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Shifting production cycle from sea to RAS – what does the fish say?

Jonna Hänninen [a,b,c,d,*], Jani Pulkkinen [c,e], Harri Vehviläinen [f]

[a] Department of Biological and Environmental Science, University of Jyväskylä, P. O. Box 35, 40014 Jyväskylä, Finland
[b] Natural Resources Institute Finland, Vilppulantie 415, 41340 Laukaa, Finland
[c] Natural Resources Institute Finland, Survontie 9 A, 40500 Jyväskylä, Finland
[d] Department of Biology, University of Turku, 20014 Turku, Finland
[e] Paras Aqua Oy, Laukaantie 4, 40320 Jyväskylä, Finland
[f] Natural Resources Institute Finland, Tekniikankatu 1, 33720 Tampere, Finland

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ABSTRACT

In combined RAS (recirculating aquaculture system) and sea cage farming, fish are first reared in RAS for about 8 months and then transferred to sea cages for the one growing season. This method allows a shorter production cycle, more efficient nutrient uptake, and avoiding risks associated with open environment rearing. However, combining two different production methods and environments challenge ability of fish to adapt to the new farming environment. In this study, rainbow trout (*Oncorhynchus mykiss*) were raised in RAS and partial RAS (PRAS) and then transferred to freshwater flow-through system and brackish water cages in June and September according to common practices. We investigated: 1) Does water quality during initial farming influences success of transfers?, 2) Does growth of rainbow trout differ in different rearing environments after transfers?, and 3) Does size of rainbow trout and/or timing of transfers affect growth and stress regulation of rainbow trout? Our results support that neither the water quality nor system (RAS or PRAS) affected the growth or welfare of fish, whereas the larger fish transferred in September had challenges (e.g. lower growth) after transfer to brackish water cages. However, there are many uncertainties associated with the transfer performed in September. Understanding the reasons behind these current problems would allow a wider use of this production method in salmonid aquaculture. It would also allow development of new, more efficient and sustainable production cycles and strategies, adapted to different needs.

1. Introduction

Unlike Atlantic salmon (*Salmo salar*), rainbow trout (*Oncorhynchus mykiss*) do not necessarily need to be reared in both fresh and saltwater. However, this is a common practise in Finland, where rainbow trout is the main cultivated species (Ministry of the Environment, 2020). A traditional production cycle of rainbow trout starts in freshwater flow-through system, from where juveniles (approximately 20 g) are transferred to sea cages located in the Baltic Sea. After the first growing season, the fish (approximately 400 g) are overwintered in the sea cages. During the second growing season, the fish reach harvest(able) size (from 1.9 kg to 3.0 kg).

The sea cage farming, while technologically relatively straightforward and low-cost production method, does not come without challenges. The longer the period of time fish are reared in the sea cages, the higher the biological risks, such as problems caused by escapees from the sea cages, fish diseases, and parasites (Bjørndal and Tusvik, 2017; Ytrestøyl et al., 2023). Furthermore, the technologies to capture nutrient effluent from the sea cages is still in its infancy. For example, increasing Finnish fish farming production to meet demand for fish in Finland is problematic due to environmental effects of sea cage farming, such as eutrophication (Ministry of the Environment, 2020). Shifting the production cycle from sea cage farming to inland/indoors could alleviate these challenges.

A potential solution to increase the production could be a use of recirculating aquaculture system (RAS), where water is recirculated between fish tanks and a water treatment system (Timmons et al., 2018). It aims to minimise the negative environmental effects of farming and provides a relatively stable rearing environment (Timmons et al., 2018). However, cost-effectiveness of RAS needs to be improved in order to RAS become economically more viable production system (Timmons et al., 2018), and optimal rearing conditions for the fish need to be ensured.

An economically and environmentally feasible production model could be a combination of RAS and sea cage farming. Fish are first reared

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[*] Corresponding author at: Natural Resources Institute Finland, Survontie 9 A, 40500 Jyväskylä, Finland.

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for about 8 months in the RAS and then transferred to sea cages and reared for one growing season (from 5 to 6 months). By increasing size of fish in the RAS, the production cycle of farming can be accelerated, and the sea cage period, which normally lasts from 16 to 27 months, can be significantly shortened (Bjørndal and Tusvik, 2017). When more production is transferred from the sea to RAS, the more nutrients can be captured. In addition, the shorter sea cage period reduces the biological risks of sea cage farming (Bjørndal and Tusvik, 2017). The shorter sea cage farming periods would also make it possible to avoid risks associated with overwintering of fish on some areas with extreme temperatures (Donaldson et al., 2008; Islam et al., 2022; Reid et al., 2022).

However, the RAS and the sea cage farming are very different production methods. When the fish are transferred from the RAS to the sea cages, many factors change. These include water quality (temperature, concentration of dissolved gases, pH, salinity, and turbidity), rate of temperature change, amount of light, water movement in tanks, and presence of predators. This challenge ability of the fish to adapt to the new environment and might cause significant stress for the fish. So, effects of combining the freshwater RAS and sea cage farming on fish growth and welfare are not well known.

Previous works have discussed an adaption period between the fresh and saltwater (Bjerknes et al., 1992; Kaneko et al., 2019). The aim of adaptation period is to ensure good survival and growth of fish in the sea cages after transfer (Bjerknes et al., 1992). Without the adaptation period, the physiology and survival of the fish may be disturbed, and the growth may be lower than planned (Bjerknes et al., 1992). Conversely, in rainbow trout, direct transfer from the fresh to the saltwater should be successful up to salinities of about 26 ‰ without disturbing osmoregulation and causing mortality (Finstad et al., 1988; Jackson, 1981; Kaneko et al., 2019). Therefore, the transfer of rainbow trout from the freshwater RAS to the brackish water sea cages should be possible without the separate adaption period between the two water salinities.

In this study, we investigated how physiological parameters change in rainbow trout of two different size after transfers from typical RAS (with biological filtration and water recycling rate of around from 98 to 99 %) and partial RAS (PRAS, without biological filtration and with water recycling rate of 80 %) to freshwater flow-through system and brackish water sea cages, and how water conditions affected on growth. Our study questions were 1) Does the water quality during initial farming (RAS or PRAS) influences the success of transfers?, 2) Does the growth of rainbow trout differ in different rearing environments (RAS, PRAS, flow-through system, and sea cages) after transfers?, and 3) Does the size of rainbow trout and/or the timing of transfers affect the growth and the stress regulation of rainbow trout? First, we hypothesise that the water quality of initial farming influences the success of transfers. Water quality of PRAS with larger relative water renewal rate is closer to natural conditions than the water quality of RAS. Therefore, the PRAS originated rainbow trout might be expected to success better in transfers than the RAS originated rainbow trout. Second, we hypothesised that the RAS and PRAS originated rainbow trout would grow better in the brackish water sea cages than in the freshwater flow-through system. The salinity of the Baltic Sea (approximately from 6 to 7 ‰, Feistel et al., 2008) is quite close to the physiological salinity of the fish (approximately from 9 to 12 ‰, Sakamoto and McCormick, 2006; Al-Jandal and Wilson, 2011). Therefore, the brackish water could be thought to suit well for rainbow trout. Studies have also shown that the brackish water (from 1 to 9 ‰) is suitable for rainbow trout (Altinok and Grizzle, 2001). Third, we hypothesised that the smaller rainbow trout would grow less than the larger rainbow trout. Studies have shown that the fish size affects their resilience to changes in environmental conditions (Ricker, 1976; Sogard, 1997). The smaller juvenile, the more sensitive it is to the changes in environmental conditions (Ricker, 1976; Sogard, 1997). For example, ability of rainbow trout to tolerate salt water improves as the fish grow (Parry, 1958). Therefore, the smaller fish might be expected to grow less after transfers than the larger fish.

2. Materials and methods

2.1. Fish

Rainbow trout hatched in January 2022 were used in the experiment. The eggs were obtained from a commercial fish farm (Hanka-Taimen Oy, Rautalampi, Finland). The fish (mean weight 20 g) were vaccinated against furunculosis and vibriosis (Alpha ject 3000, PHARMAQ AS, Overhalla, Norway) in May 2022.

2.2. Experimental setup

The experiment was carried out at the Natural Resources Institute Finland (Luke) Laukaa fish farm from 26 April 2022 to 20 October 2022 (Fig. 1). Hatching of eggs and start of feeding were carried out in a separate RAS environment. The fish were moved to the actual rearing conditions of the experiment at the end of April (26 April 2022). Half of the fish (2400 fish) were divided to three RAS tanks and half of the fish to three PRAS tanks. At the beginning of the experiment there were 800 fish in each tank.

The fish were transferred from the RAS and PRAS tanks to six freshwater flow-through tanks in Laukaa and to six brackish water sea cages in the Baltic Sea (Natural Resources Institute Finland, Rymättylä station). The first transfer took place in mid-June (16 June 2022), when 200 fish per tank were transferred equally from the RAS and PRAS tanks to both the fresh and the brackish water. The remaining fish were kept in their original RAS and PRAS tanks. After the first transfer, the fish were raised in the fresh and the brackish water for five weeks (summer period). The summer period ended on 21 July 2022.

