

Heart rates, activity, and welfare of Atlantic salmon reared to harvest size in a semi-closed prototype sea-cage or ambient conditions

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ABSTRACT

The salmon aquaculture industry is developing technologies to solve challenges with sustainability and poor animal welfare. A potential solution is to use semi-closed systems to mitigate lice infestations and provide more controlled rearing environments. Here, we tested Atlantic salmon in a novel semi-closed prototype cage and compared growth and welfare with a standard open cage to harvest sizes of ~5 kg. Additionally, data storage tags were used to record heart rate and activity in fish from both cage types. The semi-closed cage was subjected to a continuous photoperiod, constant moderate currents, and water supply from greater depths, while the open cage experienced a natural ambient surface environment. Growth trajectories differed throughout the trial, but final harvest sizes were similar in the two groups. Mortality was lower in the semi-closed cage, although welfare scores were worse, likely related to sub-optimal sampling methods. In both groups, heart rates were generally between 40 and 60 beats min⁻¹ and were influenced by seasonal temperatures. Owing to the continuous photoperiod, closed-cage fish showed weaker diurnal variations in heart rate and activity, while open-cage fish were calmer at night. Additionally, closed-cage fish had higher activity overall, indicative of higher swimming speeds. Finally, by using a refined tagging protocol, tag-related mortalities were prevented and tagged fish showed excellent growth following 7-months in sea cages. While data quality indexes did decline towards the end, this shows that bio-loggers can be used over long periods of fish production to record core welfare parameters for evaluating novel rearing systems.

1. Introduction

Norway is the world's largest producer of farmed Atlantic salmon (*Salmo salar*); however, the industry is struggling with various sustainability problems that are restricting further growth (Sjømat Norge, 2021). Key issues are the spread of salmon lice (*Lepeophtheirus salmonis*) onto wild populations, escaped farm fish interbreeding in the wild, and eutrophication of local marine environments (Glover et al., 2017; Olaussen, 2018; Dempster et al., 2021). These challenges are unlikely to be solved while fish are being reared in open sea cages within fjords and coastal areas.

Meanwhile animal welfare in salmon aquaculture is receiving increased scrutiny, not least because mortality remains high despite substantial mitigating efforts. For instance, in 2023, mortality rates in Norwegian salmon aquaculture were the highest ever recorded, with 63

million (16.7 %) Atlantic salmon dying during the seawater growth phase (Somerset et al., 2024). Owing to high mortalities and poor animal welfare, there is presently substantial pressure on the aquaculture industry to improve production standards, for instance by implementing novel technologies. One of the primary causes of mortality during the marine growth phase are the various stressful operations used for delousing fish (Overton et al., 2019).

New technologies and alternative farm concepts need to be developed and tested to facilitate sustainable industry growth and better animal welfare. Potential solutions may include the establishment of entirely new farm areas either on land or offshore (Hvas et al., 2021a; Morro et al., 2022). More imminent solutions for lice prevention at existing traditional farm sites include shielding skirts and submerged sea cages. These technologies can be helpful at mitigating infestations by reducing exposure to the upper layers in the water column where the

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infective larvae primarily exist (Sievers et al., 2022; Jónsdóttir et al., 2022).

Going a step further is the use of closed or semi-closed containment systems within the marine environment. These concepts allow for more control of inflowing and effluent water, reduce the risk of fish escape events, while also providing a physical barrier to the ambient marine environment to mitigate lice infestations (Rosten et al., 2013; Nilsen et al., 2017, 2020; Tveterås et al., 2021). Closed or semi-closed cage designs also allow for greater potential control of the rearing environment with regards to photoperiod, flow conditions, and water quality which could facilitate better growth conditions and welfare (Rosten et al., 2013; Nilsen et al., 2017, 2020). A distinction between truly closed and semi-closed is whether the intake and outlet water is adequately filtered for pathogens and waste products, respectively. For instance, a land-based recirculating aquaculture system (RAS) may be considered truly closed, but the same is difficult to achieve with sea cage systems given the extensive pumping, filtering and other infrastructure required. Therefore, most research and development has focused on semi-closed sea cage systems which offer many of the benefits of closed systems, but with lower cost and risk.

When implementing new technologies and farm concepts it is imperative that they are thoroughly tested in pilot trials before starting production at an industrial scale level. In such preliminary testing, a key factor to document is the animal welfare status of the fish, yet this is hard to measure directly in prototype systems, let alone full-scale systems (Føre et al., 2018). Welfare status can instead be assessed indirectly at the group level via monitoring of water quality parameters and appetite, while physical welfare scoring of various traits and health diagnostics can be performed on sub-samples during a production run (Noble et al., 2018; Nilsson et al., 2022). More crude is the monitoring of mortality rates. However, mortality on its own provides little information of what happened to the fish and for how long it might have suffered before dying.

To provide more detailed and continuous observations of coping abilities in aquaculture systems, implantable bio-loggers can be used on sentinel fish as representatives of the general cohort (Føre et al., 2017; Warren-Myers et al., 2021). Fluctuations in stress levels and activity patterns can then be monitored over extended time-periods from measurements of heart rates and acceleration as a proxy of swimming speed (Brijs et al., 2018; Hvas et al., 2020; Warren-Myers et al., 2023). For instance, the heart rates of Atlantic salmon show a strong diurnal rhythm by being lower at night and higher during the day, and stressful farm operations such as crowding and handling clearly elevate heart rates, thereby providing a useful indicator of the imposed stress levels (Hvas et al., 2020; Føre et al., 2021; Svendsen et al., 2021). Additionally, seasonal changes in temperature affect heart rates (Gamperl et al., 2021; Warren-Myers et al., 2021), while the lack of diurnal rhythm in heart rate may provide an indicator of chronic stress (Brijs et al., 2018; Hvas et al., 2021b).

Despite several studies utilizing bio-logging tags in aquaculture settings in recent years, it still remains uncertain whether tagged individuals truly represent untagged counterparts given that mortality rates of tagged fish tend to be higher than untagged conspecifics, if reported at all (reviewed by Macaulay et al., 2021). Most bio-logging studies also do not report growth of tagged and untagged fish (Macaulay et al., 2021). However, when fish sizes at the time of tagging and later tag retrieval have been reported, tagged individuals showed substantially worse growth (Hvas et al., 2020; Warren-Myers et al., 2021). Such negative long-term impacts on growth may be caused by surgical wound infections and inflammation, inadequate recovery following the tagging procedure, or the tag itself pressing on the digestive tract, impairing the ability to feed. In any case, it is acknowledged that most tagging processes and related stressors such as anesthetics, air exposure, and handling can impact longer term physiological and behavioural responses of fish and thereby reduce the scientific validity of the results (Hjelmstedt et al., 2020; Wright et al., 2019).

The purpose of the present study was to assess animal welfare and growth performance in Atlantic salmon reared until harvest size in a small-scale semi-closed prototype cage. For comparison, a control group was reared in parallel using a standard open sea cage with natural environmental conditions at the same farm site. We documented growth trajectories and performed welfare scoring on 30 individuals from both cage systems approximately every second month over the course of an 11-month growth period in the marine environment. Furthermore, bio-logging data storage tags were implanted on 10 fish from each cage group to monitor heart rates and activity levels. Owing to the above-mentioned challenges with negative tag-related effects, we here took extra care with the tagging procedure by allowing fish to recover in a clean land-based tank environment following surgery before being transported back to their respective cage systems. We hypothesized that the semi-closed cage group would have improved welfare owing to less sea lice infestation and need for treatment, and better growth owing to optimization of temperature by adjustment in depth of inflowing water, and by use of a continuous photoperiod. Owing to the continuous photoperiod and constant steady waterflows, we also expected to observe higher activity levels and less diurnal variation in heart rates in fish within the semi-closed cage. Finally, we hoped that our refined tagging protocol would allow for adequate growth and survival relative to untagged conspecifics.

2. Materials and methods

2.1. Animal husbandry

Atlantic salmon (Aquagen strain) were reared at the Institute of Marine Research (IMR), Matre research station, following standard production protocol for 0+ Atlantic salmon where smoltification was induced by a 12:12LD photo regime followed by 6 weeks of continuous light. The experimental fish ($n = 2400$) were from the same cohort and seawater transferred in a common tank ($\varnothing = 5$ m, 24 m³) on October 15, 2021, and were kept on a natural light regime until transfer to the experimental units on December 15, 2021 (Table 1). Upon transfer a random sample ($n = 30$ fish) weighed 298 ± 55 (mean $\pm$ SD) g and measured 29.2 ± 1.7 cm in body length. One semi-closed containment cage (see section 2.2) was stocked with 1800 fish, and an open sea cage was stocked with 855 fish (control group) at the IMR sea cage facility

Table 1

Overview of the experimental trial period with various main events and stocking densities. For each sampling of 30 fish throughout the trial, weight, length, welfare scores and health indicators were recorded.

