original draft, Supervision, Methodology, Funding acquisition, Conceptualization. **Lars Helge Stien:** Writing – original draft, Formal analysis, Data curation. **Joakim Myrland:** Validation, Software, Methodology, Data curation, Conceptualization. **Bendik Søvegjarto:** Validation, Software, Methodology, Data curation, Conceptualization. **Tim Dempster:** Writing – original draft, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Ole Folkedal reports financial support was provided by Research Council of Norway. Joakim Myrland reports a relationship with CageEye AS that includes: employment. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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