Biomass in the RAS and PRAS tanks exceeded their carrying capacity approximately three weeks after the summer period (9 August 2022) and some fish were removed from the tanks. After the removal, there were 150 fish per tank.

The second transfer took place in mid-September (13 September 2022), when 50 fish per tank were transferred equally from the RAS and PRAS tanks to both the fresh and the brackish water. The remaining fish (approximately 50 fish per tank) were kept in the same RAS and PRAS tanks. After the second transfer, the fish were raised in the fresh and the brackish water for five weeks (autumn period). The autumn period and the whole experiment ended on 20 October 2022.

The fish transferred to the flow-through tanks had a much shorter distance from the RAS environments to the new environment than the fish transferred to the sea cages. The transfer containers of fish transferred to flow-through tanks were driven by a tractor for five hours to mimic the stress levels associated with the brackish water transfer, which took also five hours. The tractor transportation was performed in both the summer and the autumn periods.

2.2.1. Tanks

The separate RAS environment was used for hatching of eggs and starting of feeding. This separate fully RAS environment consisted of 20 bottom-drained fibreglass rearing tanks (500 L) and a water treatment system. The water treatment system consisted of a drum filter with 60 μm mesh size (Faivre F2–80, Baume-les-Dames, France), two moving-bed bioreactors (1 m^3) with plastic carrier media and a fluidized bed bioreactor with fine sand as the carrier media (CycloBio, Marine Biotech Inc., Beverly, Massachusetts, USA). A cascade column filled with plastic balls was used for gas exchange. Each tank had an air stone for the oxygenation. The pH was adjusted with sodium hydrogen carbonate ($NaHCO_3$). Relative water renewal rate was set at 750 L kg^{-1} feed.

The experiment used a hybrid aquaculture experimental platform located in Laukaa fish farm consisting of the three freshwater RAS tanks and the three freshwater PRAS tanks. The RAS tank consisted of a 600 L bottom-drained plastic rearing tanks with a water volume of 500 L, followed by radial flow settlers which removed the sludge from the water. The water in the tanks was aerated using airlift pumps. Air was

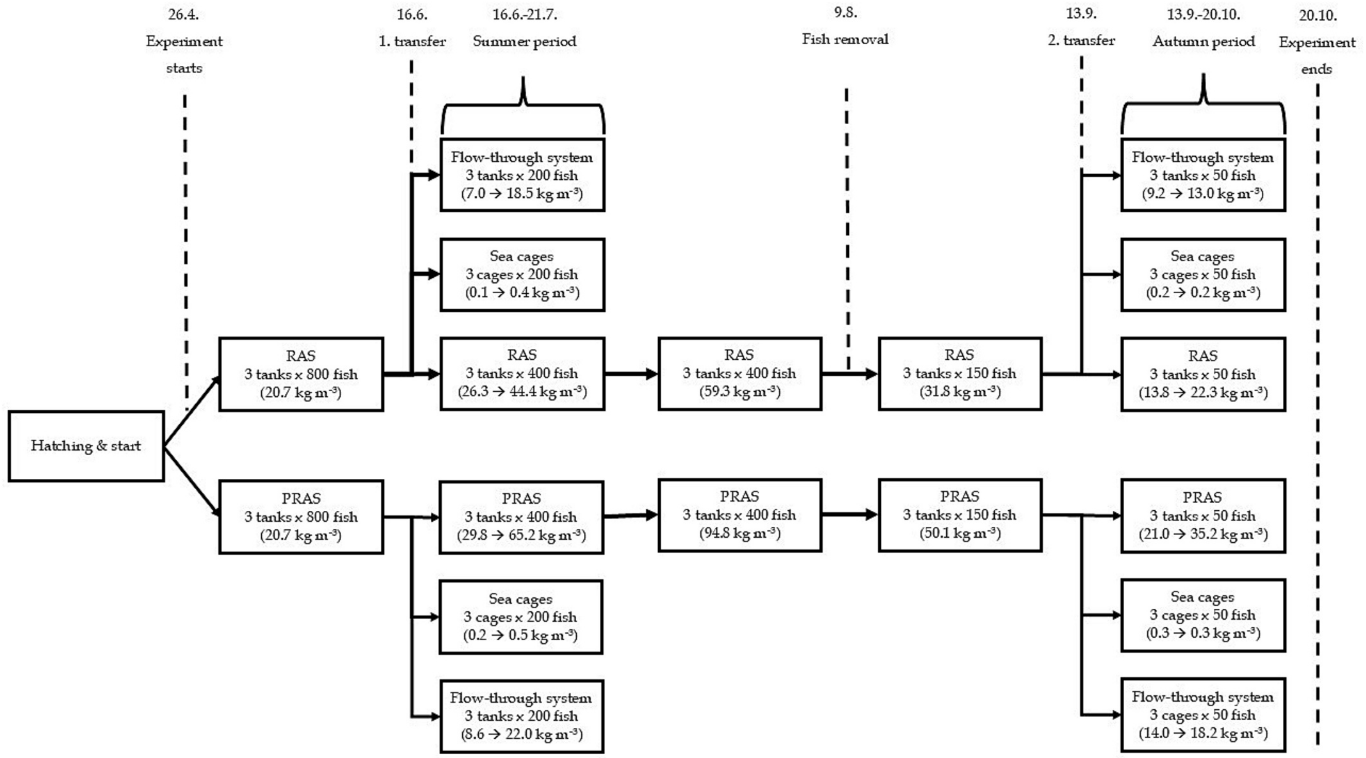

Fig. 1. Fig. 1. Experimental design. Hatching and starting of feeding were carried out in a separate RAS environment. The fish were moved to actual farming conditions of the experiment at the end of April. Half of the fish were divided to RAS tanks and half to PRAS tanks (800 fish per tank). The first transfer from the RAS and PRAS to flow-through system and sea cages was performed in mid-June (200 fish per tank or cage). The remaining fish were kept in the same RAS and PRAS tanks (400 fish per tank). The first experimental period (summer period) lasted five weeks. Biomass in the tanks exceeded carrying capacity of the RAS and PRAS tanks and some fish were removed. After the removal there were 150 fish per tank. The second transfer from the RAS and PRAS to the flow-through system and the sea cages took place in mid-September (50 fish per tank or cage). The second experimental period (autumn period) also lasted five weeks, after which the experiment was finished.

supplied to the airlift pumps by a side channel blower. The three RAS tanks were connected to a common water treatment unit consisting of two moving bed bioreactors with a total volume of 1200 L. The bioreactors contained 600 L of plastic carrier media (RK-BioElements, RK Plast A/S, Skive, Denmark). At the beginning of the experiment, the system also contained a drum filter, but it was removed due to technical problems at the beginning of June. The relative water renewal rate was set at 500 L kg^{-1} feed at the beginning of the experiment but had to be increased to 750 L kg^{-1} feed after the drum filter was removed. This fresh make-up water was supplied to the other bioreactor.

The PRAS was composed and acted in almost same way as the RAS but without the common water treatment unit (so no bioreactors were used). The system consisted of 600 L bottom-drained plastic rearing tanks with a water volume of 500 L followed by radial flow settlers. Airlift pumps were connected to the side of the tanks to aerate and circulate the water within the fish tank. The relative water renewal rate was set at 10000 L kg^{-1} feed. This fresh make-up water was supplied directly into the tanks.

In addition to the hybrid aquaculture experimental platform, the experiment used the six freshwater flow-through tanks located in Laukaa fish farm and the six brackish water sea cages located in the Baltic Sea. The flow-through tanks (3 m^2) have been made of fibreglass with a water volume of 1000 L. The sea cages (16 m^2) had a water volume of 48,000 L.

2.2.2. Rearing conditions

Rearing conditions and water quality of the separate RAS environment used for hatching and starting of feeding was kept as constant as possible. Constant lighting was used because it is a common practice in commercial RAS farming. The monitored water quality parameters were temperature, oxygen (O_2), pH, total ammonia nitrogen (TAN), nitrite nitrogen (NO_2^--N), and nitrate nitrogen (NO_3^--N). The temperature, O_2, and pH were monitored constantly. The temperature was 14.2 °C ± 0.5 °C (mean ± standard deviation). The O_2 levels remained between 8.0 mg L^{-1} and 10.0 mg L^{-1}. The pH was 7.12 ± 0.47. The TAN, NO_2^--N, and NO_3^--N were monitored (Procedure 8038 Nessler, LCK341/342, and LCK340 respectively. DS 3900, Hach Lange, Loveland, USA) every two weeks. The TAN was 0.58 mg L^{-1} ± 0.64 mg L^{-1}. The NO_2^--N was 0.04 mg L^{-1} ± 0.03 mg L^{-1}. The NO_3^--N was 21.6 mg L^{-1} ± 11.2 mg L^{-1}.