Dates (2021–2022)	Event
October 15	Transfer of fish to seawater in a common holding tank ($n = 2400$).
December 15	Sampling of 30 fish. Fish moved to closed cage ($n = 1800$, 17.4 kg m ⁻³) and control cage ($n = 850$, 1.9 kg m ⁻³).
February 10 March 3	Sampling of 30 fish per cage. Biomass (42.2 kg m ⁻³) reduced by 5 %.
April 4	Biomass (49.7 kg m ⁻³) reduced by 30 %.
April 8	Sampling of 30 fish per cage. Biomass (50.7 kg m ⁻³) reduced by 36 % in the closed cage. Subgroups transported to laboratory holding tanks on land.
April 25 June 2	Data storage tags were implanted on subgroups maintained in the laboratory.
August 17	Tagged fish were transported back to their respective sea cages. Sampling of 30 fish per cage. Biomass (46.4 kg m ⁻³) reduced by 44 % in the closed cage.
October 12	Sampling of 30 fish per cage. Biomass (39.4 kg m ⁻³) reduced by 38 % in the closed cage.
November 24	Sampling of 30 fish per cage. Biomass (31.8 kg m ⁻³) reduced by 12 %.
	Final sampling and harvest of all remaining fish (36.2 kg m ⁻³ in closed and 25.6 kg m ⁻³ in open cage).

Smørdalen (60°N). This corresponded with an initial stocking density of 17.4 kg m^{-3} in the semi-closed cage, and 1.9 kg m^{-3} in the open cage.

Prior to starting this study, the ethical use of animals in scientific research was approved by the Norwegian Food Safety Authority under permit number 28348.

2.2. The semi-closed cage prototype

This present study used a pilot scale “Watermoon” ($\varnothing = 3.5 \text{ m}$, 3 m deep, 30 m^3 , Eide Fjordbruk AS, Norway), which is a novel semi-closed cage system for submerged marine fish farming (see <https://www.efb.no/en/prosjekt/watermoon>, Fig. 1) The system used in the present study consisted of cylindrical tarpaulin attached to a rigid top and bottom that is inflated by a mild hydrostatic overpressure. At the top of the rigid structure, the fish were provided access to a circular air pocket ($\varnothing = 50 \text{ cm}$, 10 cm air height), similarly to what is used for submerged sea cages (Oppedal et al., 2020). Access to air is necessary since Atlantic salmon need to occasionally refill their swim bladder to maintain buoyancy within the water column. The cage was submerged 1 m below the sea surface throughout the experimental period.

From the initial transfer of fish into the system, and until June 2, 2022, water from 35 m depth was pumped into the system. Thereafter and until harvest the water intake was positioned at 3 m depth to attain higher temperatures to provide better growth conditions (Fig. 2). Water was supplied at a rate of 660 l min^{-1} , which corresponded to a calculated turnover rate of $\sim 45 \text{ min}$ within the cage. Furthermore, the inflowing water was evenly distributed in the vertical plane from two perforated water inlet pipes positioned in the cage periphery which provided a circular current within this closed cage system. Because direct measurement of water current velocity in the outer areas of the Watermoon was challenging, we repeatedly released a slightly negatively buoyant ping-pong ball into a flexible pipe that entered water 20 cm downstream of the water inlet and $\sim 10 \text{ cm}$ from the wall, in mid-depth. Using camera observations, we recorded the ball's travel time along half of the unit's circumference with no fish present. The resulting current velocity was measured at $22 \pm 3 \text{ cm s}^{-1}$ (mean $\pm$ SD). Oxygen levels were continuously monitored in the water outlet, while extra oxygen was added automatically if needed to always ensure normoxic conditions ($>80 \%$ saturation).

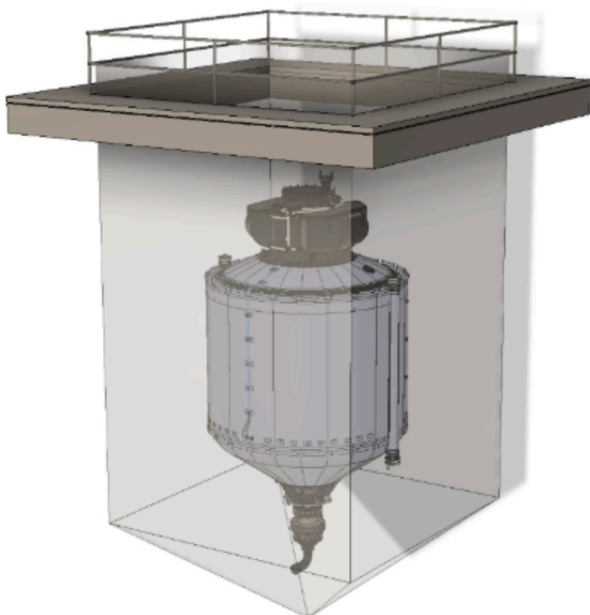


Fig. 1. Conceptual illustration of the semi-closed cage prototype used in the present study (<https://www.efb.no/en/prosjekt/watermoon>).

Two lamps (OceanLight 400, JT Electric, Faroe Islands) mounted in the top rigid structure effectively illuminated the full volume of the cage and provided a continuous (24 h) photoperiod. A continuous photoperiod is common in salmon post-smolt production in closed systems and submerged sea cages where salmon refill their swim bladder in air-filled domes, supporting welfare through visual orientation and promoting uniform growth. Consistent with industry practice when combining closed and submerged technologies, we applied continuous light primarily as a welfare precaution, but also to reflect current trends in emerging production systems. Feed was delivered between 8:00 to 20:00 from a feeding automate (Betten Maskinstasjon AS, Vågland, Norway), and daily feed control by camera monitoring ensured an ad libitum ration. Pellets (3, 4.5, 7 and 9 mm as fish grew, Skretting Optiline, Skretting, Norway) were distributed from a single point at top rigid structure and were efficiently mixed into the water by the current from inflowing water and fish movement.

2.3. Open control sea cage

The control fish group was maintained in a standard open sea cage (5 m $\times$ 5 m, 7 m deep) at the same farm site. Here, the fish were maintained in an ambient environment under natural light conditions where they were fed an ad libitum ration (same device and pellets as in the semi-closed cage) over two daily meals from 9:00 to 11:00 and again from 13:00 to 15:00.

2.4. Implantation of bio-logging data storage tags

To prepare fish for tagging, a subsample of ~ 30 individuals from both the closed cage and the control cage were netted on April 4, 2022, and transported to the land-based fish tank laboratories at the Matre research station, Institute of Marine Research, Norway. Fish from the two groups were then kept in separate holding tanks of 2 m in diameter and with a water volume of 2.4 m^3 . Aerated, filtered, and UVC treated water of 9°C and 34 ppt was supplied via an open-flow through the tanks which provided a stable high-quality environment. Additionally, the fish were kept under a 12 h light/dark cycle from 8:00 to 20:00 and were fed daily to satiation with commercial feed pellets via automatic feeding devices.

After having acclimated in these conditions, 10 fish from each group were tagged on 8 April 2022, with data storage tags (DST milli-HRT ACT, Star-Oddi, Iceland). The tag dimensions were 3.95 cm in length and 1.3 cm in diameter with a weight of 11.8 g in air. Each tag was disinfected in alcohol prior to implantation. Validation of measurements as well as methods for surgical procedures has been described previously (Brijs et al., 2018; Hvas et al., 2020). We used a similar tagging protocol in the present study starting with the netting of a random fish from its holding tank and anaesthetizing it in a 100 l water bath containing 150 mg l^{-1} Finquel (Tricaine methanesulfonate). The time to enter full anesthesia as inferred from the cessation of active gill ventilation was 5–6 min. The fish was then gently moved to the operation table and placed backside on a foam bed with an elongated cavity covered in a plastic sheet to minimize skin friction. A reduced dose of 75 mg l^{-1} Finquel was pumped over the gills via plastic tubes to maintain anesthesia. A 3 cm long incision was made with a scalpel on the ventral midline in the posterior direction roughly 4 cm behind the estimated position of the heart. The tag was then inserted into the abdominal cavity and carefully moved in the anterior direction so the flat end was situated close to the heart while the opposite rounded end of the tag would be at the start of the incision. Additionally, the side with two electrodes was ensured to face in the ventral direction as recommended previously (Brijs et al., 2018). The channel on the rounded end was then used to suture the tag to the body wall to prevent movement inside the fish whereafter the incision was closed with 4 interrupted sutures using a Resolun 3-0 sterile monofilament non-absorbable suture (RESORBA Medical GmbH, Germany) and a layer of antibacterial surgical glue