In the RAS environments used for the experiment, rearing conditions and water quality parameters were kept as constant as possible. Constant lighting was used because it is a common practice in commercial RAS farming. The water quality parameters monitored were temperature, O_2, chemical oxygen demand (CODCr), carbon dioxide (CO_2), pH, TAN, NO_2^--N, NO_3^--N, and total suspended solids (TSS) (Table 1). The

Table 1
Water quality parameters (mean ± SD) in the recirculating aquaculture system (RAS) and the partial recirculating aquaculture system (PRAS) during the experiment.

Water quality parameter	RAS	PRAS
Temperature (°C)	14.1 ± 1.4	14.1 ± 1.2
O_2 (mg L^{-1})	9.2 ± 4.9	8.5 ± 0.8
CODCr (mg L^{-1})	76.3 ± 3.5	under detection limit
CO_2 (mg L^{-1})	7.5 ± 2.0	9.3 ± 2.2
pH	6.91 ± 0.51	6.74 ± 0.27
TAN (mg L^{-1})	1.74 ± 1.40	1.58 ± 0.54
NO_2^--N (mg L^{-1})	0.37 ± 0.89	0.05 ± 0.02
NO_3^--N (mg L^{-1})	38.8 ± 14.2	0.7 ± 0.4
TSS (mg L^{-1})	30.0 ± 2.0	3.8 ± 0.1

temperature (Fig. 2), O_2, CO_2, and pH were monitored daily. The TAN, NO_2^--N, and NO_3^--N were monitored twice a week. Water samples for CODCr and TSS were taken once (13 June 2022) and sent to a commercial laboratory (Eurofins Environment Testing Finland Oy, Jyväskylä, Finland).

In the RAS tanks, fish density was from 13.8 kg m^{-3} to 59.3 kg m^{-3} (Fig. 1). In the PRAS tanks, the fish density was from 20.7 kg m^{-3} to 94.8 kg m^{-3} (Fig. 1). The densities used are typical for each of the systems (Summerfelt et al., 2004; Roque d'Orbcastel et al., 2009).

Weather conditions in the study area did not vary in a way that is not reflected in water temperature and O_2 levels. Thus, key abiotic and environmental parameters for the experiment were lighting and water temperature and O_2 levels. The freshwater flow-through tanks followed the natural light cycle. Temperature and O_2 of freshwater were monitored daily. The freshwater temperature was 15.6 ± 1.9 °C during a summer period and 8.1 ± 1.6 °C during an autumn period (Fig. 2). O_2 was 8.1 ± 0.8 mg L^{-1} during the summer period and 9.5 ± 0.6 mg L^{-1} during the autumn period. In the freshwater flow-through tanks, the fish density was from 7.0 kg m^{-3} to 22.0 kg m^{-3} (Fig. 1).

Similarly to the freshwater flow-through system, key abiotic and environmental parameters for the experiment were lighting and water temperature and O_2 levels in the brackish water sea cages. The brackish water sea cages followed natural light cycle. Temperature and O_2 levels of brackish water were monitored constantly. The brackish water temperature was 18.5 ± 1.9 °C during the summer period and 12.9 ± 1.3 °C during the autumn period (Fig. 2). The O_2 levels remained >8.0 mg L^{-1} during the experimental periods. In the brackish water sea cages, the fish density was from 0.1 kg m^{-3} to 0.5 kg m^{-3} (Fig. 1).

2.2.3. *Feeding*

Fish were fed using a commercial feeding system (Arvo-Tec T Drum 2000, Arvo-Tec Oy, Joroinen, Finland) and commercial feed (Orbit 9030. BioMar, Aarhus, Denmark). The feeding was visual observed daily during an observation period and adjusted if necessary. The fish were fed until visual satiation and overfeeding was avoided. Uneaten pellets were not collected, but the number of uneaten pellets was considered negligible. Different feeding rhythms were used in the RAS, PRAS, and freshwater tanks and the brackish water sea cages.

Due to the constant lighting in the RAS environments, the fish were fed around the clock. In the RAS environments, the feeders fed 45 % of the daily feed during 00:00–12:00, 10 % during 12:01–12:15 (the observation period) and 45 % during 12:16–23:59. In September, the 10 % of daily feed during the observation period was too small amount of the feed to observe the appetite. This is why the feeding rhythm was changed so that the feeders fed 20 % instead of 10 % during the observation period.

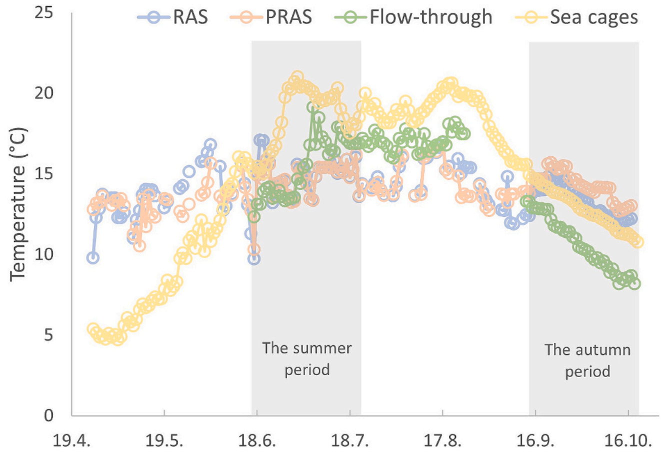

Fig. 2. Fig. 2. Temperatures (°C) in different farming environments during the experiment. The temperatures (°C) in RAS, PRAS, flow-through system, and sea cages are marked with blue, pink, green, and yellow, respectively. Experimental periods (summer and autumn periods) are marked with grey. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Due to the natural light cycle in the freshwater flow-through tanks, the fish were fed during the light period. In the freshwater flow-through tanks, the feeders fed 45 % of the daily feed during 07:00–12:15, 10 % during 12:16–12:30 (the observation period) and 45 % during 12:31–22:00. In September, feeding was also increased from 10 % to 20 % during the observation period because the 10 % was too small amount of the feed for the appetite observation.

In brackish water sea cages, feeders fed 25 % of the daily feed during 06:00–06:20, 25 % during 08:00–08:20 and 50 % during 11:00–11:20. This feeding rhythm was designed based on both to correspond to common practices in commercial sea cage farming, and to be able to monitor the feeding activity.

The fish were fasted for two days before the transfers and samplings.

2.3. *Growth parameters*

Feed conversion ratio (FCR), condition factor (CF), specific growth rate (SGR), and thermal-unit growth rate (TGC) were calculated based on the total biomasses per fish tanks for each treatment in the summer and autumn periods. Following formulas were used for the calculations: FCR = weight of feed offered in g/wet weight gain in g; CF = $(W * L^{-3}) * 100$, where W = body weight in g and L = total length in cm; SGR = $(\ln W_2 - \ln W_1)/(t_2 - t_1) * 100$, where W_2 = end weight of fish in g, W_1 = initial weight of fish in g, t_2 = end day of experimental period, and t_1 = start day of experimental period; and TGC = $((W_2^{1/3} - W_2^{1/3})/(T°C * (t_2 - t_1))) * 1000$, where W_2 = end weight of fish in g, W_1 = initial weight of fish in g, $T°C$ = heat sum, t_2 = end day of experimental period, and t_1 = start day of experimental period.

2.4. *Fish sampling*

The fish from the RAS and PRAS tanks, freshwater flow-through tanks, and brackish water sea cages were sampled after the summer and autumn periods. The samples were taken from five fish per tank. Thus, 15 fish were sampled for each group.

The sample fish were sacrificed for samplings by an overdose of anaesthetic (Tricaine Pharmaq 1000 mg g^{-1}, PHARMAQ Ltd., Fordingbridge, Hampshire, UK). First, a 2 % stock solution of anaesthetic was prepared by mixing 20 g anaesthetic in 1 L of water. The stock solution was then buffered (pH 7) with sodium hydrogen carbonate. For the fish in the brackish water sea cages, the stock solution was not buffered because the brackish water acts as a buffer. To euthanise the fish, 360 mL of 2 % stock solution was mixed with 30 L of water.

Total length (cm), weight (g) and gutted weight (g) of the sample fish were measured. Heart and liver were also weighed (g) to investigate possible pathological differences.

A blood sample was taken from the caudal vein using a heparinised needle. A haematocrit (%) sample was taken from the blood sample by using a haematocrit capillary. The haematocrit capillaries were centrifuged for 5 min (10,000 rcf). The haematocrit was then determined using a haematocrit reader.

The blood sample was then placed on ice to wait for centrifugation. The blood samples were centrifuged for 6 min (8979 rcf). Plasma osmolality (mOsmol kg^{-1}) was determined with an osmometer (K—7400S Semi-Micro Osmometer, Knauer, Berlin, Germany), chloride content (mmol L^{-1}) with a chloride titrator (Chloride Analyser 926 S, Sherwood, Cambridge, UK) and cortisol content (ng mL^{-1}) with a commercial EIA kit (Cortisol ELISA kit, Enzo Life Sciences Inc., New York, USA). The plasma cortisol content was measured only in the autumn period, because there were more significant differences (see Results: 3.2 The autumn period) in fish growth during the autumn period.

After the samplings, the sample fish were frozen, and the frozen fish were crushed. The mass was then freeze-dried and ground into powder. After the freeze-drying, the moisture content (%) of the fish was determined. The mass was then sent to a commercial laboratory (SGS Finland Oy, Helsinki, Finland) for the fat content (%) determination.

Experiment was carried out in compliance with the act on the Protection of Animals Used for Scientific or Educational Purposes (497/2013) and was approved by the national Project Authorisation Board in Finland (license number: ESAVI/27149/2022).

2.5. Statistical analyses

The data were pre-processed using Microsoft Excel (Microsoft Corporation, 2024, Redmond, Washington, USA). Means of measured response variables were calculated for each tank or cage, and then the tank or the cage could be used as an experimental unit.

Statistical analyses were performed using RStudio (R Core Team, 2024, Vienna, Austria). First, linear models were constructed in which each response variable was explained by an origin (RAS or PRAS), a location (RAS, flow-through system or sea cages) and an interaction between origin and location. A two-way ANOVA was then performed on each linear model to test the effect of origin, location and the interaction between origin and location on growth and physiological status of rainbow trout. Finally, a Tukey's test was used for pairwise mean comparisons. The threshold for statistical significance was set at $p < 0.05$.

3. Results

3.1. The summer period

In the overall model for the summer period, the origin of the fish significantly affected the initial and end weight as well as weight gain, FCR, TGC, CF, fat, and moisture content of the fish (Table 2A and 2B). The location of the fish significantly affected the end weight, weight gain, FCR, SGR, TGC, CF, fat and moisture content, relative weight of liver and heart, osmolality, chloride content, and survival of the fish (Table 2A and 2B). The interaction between the origin and the location significantly affected the end weight, weight gain, SGR, TGC, and chloride content of the fish (Table 2A and 2B).

3.1.1. The RAS originated fish in the different locations

3.1.1.1. The RAS originated fish in the RAS and the flow-through system. The RAS originated fish grew significantly better (SGR 34 %, TGC 37 %, $p < 0.001$, Table 2A and 2B) in the flow-through system than in the RAS. The RAS originated fish also gained significantly more weight (60 %, $p < 0.001$, Table 2A and 2B) in the flow-through system than in the RAS during the summer period, and the fish were significantly heavier (32 %, $p < 0.001$, Table 2A and 2B) in the flow-through system at the end of the summer period. The FCR was significantly lower (15 %, $p = 0.008$, Table 2A and 2B) in the flow-through system. For the other growth parameters of RAS originated fish, we did not observe significant differences between the RAS and the flow-through system.

Of the physiological parameters, the fat content of the RAS originated fish was significantly higher (9 %, $p = 0.028$, Table 2A and 2B) in the flow-through system than in the RAS, while the moisture content was significantly lower (3 %, $p = 0.006$, Table 2A and 2B) in the flow-through system. For the other physiological parameters of the RAS originated fish, we did not observe significant differences between the RAS and the flow-through system.

3.1.1.2. The RAS originated fish in the RAS and the sea cages. The RAS originated fish grew significantly better (SGR 27 %, $p < 0.001$, Table 2A and 2B) in the sea cages than in the RAS. The RAS originated fish also gained significantly more weight (57 %, $p < 0.001$, Table 2A and 2B) in the sea cages than in the RAS during the summer period, and the fish were significantly heavier (28 %, $p < 0.001$, Table 2A and 2B) in the sea cages at the end of the summer period. The FCR was significantly lower (14 %, $p = 0.014$, Table 2A and 2B) in the sea cages. The CF was significantly higher (14 %, $p = 0.019$, Table 2A and 2B) in the sea cages than in the RAS. For the other growth parameters of RAS originated fish, we did not observe significant differences between the RAS and the sea cages. Of the physiological parameters, only the plasma osmolality was significantly higher (3 %, $p = 0.003$, Table 2A and 2B) in the sea cages than in the RAS.

3.1.1.3. The RAS originated fish in the flow-through system and the sea cages. The RAS originated fish grew significantly better (TGC 30 %, $p < 0.001$, Table 2A and 2B) in the flow-through system than in the sea cages. For the other growth parameters of RAS originated fish, we did not observe significant differences between the flow-through system and the sea cages.

Of the physiological parameters, the fat content of the RAS originated fish was significantly higher (12 %, $p = 0.007$, Table 2A and 2B) in the flow-through system than in the sea cages. The plasma osmolality was significantly lower (5 %, $p < 0.001$, Table 2A and 2B) in the flow-through system. For the other physiological parameters of the RAS

Table 2A

Results of the summer period. Mean (± SD) values from the summer period where rainbow trout from freshwater RAS (Recirculating Aquaculture System) and freshwater PRAS (Partial Recirculating Aquaculture System) were transferred to freshwater flow-through system and brackish water sea cages. Significant values are bolded.

Location	RAS environments		Flow-through system		Sea cages		*p*-values		
Origin	RAS	PRAS	RAS	PRAS	RAS	PRAS	Origin	Location	Origin & Location
Sample fish	15	15	15	15	15	15			
Initial weight (g)	35.0 ± 0.3	43.9 ± 1.9	34.9 ± 0.8	43.2 ± 1.4	33.6 ± 0.1	42.7 ± 1.5	**p < 0.001**	0.192	0.863
End weight (g)	73.2 ± 1.4	107.9 ± 4.9	96.5 ± 3.4	117.6 ± 3.5	93.4 ± 0.9	108.5 ± 1.6	**p < 0.001**	**p < 0.001**	**p < 0.001**
Weight gain (g)	38.1 ± 1.2	64.0 ± 3.3	61.6 ± 2.8	74.4 ± 4.0	59.8 ± 0.9	65.8 ± 0.7	**p < 0.001**	**p < 0.001**	**p < 0.001**
FCR	0.91 ± 0.06	0.95 ± 0.03	0.77 ± 0.01	0.87 ± 0.06	0.78 ± 0.02	0.80 ± 0.03	**0.009**	**p < 0.001**	0.267
SGR (%)	2.30 ± 0.04	2.81 ± 0.07	3.08 ± 0.07	3.03 ± 0.14	2.92 ± 0.03	2.67 ± 0.07	0.072	**p < 0.001**	**p < 0.001**
TGC (%)	0.19 ± 0.00	0.26 ± 0.01	0.26 ± 0.01	0.27 ± 0.01	0.20 ± 0.00	0.20 ± 0.00	**p < 0.001**	**p < 0.001**	**p < 0.001**
CF	1.08 ± 0.06	1.14 ± 0.06	1.18 ± 0.09	1.24 ± 0.14	1.23 ± 0.08	1.28 ± 0.08	**0.023**	**p < 0.001**	0.995
Fat content (%)	32.2 ± 0.6	35.0 ± 0.5	35.3 ± 1.6	35.6 ± 0.9	31.6 ± 0.3	33.3 ± 1.5	**0.005**	**p < 0.001**	0.152
Moisture content (%)	70.8 ± 0.4	70.1 ± 0.1	69.2 ± 0.4	68.9 ± 0.1	70.2 ± 0.7	69.7 ± 0.5	**0.038**	**p < 0.001**	0.772
Relative weight of liver (%)	0.84 ± 0.10	0.91 ± 0.11	0.91 ± 0.12	0.86 ± 0.09	0.79 ± 0.11	0.80 ± 0.15	0.747	**0.020**	0.230
Relative weight of heart (%)	0.13 ± 0.02	0.13 ± 0.02	0.15 ± 0.02	0.13 ± 0.02	0.12 ± 0.02	0.11 ± 0.02	0.137	**0.006**	0.810
Haematocrit (%)	52 ± 7	50 ± 7	50 ± 7	49 ± 6	45 ± 5	48 ± 5	0.830	0.128	0.445
Osmolality (mOsmol kg^{-1})	321 ± 8	319 ± 9	315 ± 11	316 ± 10	332 ± 8	338 ± 11	0.158	**p < 0.001**	0.077
Chloride (mmol L^{-1})	136 ± 3	131 ± 4	135 ± 12	140 ± 9	143 ± 7	143 ± 7	0.958	**p < 0.001**	**0.038**
Survival (%)	95 ± 2	93 ± 3	98 ± 2	96 ± 3	99 ± 0	100 ± 0	0.239	**p < 0.001**	0.237

Table 2B
p-values for the results of the summer period. Significant values are bolded.