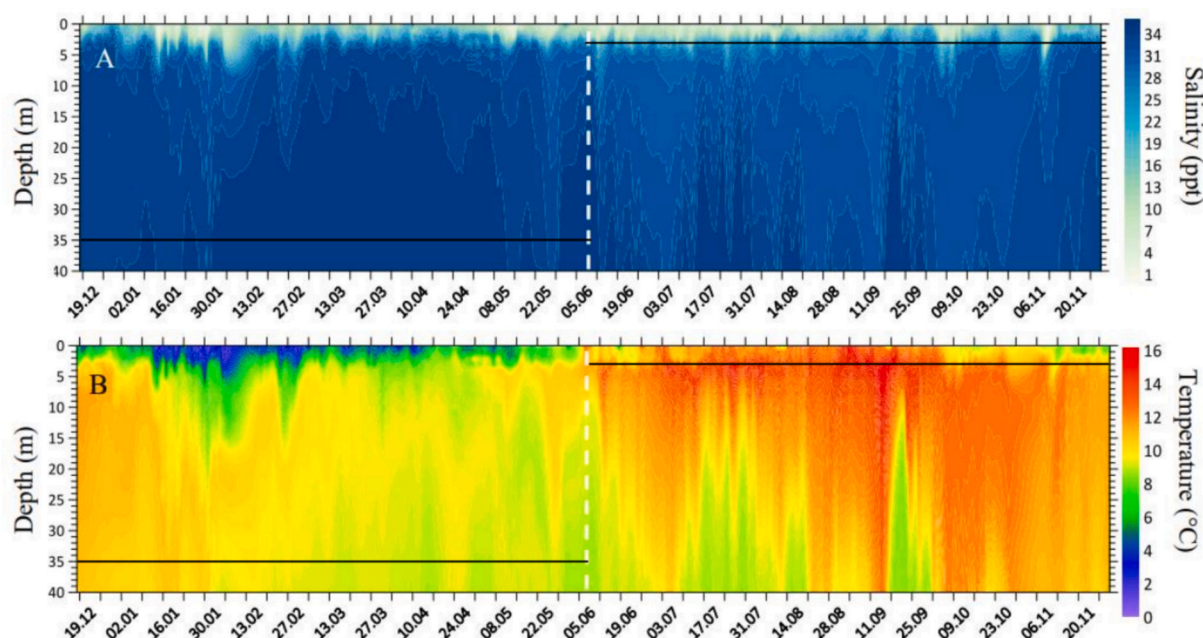


Fig. 2. Salinity (A) and temperature (B) depth-profiles during the trial period at the sea cage production site, Smørdalen in Masfjorden, Norway. The line at 35 m depth and then at 3 m depth from June 2nd onwards indicates the source of intake water for the semi-closed cage.

(Histoacryl, B. Braun, Germany). The weight and fork length of the fish were then measured before being transferred to a new holding tank of similar dimensions and properties as the previous one. Tagged fish from the two cage groups were allocated in separate holding tanks. The tagging procedure was completed within 5 min, with all fish resuming ventilation shortly after being returned to a holding tank.

Each tag was programmed with the Mercury application software (Star-Oddi, Iceland) to measure and log heart rate and acceleration in 6 h intervals at 9:00 in the morning, 15:00 in the afternoon, 21:00 in the evening, and 3:00 at night. The heart rate was obtained via three electrodes on the tag that measured at 200 Hz over a 7.5 s period to provide an electrocardiogram from which an algorithm in the tag could derive an estimate. The tag would then rate each heart rate measurement with a quality index (QI) of either 0, 1, 2, or 3 with 0 being best and 3 worst. It is also possible to store electrocardiogram data for manual calculation of heart rates, but since we also logged acceleration data, the tag did not have sufficient memory to do both for the entire duration of the planned trial.

As such, the tag was also programmed to use its accelerometer to log indicators of activity. Specifically, the activity data was logged as three-axis acceleration in relation to Earth's gravity field through an inbuilt accelerometer. The activity data was composed of burst measurements over 1 min with a sampling frequency of 5 Hz. A pre-programmed algorithm calculated EA (external acceleration) as a vectorial sum of dynamic body acceleration (VeDBA) and reports it in mg (1000 mg = 1 g, where g is the acceleration of gravity or 9.81 ms^{-2}). The algorithm presents a data summary and reports an average external acceleration. All tags were programmed to start logging on April 9 at 9:00 in the morning, the day after the surgical implantation.

The sizes of the fish at the time of tagging were $1051 \pm 60 \text{ g}$ and $44.9 \pm 0.9 \text{ cm}$ for the control group and $1198 \pm 57 \text{ g}$ and $45.4 \pm 0.6 \text{ cm}$ for the closed cage group, with 10 individuals in each group (Table 2). The tagged fish were maintained and closely monitored in their holding tanks for 16 days whereafter they were transported back to their respective sea cages at Smørdalen in Masfjorden, Norway on April 25. While recovering from surgery, the fish did not display any unusual behaviours, except that they were not yet observed to be feeding. However, an observer was not present at all times during feeding periods so the precise time when they eventually resumed feeding was not

Table 2

Size parameters and number of Atlantic salmon with data storage tags maintained in an open control cage or a closed prototype cage at the time of tagging (April 8, 2022) and at end of the trial at harvest (November 24, 2022). Data are the mean $\pm$ s.e.m.

	Weight (g)	Fork length (cm)	Condition factor	n
Control, start	1051 ± 60	44.9 ± 0.9	1.15 ± 0.01	10
Closed cage, start	1198 ± 57	45.4 ± 0.6	1.27 ± 0.02	10
Control, harvest	5134 ± 578	70.1 ± 2.5	1.44 ± 0.04	9
Closed cage, harvest	4531 ± 246	66.7 ± 1.1	1.52 ± 0.04	7

known.

2.5. Sampling events and recorded parameters

Systematic samplings of 30 fish per cage type were made for the recording of size, welfare scorings and health indicators on 10 February (Day 55), 4 April (Day 108), 2 June (Day 167), 17 August (Day 243), 12 October (Day 299), and at harvest on 24 November 2022 (Day 342) (Table 1). Additionally, the biomass in the semi-closed cage was reduced by ~ 30 to 44% at the sampling dates in April, June, and August of 2022 to maintain adequate stocking densities below 50 kg m^{-3} . The relatively high biomass throughout the study was chosen to allow assessment of fish performance towards a production strategy of transient rearing in closed system before fish transfer to larger closed or open cages (Lazado et al., 2022; Pino-Martinez and Handeland, 2025).

Sampling of fish from the semi-closed cage was carried out by pumping water from the bottom at a higher rate than the inflowing water which decreased the volume sufficiently to also pump out fish. Meanwhile, fish from the control cage was sampled conventionally by using a dip net after having lifted the net 4 m upwards in the water column to mildly crowd the fish.

The 30 fish per sample was immediately killed using an overdose of Finquel (300 mg l^{-1}) before all fish were weighed, measured for length, and scored for external appearance using the FISHWELL system (Noble et al., 2018; Nilsson et al., 2022). In this system, external traits are scored on an ordinal scale from 0 (best) to 3 (worst). Additionally, the condition factor was calculated as $100 \times \text{weight} / \text{length}^3$.

At the final sampling in November the fish were harvested, 81 and 77 fish were sampled for size metrics in the semi-closed and the open cage, respectively. Tagged fish were here identified from surgical scars on the abdomen, and the implanted bio-logger could then be retrieved for subsequent data analyses.

2.6. Bio-logger data processing

Data from the bio-loggers were downloaded as CSV files, which were then imported into R version 4.5.1 (R Core Team 2025), where the heart rate data were filtered based on the quality index, with only scores of 0 used. Other studies have included readings with QIs of 1 and have manually calculated the heart rates from the ECG raw data of QI 2 and 3 datapoints (Zrini and Gamperl, 2021). However, owing to memory limitation of the bio-logger when also storing acceleration data over a 7-month period, we did not save ECG raw data in this trial, meaning that manual verification was not possible for lower QI datapoints. Additionally, the accuracy of the bio-logger algorithm in estimating heart rate becomes reduced for QI >0 (Zrini and Gamperl, 2021). Since our study had a large sample size, we had no need to include QI >0 datapoints. Heart rates below 10 or above 110 beats min⁻¹ were classified as outliers and excluded from further analyses.