	RAS originated fish in different locations			PRAS originated fish in different locations			RAS and PRAS originated fish in same location		
	RAS vs. flow-through system	RAS vs. sea cages	Flow-through system vs. sea cages	PRAS vs. flow-through system	PRAS vs. sea cages	Flow-through system vs. sea cages	RAS environments	Flow-through	Sea cages
Initial weight	1.000	0.705	0.766	0.983	0.810	0.990	**<0.001**	**<0.001**	**<0.001**
End weight	**<0.001**	**<0.001**	0.785	**0.017**	1.000	**0.026**	**<0.001**	**<0.001**	**<0.001**
Weight gain	**<0.001**	**<0.001**	0.939	**0.003**	0.941	**0.012**	**<0.001**	**<0.001**	0.093
FCR	**0.008**	**0.014**	1.000	0.158	**0.006**	0.391	0.747	0.071	0.956
SGR	**<0.001**	**<0.001**	0.182	**0.040**	0.274	**<0.001**	**<0.001**	0.973	**0.019**
TGC	**<0.001**	0.720	**<0.001**	0.622	**<0.001**	**<0.001**	**<0.001**	0.236	0.948
CF	0.147	**0.019**	0.812	0.172	**0.024**	0.830	0.624	0.682	0.703
Fat content	**0.028**	0.960	**0.007**	0.974	0.342	0.116	**0.049**	0.998	0.361
Moisture content	**0.006**	0.596	0.094	**0.034**	0.854	0.218	0.471	0.957	0.744
Relative weight of liver	0.636	0.812	0.125	0.902	0.185	0.656	0.677	0.875	1.000
Relative weight of heart	0.633	0.629	0.072	0.981	0.506	0.209	0.992	0.704	0.968
Haematocrit	0.925	0.206	0.658	1.000	0.987	0.998	0.915	1.000	0.948
Osmolality	0.105	**0.003**	**<0.001**	0.563	**<0.001**	**<0.001**	0.976	0.995	0.122
Chloride	0.997	0.155	0.076	**0.028**	**0.003**	0.696	0.287	0.445	1.000
Survival	0.427	0.245	0.998	0.236	**0.005**	0.239	0.578	0.820	0.973

originated fish, we did not observe significant differences between the flow-through system and the sea cages.

3.1.2. *The PRAS originated fish in the different locations*

3.1.2.1. The PRAS originated fish in the PRAS and the flow-through system. The PRAS originated fish grew significantly better (SGR 8 %, $p = 0.040$, Table 2A and 2B) in the flow-through system than in the PRAS. The PRAS originated fish also gained significantly more weight (16 %, $p = 0.003$, Table 2A and 2B) in the flow-through system than in the PRAS during the summer period, and the fish were significantly heavier (9 %, $p = 0.017$, Table 2A and 2B) in the flow-through system at the end of the summer period. For the other growth parameters of the PRAS originated fish, we did not observe significant differences between the PRAS and the flow-through system.

Of the physiological parameters, the moisture content of the PRAS originated fish was significantly lower (1 %, $p = 0.034$, Table 2A and 2B) in the flow-through system than in the PRAS. The plasma chloride content was higher (7 %, $p = 0.028$, Table 2A and 2B) in the flow-through system. For the other physiological parameters of the PRAS originated fish, we did not observe significant differences between the PRAS and the flow-through system.

3.1.2.2. The PRAS originated fish in the PRAS and the sea cages. The PRAS originated fish grew significantly less (TGC 33 %, $p < 0.001$, Table 2A and 2B) in the sea cages than in the PRAS. The FCR was significantly lower (16 %, $p = 0.006$, Table 2A and 2B) in the sea cages. The CF (12 %, $p = 0.024$, Table 2A and 2B) was higher in the sea cages. For the other growth parameters of the PRAS originated fish, we did not observe significant differences between the PRAS and the sea cages.

Of the physiological parameters, the plasma osmolality (6 %, $p < 0.001$, Table 2A and 2B) and the plasma chloride content (9 %, p = 0.003, Table 2A and 2B) were significantly higher in the sea cages than in the PRAS. For the other physiological parameters of the PRAS originated fish, we did not observe significant differences between the PRAS and the sea cages. In addition, survival of the PRAS originated fish was significantly better (8 %, $p = 0.005$, Table 2A and 2B) in the sea cages.

3.1.2.3. The PRAS originated fish in the flow-through system and the sea cages. The PRAS originated fish grew significantly better (SGR 8 %, TGC 35 %, $p < 0.001$, Table 2A and 2B) in the flow-through system than in the sea cages. The PRAS originated fish also gained significantly more weight (13 %, $p = 0.012$, Table 2A and 2B) in the flow-through system than in the sea cages during the summer period, and the fish were significantly heavier (8 %, $p = 0.026$, Table 2A and 2B) in the flow-through system at the end of the summer period. For the other growth parameters of the PRAS originated fish, we did not observe significant differences between the flow-through system and the sea cages. Of the physiological parameters, only the plasma osmolality was significantly lower (7 %, $p < 0.001$, Table 2A and 2B) in the flow-through system than in the sea cages.

3.1.3. *The RAS and the PRAS originated fish in the same location*

3.1.3.1. The RAS and the PRAS originated fish in the different RAS environments. At the beginning of the summer period, the initial weight of the PRAS originated fish was significantly higher (25 %, p < 0.001, Table 2A and 2B) than the initial weight of the RAS originated fish in the different RAS environments. The PRAS originated fish grew significantly better (SGR 22 %, TGC 37 %, $p < 0.001$, Table 2A and 2B) than the RAS originated fish in the different RAS environments. The PRAS originated fish also gained significantly more weight (68 %, $p < 0.001$, Table 2A and 2B) than the RAS originated fish during the summer period, and the PRAS originated fish were significantly heavier (47 %, $p < 0.001$, Table 2A and 2B) at the end of the summer period. For the other growth parameters of the RAS and the PRAS originated fish, we did not observe significant differences in the different RAS environments. Of the physiological parameters, only the fat content of the PRAS originated fish was significantly higher (9 %, $p = 0.049$, Table 2A and 2B) than the fat content of the RAS originated fish.

3.1.3.2. The RAS and the PRAS originated fish in the flow-through system. At the beginning of the summer period, the initial weight of the PRAS originated fish was significantly higher (24 %, $p < 0.001$, Table 2A and 2B) than the initial weight of the RAS originated fish in the flow-through system. The PRAS originated fish also gained significantly more weight (21 %, $p < 0.001$, Table 2A and 2B) than the RAS originated fish during the summer period, and were significantly heavier (22 %, $p < 0.001$, Table 2A and 2B) at the end of the summer period. For the other parameters of the RAS and the PRAS originated fish, we did not observe significant differences in the flow-through system.

3.1.3.3. The RAS and the PRAS originated fish in the sea cages. At the beginning of the summer period, the initial weight of the PRAS originated fish was significantly higher (27 %, $p < 0.001$, Table 2A and 2B) than the initial weight of the RAS originated fish in the sea cages. The RAS originated fish grew significantly better (SGR 9 %, $p = 0.019$, Table 2A and 2B) than the PRAS originated fish, although the PRAS originated fish were still significantly heavier (16 %, $p < 0.001$, Table 2A and 2B) at the end of the summer period. For the other parameters of the RAS and the PRAS originated fish, we did not observe significant differences in the sea cages.

3.2. *The autumn period*

In the overall model for the autumn period, similarly to the summer period, the origin of the fish significantly affected the initial and end weight as well as TGC, CF, fat, and moisture content of the fish (Table 3A and 3B). During the autumn period, the origin also affected significantly the SGR and the survival of the fish (Table 3A and 3B). Contrary to the summer period, origin did not significantly affect the weight gain and the FCR during the autumn period (Table 3A and 3B, see also Discussion).

Again, similarly to the summer period, the location of the fish significantly affected the end weight, weight gain, SGR, TGC, CF, fat and moisture content, relative weight of the liver and the heart, and chloride content of the fish (Table 3A and 3B). During the autumn period, location also affected significantly the haematocrit (Table 3A and 3B). Contrary to the summer period, the location did not significantly affect the FCR, osmolality, and survival of the fish during the autumn period (Table 3A and 3B).

Similarly to the summer period, the interaction between the origin and the location of the fish significantly affected the end weight, weight gain, SGR, TGC, and chloride content of the fish during the autumn period (Table 3A and 3B).

3.2.1. *The RAS originated fish in the different locations*

3.2.1.1. The RAS originated fish in the RAS and the flow-through system. The moisture content of RAS originated fish was significantly lower (10 %, $p < 0.001$, Table 3A and 3B) in the flow-through system than in the RAS at the end of the autumn period. The relative weight of the heart was significantly higher (18 %, $p = 0.027$, Table 3A and 3B) in the flow-through system. For the other parameters of the RAS originated fish, we did not observe significant differences between the RAS and the flow-through system.

3.2.1.2. The RAS originated fish in the RAS and the sea cages. The RAS originated fish grew significantly better (SGR 295 %, TGC 283 %, $p < 0.001$, Table 3A and 3B) in the RAS than in the sea cages. The RAS originated fish also gained significantly more weight (346 %, $p < 0.001$, Table 3A and 3B) in the RAS during the autumn period, and were significantly heavier (46 %, $p < 0.001$, Table 3A and 3B) in the RAS at the end of the autumn period. The CF of the RAS originated fish was also significantly higher (16 %, $p = 0.001$, Table 3A and 3B) in the RAS. For the other growth parameters of the RAS originated fish, we did not observe significant differences between the RAS and the sea cages.

Of the physiological parameters, the fat (21 %, $p = 0.002$, Table 3A and 3B) and the moisture content (6 %, $p < 0.001$, Table 3A and 3B) of the RAS originated fish were significantly higher in the RAS than in the sea cages. On the other hand, the plasma chloride content was significantly lower (8 %, $p = 0.009$, Table 3A and 3B) in the RAS. For the other physiological parameters of the RAS originated fish, we did not observe significant differences between the RAS and the sea cages.

3.2.1.3. The RAS originated fish in the flow-through system and the sea cages. The RAS originated fish grew significantly better (SGR 270 %, TGC 333 %, $p < 0.001$, Table 3A and 3B) in the flow-through system than in the sea cages. The RAS originated fish also gained significantly more weight (306 %, $p < 0.001$, Table 3A and 3B) in the flow-through system during the autumn period, and were significantly heavier (37 %, $p < 0.001$, Table 3A and 3B) in the flow-through system at the end of the autumn period. The CF of the RAS originated fish was significantly higher (19 %, $p < 0.001$, Table 3A and 3B) in the flow-through system than in the sea cages. For the other growth parameters of the RAS originated fish, we did not observe significant differences between the flow-through system and the sea cages.

Of the physiological parameters, the fat content of the RAS originated fish was significantly higher (23 %, $p < 0.001$, Table 3A and 3B) in the flow-through system than in the sea cages, while the moisture

Table 3A

Results of the autumn period. Mean (± SD) values from the autumn period where rainbow trout from freshwater RAS (Recirculating Aquaculture System) and freshwater PRAS (Partial Recirculating Aquaculture System) were transferred to freshwater flow-through system and brackish water sea cages. Significant values are bolded.

Location	RAS environments		Flow-through system		Sea cages		p-values		
Origin	RAS	PRAS	RAS	PRAS	RAS	PRAS	Origin	Location	Origin & Location
Sample fish	15	15	15	15	15	15			
Initial weight (g)	190.8 ± 10.5	289.5 ± 14.7	181.9 ± 3.7	277.3 ± 9.8	187.2 ± 10.1	295.2 ± 14.6	**p < 0.001**	0.183	0.609
End weight (g)	313.5 ± 16.2	463.7 ± 15.1	293.6 ± 9.3	400.8 ± 19.7	214.8 ± 14.9	288.0 ± 11.0	**p < 0.001**	**p < 0.001**	**0.003**
Weight gain (g)	122.7 ± 5.8	174.2 ± 19.3	111.7 ± 6.4	123.5 ± 10.5	27.6 ± 5.3	−7.2 ± 5.5	0.070	**p < 0.001**	**p < 0.001**
FCR	1.45 ± 0.31	1.46 ± 0.19	1.28 ± 0.03	1.41 ± 0.10	1.46 ± 0.22	−9.19 ± 11.2	0.129	0.110	0.103
SGR (%)	1.46 ± 0.02	1.39 ± 0.16	1.37 ± 0.05	1.05 ± 0.05	0.37 ± 0.05	−0.07 ± 0.05	**p < 0.001**	**p < 0.001**	**0.006**
TGC (%)	0.23 ± 0.00	0.23 ± 0.03	0.26 ± 0.01	0.23 ± 0.01	0.06 ± 0.01	−0.01 ± 0.01	**p < 0.001**	**p < 0.001**	**0.003**
CF	1.29 ± 0.06	1.41 ± 0.10	1.32 ± 0.13	1.39 ± 0.10	1.11 ± 0.10	1.13 ± 0.07	**0.003**	**p < 0.001**	0.162
Fat content (%)	37.9 ± 0.4	42.5 ± 1.2	38.3 ± 1.1	42.5 ± 1.3	31.2 ± 0.4	31.0 ± 3.0	**p < 0.001**	**p < 0.001**	0.083
Moisture content (%)	66.6 ± 0.0	64.9 ± 0.6	60.2 ± 0.5	58.8 ± 0.1	62.7 ± 0.3	61.7 ± 0.5	**p < 0.001**	**p < 0.001**	0.274
Relative weight of liver (%)	0.99 ± 0.13	1.00 ± 0.13	1.02 ± 0.10	0.97 ± 0.11	0.82 ± 0.09	0.73 ± 0.11	0.155	**p < 0.001**	0.484
Relative weight of heart (%)	0.11 ± 0.01	0.12 ± 0.01	0.13 ± 0.01	0.13 ± 0.01	0.12 ± 0.01	0.11 ± 0.01	0.666	**0.001**	0.403
Haematocrit (%)	45 ± 5	47 ± 6	50 ± 6	49 ± 8	39 ± 3	41 ± 7	0.631	**0.003**	0.673
Osmolality (mOsmol kg^{-1})	311 ± 12	320 ± 18	321 ± 16	315 ± 14	308 ± 10	310 ± 8	0.661	0.162	0.240
Chloride (mmol L^{-1})	125 ± 6	134 ± 4	133 ± 8	129 ± 8	136 ± 4	136 ± 5	0.160	**0.007**	**0.010**
Cortisol (ng mL^{-1})	6 ± 6	7 ± 5	7 ± 6	7 ± 6	8 ± 7	9 ± 5	0.199	0.705	0.488
Survival (%)	97 ± 3	100 ± 0	98 ± 0	100 ± 0	99 ± 1	100 ± 0	**0.013**	0.400	0.400

content was significantly lower (5 %, $p < 0.001$, Table 3A and 3B) in the flow-through system. The relative weight of the liver (24 %, $p = 0.023$, Table 3A and 3B) and the blood haematocrit (28 %, $p = 0.027$, Table 3A and 3B) were significantly higher in the flow-through system. For the other physiological parameters of the RAS originated fish, we did not observe significant differences between the flow-through system and the sea cages.

3.2.2. *The PRAS originated fish in the different locations*

3.2.2.1. The PRAS originated fish in the PRAS and the flow-through system. The PRAS originated fish grew significantly better (SGR 32 %, $p = 0.002$, Table 3A and 3B) in the PRAS than in the flow-through system. The PRAS originated fish also gained significantly more weight (41 %, $p < 0.001$, Table 3A and 3B) in the PRAS during the autumn period, and were significantly heavier (16 %, $p = 0.002$, Table 3A and 3B) in the PRAS at the end of the autumn period. For the other growth parameters of PRAS originated fish, we did not observe significant differences between the PRAS and the flow-through system. Of the physiological parameters, only the moisture content of the PRAS originated fish was significantly higher (10 %, $p < 0.001$, Table 3A and 3B) in the PRAS than in the flow-through system.

3.2.2.2. The PRAS originated fish in the PRAS and the sea cages. The PRAS originated fish grew significantly better in the PRAS than in the sea cages ($p < 0.001$, Table 3B). In the PRAS, the fish continued to grow (SGR 1.39, TGC 0.23, Table 3A), while in the sea cages, the fish did not eat and subsequently lost weight (SGR -0.07, TGC -0.01, Table 3A). Thus, the PRAS originated fish gained significantly more weight in the PRAS (174.2 g, Table 3A) than in the sea cages (-7.2 g, Table 3A) during the autumn period ($p < 0.001$, Table 3B). At the end of the autumn period, the PRAS originated fish were significantly heavier (66 %, $p < 0.001$, Table 3A and 3B) in the PRAS than in the sea cages. The CF of the PRAS originated fish was also significantly higher (25 %, $p < 0.001$, Table 3A and 3B) in the PRAS. For the other growth parameters of PRAS originated fish, we did not observe significant differences between the PRAS and the sea cages.

Of the physiological parameters, the fat (33 %, $p < 0.001$, Table 3A and 3B) and the moisture content (5 %, $p < 0.001$, Table 3A and 3B) of the PRAS originated fish were significantly higher in the PRAS than in the sea cages. The relative weight of the liver was also significantly higher (37 %, $p = 0.003$, Table 3A and 3B) in the PRAS. For the other physiological parameters of the PRAS originated fish, we did not observe significant differences between the PRAS and the sea cages.

3.2.2.3. The PRAS originated fish in the flow-through system and the sea cages. The PRAS originated fish grew significantly better in the flow-through system than in the sea cages ($p < 0.001$). In the flow-through system, the fish continued to grow (SGR 1.05, TGC 0.23, Table 3A and 3B), while in the sea cages, the fish did not eat and subsequently lost weight (SGR -0.07, TGC -0.01, Table 3A and 3B). Thus, the PRAS originated fish gained significantly more weight in the flow-through system (123.5 g, Table 3A) than in the sea cages (-7.2 g, Table 3A) during the autumn period ($p < 0.001$, Table 3B). At the end of the autumn period, the PRAS originated fish were significantly heavier (39 %, $p < 0.001$, Table 3A and 3B) in the flow-through system than in the sea cages. The CF of the PRAS originated fish was also significantly higher (23 %, $p < 0.001$, Table 3A and 3B) in the flow-through system. For the other growth parameters of the PRAS originated fish, we did not observe significant differences between the flow-through system and the sea cages.