2.7. Data analyses and statistics

Statistical analysis was performed using R with RStudio (Posit Software). Model 1 compared growth rates between cages based on regular subsamples of untagged fish over the duration of the trial. Three versions were fitted to compare weight, length and condition factor (Models 1 A-C, respectively). Linear models were used (lm function), with factors for cage (open and semi-closed) and sample (7 samples), including an interaction term. Good model fit was assessed by viewing simulated residual plots comparing observed versus expected residual distribution (DHARMa package, Hartig 2019) before the models were interpreted using analysis of variance tables (Anova function, car package, Fox and Weisberg 2019), pairwise contrasts (emmeans package, Lenth 2020) and marginal means (ggeffects package, Lüdtke 2018). Model 2 compared growth of tagged and untagged fish, to check for negative effects of tagging. Models 2 A-C compared weight, length and condition factor, respectively, with factors for sample (start, end) and tagging status (tagged, untagged), with an interaction term. Because only tagged fish were sampled repeatedly, we did not use a repeated measures design. These models were evaluated as Model 1. Model 3 compared long-term patterns in heart rate (3 A) and activity (3B) using a time series with 6-hourly temporal resolution. Generalized additive models were fitted using the gam function in the mgcv package (Wood 2011), with time represented by a numerical variable 'Days'. Independent smooths were fitted for each cage to account for an expected cage × time interaction (Response ~ Cage + s(Days, by = Cage). Although there were repeated measures of tagged fish to reduce model complexity, we did not account for this. Default settings were used, with k = 50. Model fit was assessed using the gam.check function in mgcv, and results interpreted using summary.gam, the gratia package (Simpson 2024) and ggeffects. Model 4 compared diurnal heart rate (4 A) and activity (4B) patterns between cages, while also accounting for seasonal effects. There were fixed effects for time of day (unordered factor with 4 levels: 03:00, 09:00, 15:00, 21:00), cage and month, including full interactions. As tagged fish were repeatedly measured, we included a random intercept term for each one (fish ID). The model was a linear mixed effects model fitted using the glmmTMB package (Brooks et al. 2017) and evaluated as for Models 1–3. Model 5 assessed the correlation between heart rate and activity while accounting for fish size and temperature. Heart rate was specified as the response variable, with fixed effects for activity, weight, temperature, and full interactions. As fish weight and temperature were correlated with each other and with other seasonal changes, we included month as a random intercept term, and to account for repeated

measures, a random intercept term for fish ID. Summary of statistical results from all five models are included in the supplementary material.

3. Results

3.1. Fish welfare scores

Overall, fish from both treatment groups showed relatively good scores for individual welfare indicators throughout the trial, with the same minimum, median and maximum values for overall welfare, although the semi-closed cage had higher maximum values for sores and fin erosion at the final assessment (Table 3). These traits were never prominent in fish from the open cage, while the scoring frequency and severity of these indicators increased over the trial period in the semi-closed cage. At all the sampling events, these types of injuries were consistently evaluated as newly inflicted by the sampling method of crowding and pumping the fish in the semi-closed cage. Furthermore, general risks for collision damage appeared to increase as the fish became larger in size.

3.2. Growth performance, maturation, and mortality in the two cage systems

Early in the trial, fish in the semi-closed cage grew faster than their counterparts in the open cage, with significantly higher weight in June and August, length in February, and condition from February to August (Fig. 3). During this early period of the trial, it was necessary to treat the open cage group for salmon lice infestations, which involved 3 days of fasting and then a treatment in which the fish were anaesthetized so that lice could be removed by hand using vacuum suction. During the sampling event in August, the semi-closed cage fish were unintentionally subjected to severe crowding causing a 16 % mortality rate. Appetite in the remaining fish was hereafter observed to be reduced over the following 3 weeks, which presumably contributed to a period of low growth. Indeed, fish in the open cage were significantly heavier and longer than those in the semi-closed cage by the October sample and November harvest (Fig. 3).

At harvest, the proportion of sexual maturation was 1.5 % (6 fish) in the open cage group and 2.5 % (6 fish) in the semi-closed cage group. Additionally, 5 of the 30 fish sampled in semi-closed cage in October were sexually mature, effectively increasing the maturation rate to 4 %. All the mature fish were males, and the mature fish sampled in October were on average 31 lighter than the non-mature ones, thus affecting the estimated weight. Although relatively few fish matured, coincidentally two of them were tagged, one from each cage system.

Over the first 2 months of the trial until the first sampling, the accumulated mortality was 0.4 % (7 fish) in the semi-closed cage while it was substantially higher in the open cage at 3.5 % (30 fish). For the remaining period of the trial, natural mortality was low with a total of 17 and 11 dead fish in the semi-closed and open cage, respectively.

Table 3

Welfare summary statistics, including overall welfare score and specific metrics relevant to submergence (fin erosion, snout injury, sores). In this system, 0 is a perfect score, 1 a mild deviation, 2 a notable deviation, and 3 a severe deviation. Values are reported as median (range), grouped by cage for the first (T0, 21/12/2021) and last (T5, 12/10/2022) sampling events where full welfare assessments were conducted.

Cage	Sample	Overall	Fin erosion	Snout	Sores
Open	T0	1 (1–1)	2 (1–2)	0 (0–0)	0 (0–0)
	T5	1 (1–2)	2 (1–2)	0 (0–1)	0 (0–0)
Semi-closed	T0	1 (1–1)	2 (1–2)	0 (0–0)	0 (0–0)
	T5	1 (1–2)	2 (1–3)	0 (0–1)	0 (0–1)

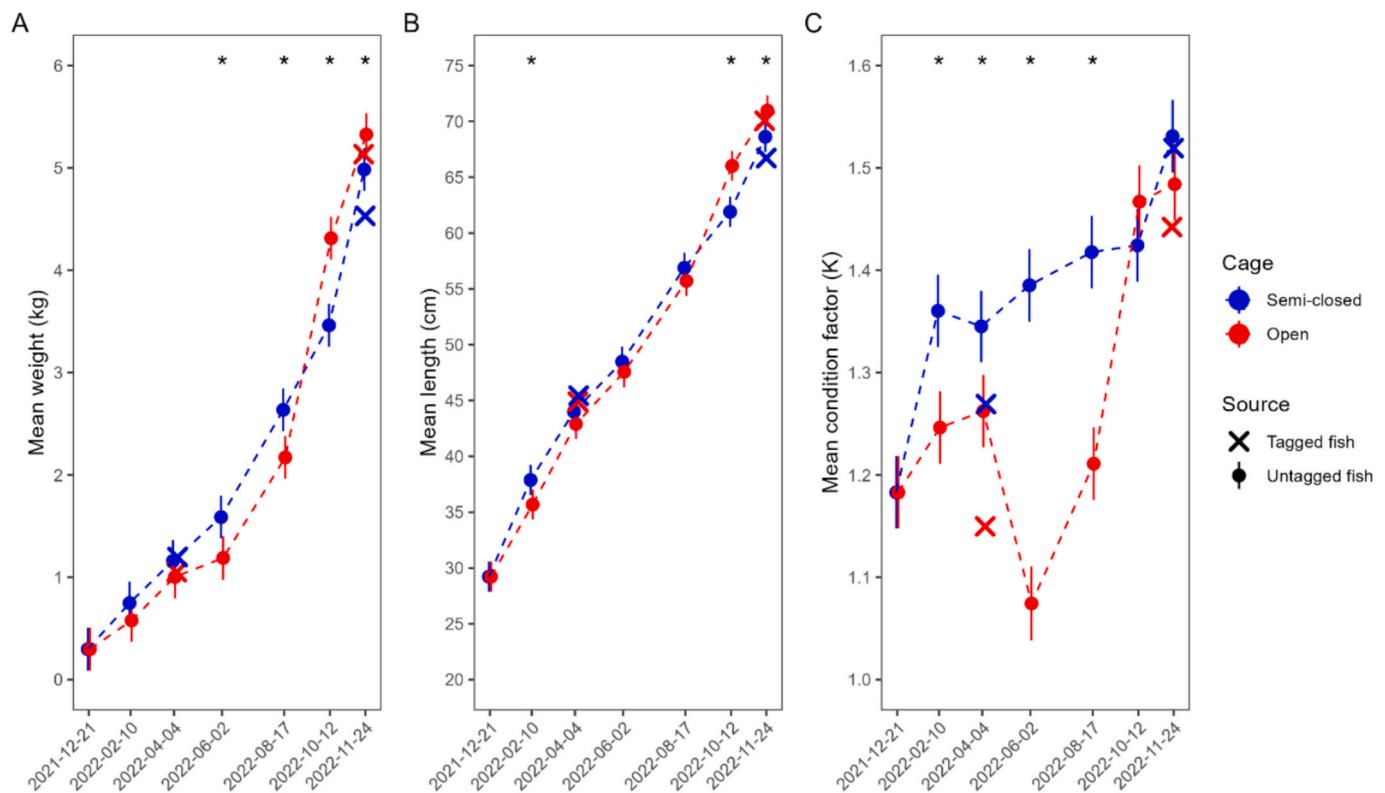


Fig. 3. Weight (A), length (B) and condition factor (C) in Atlantic salmon over the trial period in the two cage groups. Points and error bars indicate the marginal mean and 95 % confidence for each cage and sample. Asterisks indicate significant differences between cages. Sample sizes were $n = 30$ untagged fish during intermediate sampling events and $n = 77$ and 81 untagged fish in open and semi-closed cages, respectively, at the final sampling. Mean values for tagged fish are also shown where available (measuring during tagging and at the end of the trial).