Of the physiological parameters, the fat content of the PRAS originated fish was significantly higher (33 %, $p < 0.001$, Table 3A and 3B) in the flow-through system than the sea cages, while the moisture content was significantly lower (5 %, $p < 0.001$, Table 3A and 3B) in the flow-through system. The relative weight of the liver was also significantly higher (33 %, $p = 0.009$, Table 3A and 3B) in the flow-through system. For the other physiological parameters of the PRAS originated fish, we did not observe significant differences between the flow-through system and the sea cages.

3.2.3. *The RAS and the PRAS originated fish in the same location*

3.2.3.1. The RAS and the PRAS originated fish in the different RAS environments. At the beginning of the autumn period, the initial weight of the PRAS originated fish was significantly higher (52 %, $p < 0.001$, Table 3A and 3B) than the initial weight of the RAS originated fish in the different RAS environments. The PRAS originated fish also gained significantly more weight (41 %, $p < 0.001$, Table 3A and 3B) than the RAS originated fish during the autumn period, and were significantly heavier (48 %, $p < 0.001$, Table 3A and 3B) at the end of the autumn period. The CF of PRAS originated fish was also significantly higher (9 %, $p = 0.028$, Table 3A and 3B) in the RAS environments. For the other growth parameters, we did not observe significant differences between

Table 3B
p-values for the results of the autumn period. Significant values are bolded.

	RAS originated fish in different locations			PRAS originated fish in different locations			RAS and PRAS originated fish in same location		
	RAS vs. flow-through system	RAS vs. sea cages	Flow-through system vs. sea cages	PRAS vs. flow-through system	PRAS vs. sea cages	Flow-through system vs. sea cages	RAS environments	Flow-through	Sea cages
Initial weight	0.919	0.998	0.991	0.763	0.986	0.415	**<0.001**	**<0.001**	**<0.001**
End weight	0.585	**<0.001**	**<0.001**	**0.002**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.001**
Weight gain	0.763	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.713	**0.012**
FCR	1.000	1.000	1.000	1.000	0.113	0.116	1.000	1.000	0.114
SGR	0.697	**<0.001**	**<0.001**	**0.002**	**<0.001**	**<0.001**	0.855	**0.004**	**<0.001**
TGC	0.128	**<0.001**	**<0.001**	0.997	**<0.001**	**<0.001**	1.000	0.090	**<0.001**
CF	0.865	**0.001**	**<0.001**	0.991	**<0.001**	**<0.001**	**0.028**	0.385	0.961
Fat content	0.999	**0.002**	**<0.001**	1.000	**<0.001**	**<0.001**	**0.024**	**0.048**	0.991
Moisture content	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.002**	**0.010**	0.089
Relative weight of liver	0.991	0.061	**0.023**	0.989	**0.003**	**0.009**	1.000	0.878	0.596
Relative weight of heart	**0.027**	0.774	0.223	0.178	0.983	0.062	0.780	1.000	0.982
Haematocrit	0.538	0.399	**0.027**	0.980	0.460	0.181	0.990	0.997	0.977
Osmolality	0.594	0.996	0.343	0.939	0.611	0.978	0.682	0.890	0.999
Chloride	0.054	**0.009**	0.890	0.444	0.907	0.105	**0.027**	0.675	0.999
Cortisol	0.998	1.000	1.000	0.912	0.998	0.729	0.999	0.507	1.000
Survival	0.969	0.409	0.823	1.000	1.000	1.000	0.174	0.486	0.988

the RAS and the PRAS originated fish in the different RAS environments.

Of the physiological parameters, the fat content of the PRAS originated fish was significantly higher (12 %, $p = 0.024$, Table 3A and 3B) than the fat content of the RAS originated fish, while the moisture content of PRAS originated fish was significantly lower (3 %, $p = 0.002$, Table 3A and 3B). The plasma chloride content of the PRAS originated fish was also significantly higher (7 %, $p = 0.027$, Table 3A and 3B). For the other physiological parameters, we did not observe significant differences between the RAS and the PRAS originated fish in the different RAS environments.

3.2.3.2. The RAS and the PRAS originated fish in the flow-through system. At the beginning of the autumn period, the initial weight of the PRAS originated fish was significantly higher (52 %, $p < 0.001$, Table 3A and 3B) than the initial weight of the RAS originated fish in the flow-through system. The PRAS originated fish grew significantly less (29 %, $p = 0.004$, Table 3A and 3B) than the RAS originated fish, but the PRAS originated fish were still significantly heavier (36 %, $p < 0.001$, Table 3A and 3B) than the RAS originated fish at the end of autumn period. For the other growth parameters, we did not observe significant differences between the RAS and the PRAS originated fish in the flow-through system.

Of the physiological parameters, the fat content of the PRAS originated fish was significantly higher (11 %, $p = 0.048$, Table 3A and 3B) than the fat content of the RAS originated fish, while the moisture content was significantly lower (2 %, $p = 0.010$, Table 3A and 3B). For the other physiological parameters, we did not observe significant differences between the RAS and the PRAS originated fish in the flow-through system.

3.2.3.3. The RAS and the PRAS originated fish in the sea cages. At the beginning of the autumn period, the initial weight of the PRAS originated fish was significantly higher (58 %, $p < 0.001$, Table 3A and 3B) than the initial weight of the RAS originated fish in the sea cages. The PRAS originated fish grew significantly less than the RAS originated fish ($p < 0.001$, Table 3B). The RAS originated fish continued to grow (SGR 0.37, TGC 0.06, Table 3A), while the PRAS originated fish did not eat and lost weight (SGR -0.07, TGC -0.01, Table 3A). The RAS originated fish gained significantly more weight than the PRAS originated fish during the autumn period ($p = 0.012$, Table 3B). The RAS originated fish gained weight 27.6 g (Table 3A), while the PRAS originated fish lost weight 7.2 g (Table 3A). However, the PRAS originated fish were still significantly heavier (34 %, $p = 0.001$, Table 3A and 3B) at the end of the autumn period. For the other parameters, we did not observe significant differences between RAS- and PRAS-farmed fish in the sea cages.

4. Discussion

Saltwater transfer plays an important role in salmonid production, where juveniles are produced on land in freshwater and transferred after smoltification to the saltwater for the rest of their life (Thorstad et al., 2012; van Rijn et al., 2021). Unlike Atlantic salmon, rainbow trout do not require both fresh and saltwater environments for rearing. Nevertheless, this practice is commonly followed in Finland, where majority (approximately 90 %) of grow-out production is done in sea cage farming (Ministry of the Environment, 2020). This study investigated the transfer of two different sizes of rainbow trout from two different RAS environments to freshwater flow-through system and brackish water sea cages. Contrary to the hypothesis, the larger rainbow trout (from 200 to 300 g), transferred in the autumn, had difficulties adapting to the brackish water cage farming. Therefore, combining these two production methods is not straightforward and more studies are needed.

In general, the results of the rearing experiment were in line with those reported in the literature: FCR (from 0.77 to 0.95 during the summer period and from 1.28 to 1.46 during the autumn period), SGR (from 2.30 to 3.08 during the summer period and from 1.05 to 1.46 during the autumn period), and TGC (from 0.19 to 0.27 during the summer period and from 0.23 to 0.26 during the autumn period) are typical for rainbow trout of this size (Austreng et al., 1987; Davidson et al., 2014; Pulkkinen et al., 2019). Both CF (from 1.08 to 1.28 during the summer period and from 1.11 to 1.41 during the autumn period) and fish fat (from 31.6 to 35.6 % during the summer period and from 31.0 to 42.5 % during the autumn period) and moisture content (from 68.9 to 70.8 % during the summer period and from 58.8 to 66.6 % during the autumn period) were also typical for rainbow trout (Storebakken and Austreng, 1987). The most striking exception was the results for PRAS originated fish in the brackish water sea cages during the autumn period. Despite the continuous offering of the feed, the fish did not eat and therefore lost weight. This is reflected in the negative FCR and the significant differences in CF, fat and moisture content. In the overall model, the origin significantly affected the survival during the autumn period because some RAS originated fish died while PRAS originated fish did not. However, the survival rate of RAS originated fish was high, and therefore there were no significant differences on the pairwise tests.