3.3. Biologger retrieval and tagged fish health

During the sampling event in August in the semi-closed cage, the imposed crowding unfortunately becomes more severe than intended which caused some mortality (see section 3.1.). These mortalities included two tagged fish. As the crowding related mortality of tagged fish (20 %) was in proportion with untagged conspecifics (~ 16 %), it was not believed to be tag related. The two tagged fish were 2072 g and 52.8 cm, and 2420 g and 55.5 cm, respectively, and were following a normal growth trajectory. At the sampling event in October, a tagged fish from the open cage was accidentally sampled and killed. It appeared to have been in excellent health and on a normal growth trajectory (4440 g, 67 cm). In November at harvest, all the 9 remaining tagged fish were found in the open cage group. In the semi-closed cage, 7 of the 8 remaining tagged fish were identified, while the final tagged fish was not found. At harvest 7 months after the tagging procedure, the surgical wound on the abdomen had healed well in all cases, and in some individuals only a faint scar remained visible (Fig. 4). It is therefore possible that the final fish was not found owing to excellent wound healing making tagged fish difficult to identify. In total, this meant that 95 % of the tags were retrieved for partial data and 80 % for the full 7-month trial period, and that no mortalities are attributed to tagging. However, there was some evidence that growth rates were affected (Table 2). While low sample sizes limited statistical power, there was a significant interaction effect between sample and tagged status in Model 2, consistent with slower length growth in tagged fish (Fig. 3). The non-significant effect on weight occurred in the same direction (Fig. 3).

3.4. Heart rates following surgical recovery on land

The heart rates rapidly declined over the first 24 h after the surgical implantation of the bio-logger, before gradually stabilizing over the



Fig. 4. Photos of two Atlantic salmon with healed surgical wounds and partially remaining sutures (fish on right) at harvest ~ 7 months after being tagged.

following 2 weeks in the land-based recovery tanks (Fig. 5). Mean heart rates for all fish over the course of the first day after tagging was 54.6 ± 6.5 beats min^{-1} , which declined to 45.6 ± 7.8 beats min^{-1} on the second day, and then further declined to 36.0 ± 5.9 beats min^{-1} prior to fish being transferred back to their respective cages. The mean of all individual fish had a negative linear slope corresponding to -0.9 beats $\text{min}^{-1} \text{ day}^{-1}$.

3.5. Patterns of heart rate and activity level in the two cage systems

Heart rate and activity data in the two groups followed significantly

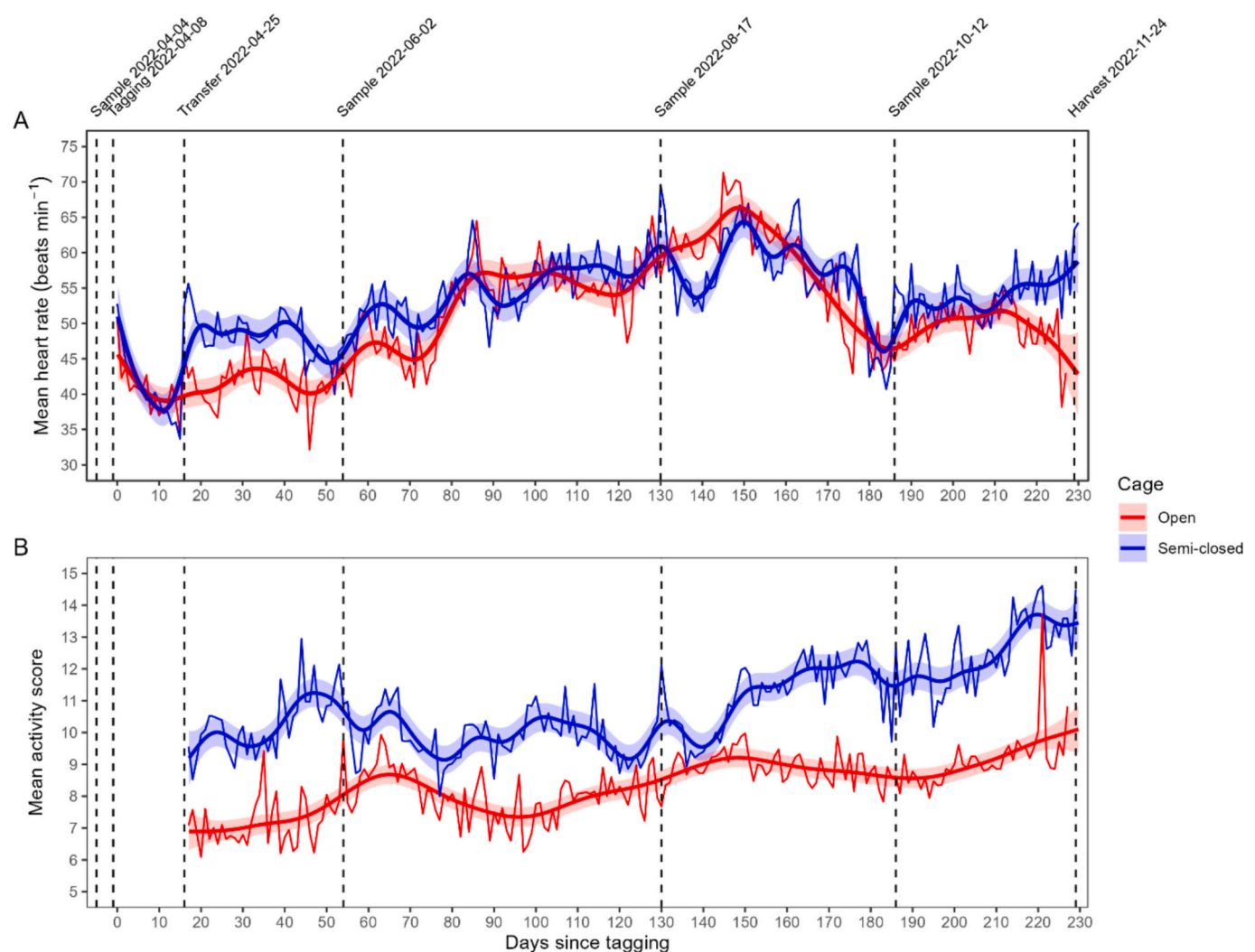


Fig. 5. Mean weekly heart rate (A) and activity (B) of Atlantic salmon in the semi-closed cage and the open cage groups. Smoothed lines and shaded ribbons are generalized additive model fits with 95 % confidence intervals from Models 3 A and 3B. Daily cage means are indicated by the jagged lines.

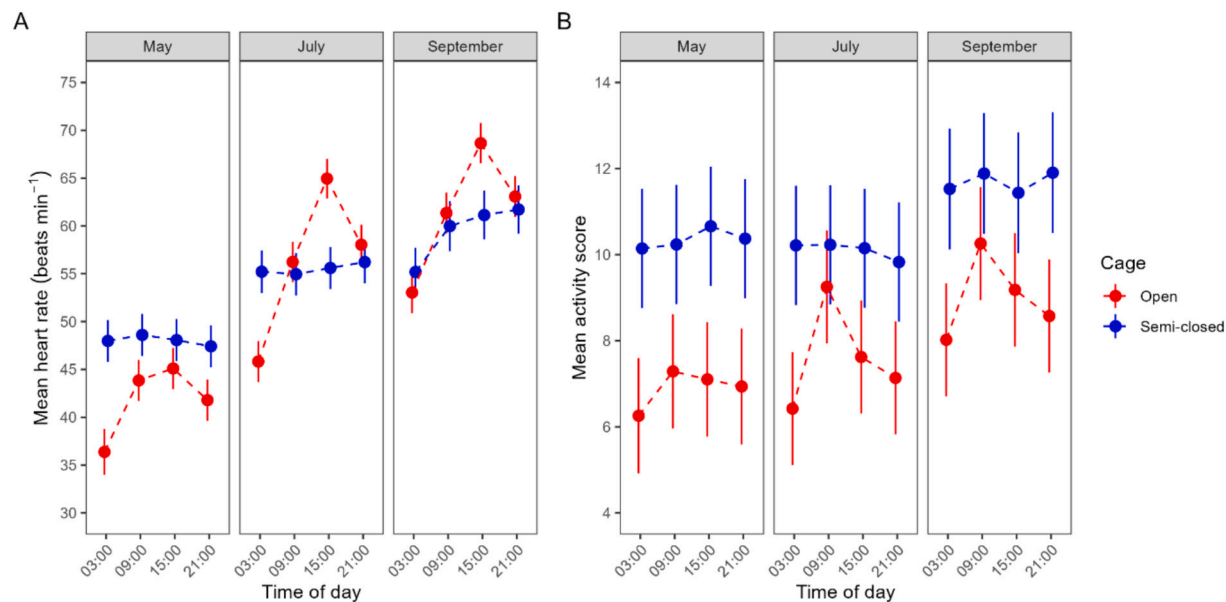


Fig. 6. Diurnal variation in heart rate (A) and activity (B) of Atlantic salmon in open and semi-closed cages. Points and error bars show predicted marginal means and 95 % confidence intervals from Models 4 A and 4B. For brevity, results are shown for three representative months only.