4.1. Water quality in initial farming

Firstly, we explored whether the water quality in initial farming (the RAS or the PRAS) influences the success of transfers. Our water quality results in initial farming are mostly within the recommended limits for temperature (from 14.0 to 16.0 °C), O_2 (at least from 6.0 to 8.0 mg L^{-1}), CO_2 (< 20.0 mg L^{-1}), pH (from 6.5 to 8.5), TAN (< 1.0 mg L^{-1}), NO_2^--N (< 0.1 mg L^{-1}), NO_3^--N (< 75.0 mg L^{-1}), and TSS (< 25.0 mg L^{-1}, Timmons et al., 2018). The exceptions were the TAN results, the NO_2^--N. results in the RAS, and the TSS results in the RAS. Even though our TAN (1.74 mg L^{-1} in the RAS and 1.58 mg L^{-1} in the PRAS) and NO_2^--N (0.37 mg L^{-1} in the RAS) results were slightly above the recommended limits, these values have also reported in the literature (von Ahnen et al., 2018; Pulkkinen et al., 2019). In addition, although TAN values were slightly high, the pH was quite low, meaning that levels of free, toxic unionised ammonia (NH_3) were not harmful to fish. The slightly high total suspended solid levels (30.0 mg L^{-1}) was due to technical problems with the drum filter. Elevated TSS levels could increase bacterial load in the RAS (Pedersen et al., 2017), which can be harmful, especially to stressed fish (Bullock et al., 1997; Vadstein et al., 2004; Attramadal et al., 2014). However, Becke et al. (2019) found no evidence for bacterially mediated physiological stress in rainbow trout reared in RAS.

The water quality parameters such as nitrogen compounds and TSS were better in the PRAS than in the RAS. Nevertheless, there was no significant difference in the growth of the RAS and the PRAS originated fish (flow-through system, summer period) or the RAS originated fish grew better (sea cages, summer period and flow-through system and sea cages, autumn period). This could be explained by compensatory growth of RAS originated fish, because there were significant differences in the initial weight between the RAS and the PRAS originated fish. Therefore, our results support that the water quality in the initial farming in itself had no effect on the fish growth after the transfers.

4.2. Feeding behaviour and growth

Secondly, we wanted to explore whether the growth of rainbow trout differ in the different rearing environments after transfers. During the summer period, the RAS originated fish had the lowest growth in the RAS environment. This was probably due to the slightly high TSS levels. The high TSS levels generally indicate a deterioration in water quality, which may have affected fish growth (Pulkkinen et al., 2018), although the high TSS levels have not been found to affect in itself rainbow trout growth and welfare (Becke et al., 2018; Becke et al., 2019).

Both the PRAS originated fish during the summer period and the RAS and the PRAS originated fish during the autumn period had the lowest growth in the sea cages. The salinity in the Baltic Sea is quite close to the physiological salinity of rainbow trout (Sakamoto and McCormick, 2006; Feistel et al., 2008; Al-Jandal and Wilson, 2011). According to Morgan and Iwama (1991) rainbow trout grow equally well in fresh and salt water with a salinity of 9 ‰, but as the salinity increases to 18 ‰, their growth decreases significantly from 52 to 53 %. Therefore, the brackish water as such should not have posed a challenge for growth of rainbow trout, and other environmental conditions could have a larger influence on growth. On the other hand, Tsintsadze (1991) found that rainbow trout growth is fastest at salinities of from 15 to 18 ‰ (the highest salinity tested in the experiment) and decreases significantly as salinity decreases. So, varied results have been obtained on the growth of rainbow trout at different salinities.

During the summer period, the plasma osmolality of the fish was slightly (from 3 to 7 %) higher in the brackish water sea cages than in the freshwater RAS, PRAS, or flow-through system. When fish are transferred from fresh to saltwater, more ions passively flow into the fish increasing osmolality, and the fish must start actively excreting the ions (McCormick, 2024). So, it is typical for the osmolality to increase when rainbow trout are transferred from fresh to saltwater (Jackson, 1981; Al-Jandal and Wilson, 2011). Otherwise, there were no significant differences with a clear pattern in the physiological parameters. Thus, stress does not seem to explain the differences in the feeding behaviour that resulted in low growth. According to Finstad et al. (1988), direct transfer of rainbow trout from fresh to saltwater should be successful up to salinities of 26 ‰ without visible signs of stress. So, our results seem to be in line with the earlier literature in this respect.

The constant lighting was used in the initial farming, because it is the common practice in RAS farming. The constant lighting (and feeding) aims to maintain a constant yield of fish metabolites, thus eliminating the need to plan the water treatment system according to the feeding peaks. This maintains constant water quality, which is believed to benefit the fish welfare and the performance of RAS. However, constant lighting has been shown to affect the fish physiology. For example, it has been found to impair the immune response of rainbow trout (Leonardi and Klempau, 2003; Goldstein et al., 2023). Light cycles have been shown to affect the growth of rainbow trout in freshwater (Taylor et al., 2005), but no effect on saltwater adaptation has been found with different light cycles (Morro et al., 2019). In addition, Ytrestøyl et al. (2023) found that the use of constant lighting in RAS does not have adverse effects on growth or mortality in saltwater. In our experiment, we observed low growth only in the brackish water sea cages, not in the freshwater flow-through system. Therefore, we do not believe that the continuous lighting in the initial farming alone explains low growth in the brackish water sea cages.

The natural lighting was used in the freshwater flow-through system and in the brackish water sea cages. The flow-through tanks were much shallower than the sea cages. Thus, it is possible that the depth of the sea cages and the resulting sudden darkness after transfers from continuous lighting environments (the RAS and the PRAS) negatively affected the feeding behaviour, resulting in low growth.

Other factors that could affect the results were different densities and feeding rhythms in the different rearing environments. There were even smaller densities and same feeding rhythm during the summer period than during the autumn period and the growth (SGR from 2.30 to 3.08, TGC from 0.19 to 0.27) was similar to those previously reported (Austreng et al., 1987; Davidson et al., 2014; Pulkkinen et al., 2019), whereas the growth was low during the autumn period. Therefore, we do not believe that those factors affected our results.

4.3. *Fish size and timing of transfers*

This study shows that the size of rainbow trout and timing of transfers affects the growth of rainbow trout. Fish size affects ability of fish to adapt to environmental changes (Ricker, 1976; Sogard, 1997). For example, larger rainbow trout individuals have been found to tolerate salt water better than smaller ones (Parry, 1958). Smaller fish are more sensitive to environmental changes (Ricker, 1976; Sogard, 1997), which could be expected to negatively affect feeding behaviour and growth. Thus, the growth of smaller fish after environmental change could be hypothesised to be weaker. However, the size is not the only factor that determines whether fish can adapt to saltwater. For example, the onset of Na^+/K^+-ATPase in the gills, kidney, and gut is important for saltwater adaptation (McCormick, 2024).

We observed the smaller rainbow trout transferred in the summer grew better than the larger rainbow trout transferred in autumn. The larger rainbow trout have lived in the RAS and PRAS environments for longer and have been used to those conditions. This may have made it more difficult for the larger fish to adapt to changes in environmental conditions. There are only a few studies on this topic, but a similar phenomenon has also been observed in other salmonids. For example, 100 g and 200 g Atlantic salmon smolts grew better in seawater than 600 g salmon smolts after transfer from RAS (Ytrestøyl et al., 2023), although the size differences are bigger than in our study.

On the other hand, feeding behaviour and growth is not only influenced by fish size but also by the seasonal environmental conditions that fish face after transfer to new environment. In this experiment, the smaller fish were transferred to the new farming environments when the water warmed up and the lighting increased (the summer period), whereas the larger fish were transferred when the water cooled down and the lighting decreased (the autumn period). We believe that the transfer from the stable environments to the environments with varying circadian and annual rhythms affects the fish physiology. Therefore, successful growth and achieved fish size in stable RAS environments (14.1 ± 1.4 °C in RAS and 14.1 ± 1.2 °C in PRAS and constant lighting) do not automatically guarantee good growth in further farming environments.

In our experimental set-up, we could not fully separate the effects of the fish size and the timing of the transfer. However, the fish transferred to the freshwater flow-through system in autumn grew well. Thus, the causes for the refusal to eat and extremely low growth found in the brackish water sea cages during the autumn period remain yet to be fully investigated. We hypothesise that the fish size (desmoltification), the salty water, the falling temperature, and the shortening day possibly induced winter signal for the fish in the brackish water sea cages (Morro et al., 2019).

5. Conclusions

We found that larger rainbow trout reared in stable RAS or PRAS environments had difficulties adapting to the brackish water cage farming. Our results support that the water quality (RAS vs PRAS) during the initial farming does not itself influence the success of transfers, whereas the fish size and timing of transfer seem to do so. However, there are many uncertainties associated with the transfer performed in autumn. In the future, studies could explore our results further, with a need for mechanistic and physiological understanding. Understanding the reasons behind current problems would allow a wider use of combined RAS and sea cage farming. It would also allow development of new, more efficient and sustainable production cycles and strategies, adapted to different needs. The developing production cycles and strategies could also potentially increase fish production and better meet the increasing demand for fish.

CRediT authorship contribution statement

Jonna Hänninen: Writing – original draft, Visualization, Methodology, Investigation. **Jani Pulkkinen:** Writing – review & editing, Visualization, Methodology, Investigation, Conceptualization. **Harri Vehviläinen:** Writing – review & editing, Visualization, Project administration, Funding acquisition.

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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Data availability

Data will be made available on request.

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