different patterns over short and long timescales, including the full trial duration (Fig. 5) and diurnal cycles (Fig. 6). Both heart rate and activity levels in the open cage group exhibited more variation throughout the day (Fig. 6). In the open cage, the lowest heart rate typically occurred pre-dawn (03:00), and the highest in the afternoon (15:00) (Fig. 6A), while the semi-closed cage had a more subdued diurnal pattern, with 03:00 not always having the lowest mean value (Fig. 6A).

Overall, there was a positive but weak correlation in activity and heart rate over the trial duration (Figs. 5–7). Fish exhibited higher activity levels as the trial progressed (Fig. 5), likely due to absolute swimming speeds and associated movements increasing with fish size over time. Heart rate scaling showed a more complex pattern, with a gradual but inconsistent increase in heart rate until late August in both cages, likely to reflect increasing water temperature, followed by a rapid decline and diverging trends at the end of the trial (Fig. 5). The heart rate increased significantly with activity, fish weight, and temperature (Fig. 7). Notably, there was a significant weight $\times$ temperature interaction indicating that temperature modulates the effect of fish size (or vice versa), such that fish weight has a stronger effect on heart rate at higher temperatures (Fig. 7).

3.6. Response and recovery from severe crowding stress

The August sampling event in the semi-closed cage imposed substantially more severe crowding than planned, which was apparent in the heart rate data (Fig. 5A). In the week leading up to the sampling day, the semi-closed cage had a mean heart rate of 58 beats min^{-1} , nearly identical to the 59 beats min^{-1} in the open cage, albeit with a different diurnal range. On the sampling day, mean heart rate in the semi-closed cage was normal at 03:00 and 09:00 (54 beats min^{-1} at each), but had increased to 71 beats min^{-1} by 15:00 and 78 beats min^{-1} by 21:00. Heart rate remained high at 09:00 the next day (73 beats min^{-1}) but had recovered by 15:00 (56 beats min^{-1}). The open cage exhibited a much smaller increase of 66 beats min^{-1} at 15:00 on the sampling day and had recovered to 56 beats min^{-1} by 21:00. Heart rates in the semi-closed cage continued to decline in the week following, and by 10 days post sampling were substantially lower than in the open cage yet had increased to match the open cage by 20 days post sampling (Fig. 5).

3.7. Quality index of heart rate data across time

There was some evidence that the quality of heart rate data changed

over time in both cages. Most fish in both groups had a period of low-quality readings in the month following tagging, especially while in the recovery tank (Fig. 8). Quality had improved substantially by May–June in the semi-closed cage (88 % with QI = 0 throughout June) but remained relatively poor in the open cage until July–August (79 % with QI = 0 throughout August) (Fig. 8). There was then a decline in quality in both cages that continued to the end of the trial, strongly driven by a subset of individuals, with approximately half of the cohort maintaining high quality readings to the end of the trial, while the other half began declining in quality from August onwards (Fig. 8). Mean QI values for individuals over the trial ranged from 0.31 to 1.2 (best to worst individuals).

4. Discussion

In this study we successfully produced harvest sized Atlantic salmon of ~ 5 kg in a semi-closed prototype cage, showing that these emerging cage designs can accommodate the biological requirements throughout the entire marine production phase. Furthermore, the mortality was lower overall than in the companion open cage group, and treatment for lice infestation was also completely avoided during the 11-month period. This highlights the potential for improving animal welfare in semi-closed cages. However, we encountered technical challenges during sampling events that resulted in excessive crowding stress in the semi-closed cage. We expect that more practical experience along with technological refinement will improve handling procedures going forward as semi-closed cage technology continues to evolve. Since the present study was a small-scale proof of concept trial, the next steps for the development of these designs will involve documenting welfare and growth performance at a larger production scale and in replicated designs.

The bio-logger component of this experiment with a refined tagging protocol was highly successful. Tagged fish had only slightly reduced growth over a 7-month period, perhaps reflecting the two additional transfers (sea to tank and tank to sea) as well as any negative effects of tagging, with no tag-related mortalities. This shows that long time series of physiology and behaviour can be obtained to provide detailed assessments of fish coping ability in novel aquaculture systems. Useful metrics documented in this trial included how differences in photoperiod and water flow in the two cage systems affected heart rate and activity patterns in Atlantic salmon. Additionally, the general effects of water temperature, size as the fish grew larger, and stress following

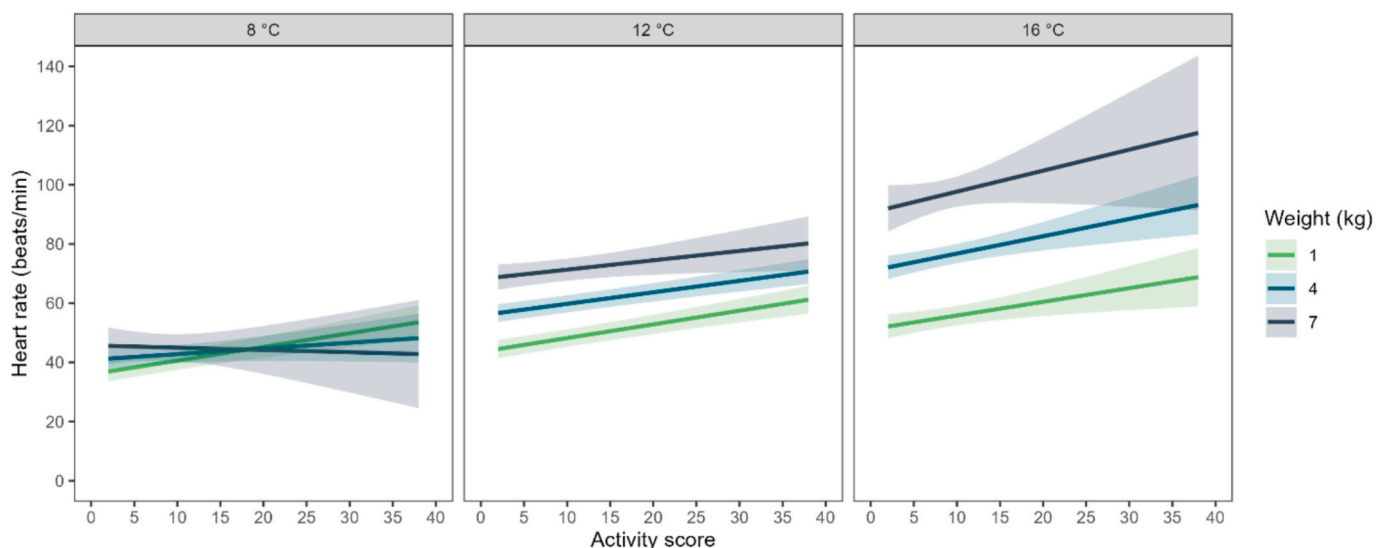


Fig. 7. Relationship between activity and heart rate, accounting for effects of temperature (8, 12, 16 °C) and fish size (1, 4, 7 kg) in Atlantic salmon. Lines and shaded ribbons indicate predicted marginal means and 95 % confidence intervals from Model 5.

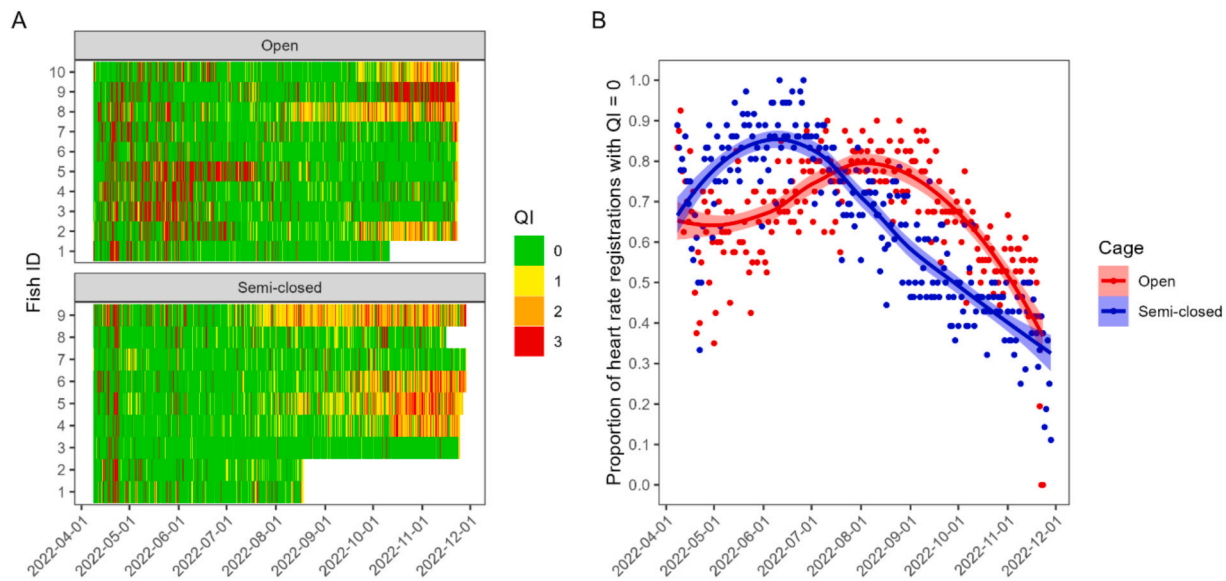


Fig. 8. Quality index (QI) scores of heart rate biollogger data over the 7-month trial period. A: Tile plot of QI scores over time, grouped by fish and cage. The time series ends for each fish when the fish dies or is harvested. B: Daily distribution of QI values within each cage, presented as the proportion of registrations with QI = 0. The data are fitted by a locally estimated regression model (LOESS) for illustrative purposes, where the shaded areas indicate 95 % confidence intervals.

crowding were also reported.

4.1. Mortality, welfare, and maturation in the two cage systems

The semi-closed cage group had a slightly lower accumulated mortality rate than the open cage group over the 11-month marine growth period when omitting the accidental crowding related mortalities during the August sampling event in the semi-closed cage. Mortality rates were low in both cage systems and markedly lower than the high mortality observed in commercial-scale aquaculture in the same production region that year (18 % in western Norway), which was largely driven by the frequent use of non-medicinal delousing operations (Agnalt et al., 2024). The present production with minimal such interventions demonstrates that low mortality is achievable throughout a full marine production cycle, both in open and closed farming. This is further supported by the observed growth rates to harvest size and consistently high welfare scores, indicating good overall fish welfare. Fish mortality in Norwegian aquaculture is widely acknowledged to be unacceptably high and ongoing legislative initiatives has proposed a target rate of 5 % maximum. To reach this goal, the aquaculture industry will likely need a major shift towards lice prevention technologies such as semi-closed cages in the coming years (Barrett et al., 2020; Sievers et al., 2022). Hence, one of the major purposes of closed containment farming is to avoid lice infestations (Nilsen et al., 2017), as treatment for lice is associated with poor animal welfare and elevated mortality (Overton et al., 2019). In the present study, lice treatments never became necessary in the semi-closed cage, while one treatment was required in the open cage in February. Similarly, lice treatments were not needed in larger closed cages, as reported by Nilsen et al. (2017), where deep water inlets were used. In our study, the depth of the water inlet was adjustable and moved closer to surface to benefit from higher temperatures that provide better growth conditions in summer and autumn. This would normally give increased lice infestations as the lice larvae swim up and are found close to the surface. However, lice levels did not increase, probably as the lice avoid surface brackish water. Also, the infestation pressure at the site was generally low. For choice of future inlet depths, a balance between temperature benefits and potential lice infestations must be considered.

Welfare scoring was overall similar between cage groups where minor scale loss, snout wounds, skin bleeding, skin wounds, and fin

damage were the most prevailing observations. These types of injuries generally appeared fresh upon scoring. We therefore ascribe them to the sampling methods. In both of the cage types, fin erosion worsened over time, and this was likely owing to general wear and tear in confined aquaculture settings with high stocking densities. Contrasting to this, occurrences of skin bleeding and wounds decreased over time indicating that welfare became better for these metrics. These observations may be explained by higher temperatures in the latter part of the trial period in combination with lower salinities in the semi-closed cage from June onwards when the water intake pumps were raised, as brackish and warmer water is known to facilitate better wound healing (Jensen et al., 2015).

The proportion of sexual maturation was higher in the semi-closed cage group (2.5 %) than in the open cage group (1 %). This difference was anticipated owing to the persistent use of a continuous photoperiod in the semi-closed cage, as such prolonged environmental stimuli are well known to eventually stimulate sexual maturation in farmed Atlantic salmon (Oppedal et al., 1997; Endal et al., 2000; Taranger et al., 2010). Although maturation is undesired as it reduces product quality, a continuous photoperiod was nevertheless applied in the semi-closed cage group to safeguard welfare by maintaining the visual orientation of the fish under novel rearing conditions. As such, injuries may occur more frequently from collisions with cage structures and between fish if they were subjected to periods with complete darkness (Sievers et al., 2018). Future efforts will need to clarify whether constant illumination is required in semi-closed technologies, or if the fish can adapt to alternating photoperiods. If not, this may set an upper limit to the maximum sizes that reliably can be produced while avoiding high proportion of sexual maturation.

4.2. Stocking density and growth performance in the two cage systems

Despite several reductions in biomass over the trial period, stocking density in the semi-closed cage remained persistently higher than in the open cage group. We maintained a relatively high stocking density from the onset in the semi-closed cage to better reflect the intended production strategy of the industry in this type of technology. As such, from a cost-efficiency perspective, higher stocking densities are inherent to closed containment systems due to both operational costs and the controlled environmental conditions that support such densities. It was

therefore not feasible nor relevant to aim for a similar stocking density in the open cage group.

Stocking densities reaching up to $\sim 36\text{--}51\text{ kg m}^{-3}$ (Table 1) across a wide fish size range (0.9 to 2.7 kg) did not appear to restrict growth, indicating that the Watermoon environment is suitable for high-capacity utilization in transient semi-closed rearing strategies. However, the experimental design of periodic biomass reduction necessitated more extensive crowding than would normally be required for sampling only 30 fish. If the stocking density becomes too high, it can have negative effects on growth and external welfare parameters in Atlantic salmon post-smolts (Calabrese et al., 2017). However, the stocking densities in the present study never surpassed the thresholds previously recommended (Calabrese et al., 2017). Meanwhile, elevated fish densities could influence swimming behaviours where local fish density is determined by the spatial availability of preferred environmental conditions such as light and temperature (Oppedal et al., 2011).

The semi-closed group outperformed the open cage group in terms of weight, fork length and condition factors for large parts of the trial, up until the two latest sampling events in October and November. This can be attributed to the more ideal rearing conditions in the semi-closed cage between December and June. During this period, intake water was supplied from a depth of 35 m, providing more stable and higher temperatures especially during the winter. The semi-closed group was also exposed to constant moderate flow conditions. Moderate flow conditions have previously been shown to improve growth metrics (Christiansen et al., 1992; Solstorm et al., 2015; Nilsen et al., 2019). Furthermore, the semi-closed cage group was subjected to a continuous photoperiod. This can aid in delaying maturation and facilitate somatic growth during winter and spring, while a natural seasonal photoperiod experienced by the open cage group may cause slower growth and a reduction in condition factor during winter and spring, which then becomes compensated for by higher growth rates in summer and autumn (Oppedal et al., 1999; 2006). These respective patterns were evident in the two cage systems.

The problematic sampling event in August in the semi-closed group, which imposed severe crowding stress, likely also contributed to the slower growth in the latter part of the trial, as recovery of appetite following exhaustive stress events can take several days to weeks in sea caged Atlantic salmon (Walde et al., 2022; Morin et al., 2025). In addition, the October sample contained a sampling bias by a relatively high proportion of sexually mature fish, which were on average smaller than non-mature individuals and therefore contributed to the pronounced size difference between the groups at that time. Although some growth compensation appeared in the semi-closed group towards the final sampling, we cannot rule out negative effects of the relatively small rearing unit volume on growth towards harvest, particularly related to the limited size of the air-filled dome, or possible biases in fish size estimates resulting from the sampling method (Nilsson & Folkedal, 2019). The fluctuating growth trajectories over the 11-month trial period highlight the importance of following fish groups all the way to harvest size for a complete evaluation of realized growth potential reflecting rearing conditions at different production phases (Hvas et al., 2022).

4.3. Growth and survival in tagged fish

In previous bio-logging aquaculture studies a recurring concern has been whether tagged fish adequately represent untagged conspecifics owing to issues with reduced growth and higher relative mortality rates in tagged individuals (Hvas et al., 2020; Warren-Myers et al., 2021; Macaulay et al., 2021). A major purpose of the present study was therefore the incorporation of a refined tagging protocol to hopefully improve long-term growth and survival prospects in tagged fish.

The surgical tagging procedure involves multiple stressors, and the fish will therefore be most vulnerable in the immediate period after being tagged, where recovery of resting heart rates can take 2–3 weeks in Atlantic salmon (Hvas et al., 2020; Zrini and Gamperl, 2021). To

facilitate a more lenient surgical recovery environment, we therefore maintained tagged fish in clean and undisturbed land-based flow-through tanks for ~ 2 weeks before transferring them back to their respective cage types. This contrasted with previous sea cage-based bio-logger studies where fish were tagged on-site and immediately returned to their marine environment (Brijs et al., 2018; Gamperl et al., 2021; Warren-Myers et al., 2021). The ambient sea cage environment is generally more stressful and contains more health hazards (Morin et al., 2025). Risks of wound infections and other injuries during the initial surgical recovery period would therefore most likely be higher in sea cages compared to laboratory holding tanks.

We did not observe any tag-related mortalities over the 7-month period that the tagged fish were maintained in the two sea cage types. However, a few tagged fish were accidentally sampled prior to harvest, but these all appeared in good health. At the end of the trial 19 out of 20 tags were retrieved, and tagged fish were of comparable sizes relative to untagged fish, indicating normal growth. Wound healing from the surgical implantation was excellent, and in some cases, it was difficult to identify tagged fish as only a faint abdominal scar remained visible. It is therefore possible that the final tagged fish was not found owing to these reasons. As such, the refined protocol with a more lenient recovery period appeared to have aided in improving the overall health of tagged fish and helped avoid long-term growth and appetite impairments. It is therefore reasonable to consider tagged fish from the present study as true sentinels that represent the general status of the group.

4.4. Long term bio-logger studies and decreasing quality index

All heart rate measurements recorded by the bio-logger are assigned a quality index score (e.g., 0, 1, 2 or 3), indicating the accuracy of each data point. A score of 0 is highly accurate, while increasing scores progressively decrease data reliability (Zrini and Gamperl, 2021). To obtain a consistent high-quality index it is important that the bio-logger is situated adequately in the abdomen of the fish in near proximity to the pericardium (Brijs et al., 2019; Muller et al., 2020). However, over time the bio-logger may dislocate and thereby reduce the quality of heart rate data. Dislocated bio-loggers will be a greater concern in long-running trials as the tagged fish grow larger. At the end of the present study, tagged fish had increased in size by $\sim 4\text{--}5$ fold since being tagged 7-months prior. Position of the bio-logger in the abdomen was therefore anticipated to become less optimal over time.

We found that quality index scores displayed a non-linear change over time, where the proportion of 0 scores increased over the first two months, whereafter the proportion steadily declined towards the end of the trial were less than half of the datapoints were assigned a 0 score. Upon fish dissection for tag retrieval, the bio-logger generally appeared to still be anchored adequately in the abdomen, although the distance to the pericardium had likely increased simply from the fish growing substantially larger over the trial period. Consequently, data will become more fragmented with time. This imposes some limitations on how long heart rate bio-logger trials effectively can be run, particularly if the fish increase drastically in size. Hence, the final period of the present trial (e.g., 5–7 months post-tagging) may be considered a soft time limit for such bio-logger trials.

4.5. Heart rate patterns – Influence of photoperiod, body size, and temperature

Earlier bio-logging studies have consistently reported strong diurnal cycles in heart rates in farmed Atlantic salmon and rainbow trout, reflecting resting periods at night and increased activity during the day (Brijs et al., 2018; Hvas et al., 2020; Warren-Myers et al., 2021). However, owing to the use of a continuous photoperiod in the semi-closed cage, we hypothesized that diurnal heart rate patterns here would become more relaxed when compared to the open cage group. The differences between night and day were indeed much lower in the semi-

closed cage group while the open cage group had a much more pronounced increase in heart rate between night and day. This indicates that photo-period is the dominant factor for diurnal heart rate variations, and that endogenous circadian rhythms in metabolism have a more subtle effect on the heart rate in Atlantic salmon.

The tagged fish increased in size from ~1.1 kg to ~4.8 kg over the trial period, and physiological scaling effects were therefore anticipated to affect heart rate measurements. We found that larger sizes were associated with increasing heart rate, and moreover, interacted with temperature so that larger fish at higher temperatures tended to have higher heart rates. Meanwhile, in mammals it is well established that resting heart rates decrease at larger body sizes (Dawson, 2014). Although in fish, the size-scaling effects of heart rates and the general cardio-vascular system remains less clear. For instance, no evidence for allometric scaling in heart rates was found among larger-sized adult chinook salmon in one study (Clark and Farrell, 2011), while another study on adult chinook salmon found a slight decrease in heart rate among longer individuals (Twardek et al., 2021). A more focused experiment on heart functionality across greater size differences in Atlantic salmon would be needed to fully clarify these effects. However, based on the present study, scaling effects of heart rate appear to be on the subtle side in this species at the post-smolt life-stage.

Ambient water temperature directly affects all physiological functions in ectothermic fish (Scholander et al., 1953; Brett, 1971; Fry, 1971). It was therefore expected that seasonal changes in temperature would have a significant impact on heart rates of Atlantic salmon in the present study, as has also been reported in previous bio-logger studies (Gamperl et al., 2021; Warren-Myers et al., 2021). Increasing temperatures substantially accelerate metabolism and oxygen requirements in Atlantic salmon (Remen et al., 2016; Hvas et al., 2017), and this necessitates an accompanying increase in cardiac output to supply sufficient oxygen to receiving tissues (Farrell, 2002, 2007; Anttila et al., 2014).

Our model estimated an increase in heart rate with temperature in both cage groups, similarly as in previous bio-logger studies on Atlantic salmon (Zrini and Gamperl, 2021; Bloecher et al., 2024; Gamperl et al., 2021). However, the semi-closed group response to increasing temperature was lower than in the open cage group. This may be explained by the role of stroke volume as the primary modulator of cardiac output in response to increasing swimming speeds in salmonids (Stevens and Randall, 1967; Thorarensen et al., 1996), as the semi-closed cage fish consistently showed higher activity levels. Furthermore, an increase in heart rate is the primary modulator of cardiac output in response to higher temperatures (Gamperl et al., 2022). The slower swimming fish in the open cage would therefore be more sensitive to temperature changes with regards to their heart rate.

4.6. Activity patterns

Activity levels tended to increase over the course of the trial. This can be ascribed to increasing body sizes which would increase absolute levels of acceleration, as larger fish generally swim faster when expressed in absolute units such as meter s^{-1} , while relative speeds (e.g., body lengths s^{-1}) decrease with size (Hvas et al., 2018; Oldham et al., 2019).

The semi-closed group showed higher activity levels overall, indicating higher swimming speeds. A higher swimming speed was anticipated owing to the constant moderate flow conditions provided in the semi-closed cage relative to the open cage group that would have experienced weak ambient current with some tide driven variation. Furthermore, submerged fish may increase their swimming speed owing to progressively increasing negative buoyancy if they are unable to refill their swim bladders (Sievers et al., 2022). However, our fish were given access to an air reservoir and were only submerged one meter. Increased swimming to compensate for negative buoyancy were therefore unlikely here.

We also observed differences in activity between time of day in the open cage group subjected to natural photoperiods. Here activity was highest in the morning at 9:00, coinciding with the onset of feeding whereafter it decreased and was lowest at night. This reflects the diurnal heart rate patterns discussed previously and is in line with the typically observed behaviours of Atlantic salmon in sea cages where fish are most active during feeding, while schooling behaviours becomes less tight and more dispersed at night with calmer swimming (Fernö et al., 1995; Korsøen et al., 2009). Meanwhile, the semi-closed cage showed negligible diurnal variation in activity, which can be ascribed to a continuous feeding protocol throughout the day in combination with constant illumination.

CRediT authorship contribution statement

Malthe Hvas: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Luke T. Barrett:** Writing – review & editing, Visualization, Validation, Supervision, Software, Methodology, Investigation, Data curation. **Lisa Marie Gjerde:** Writing – review & editing, Visualization, Software, Methodology, Investigation, Formal analysis. **Tone Vågseth:** Writing – review & editing, Visualization, Software, Methodology, Investigation. **Frode Oppedal:** Writing – review & editing, Funding acquisition, Conceptualization. **Ole Folkedal:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

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Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.aquaculture.2025.743601>.

Data availability

Data will be made available on request.

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