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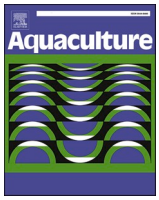

Understanding how winter conditions in the North Atlantic affect the physiology and behaviour of Atlantic Salmon in sea-cages

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ABSTRACT

In recent years there have been a number of instances where declines in water temperature are suspected to have contributed to winter mortalities at salmon cage-sites in Atlantic Canada. In addition, it is expected that temperature variability due to more intense and frequent winter storms will increase with climate change, and this may further threaten Atlantic salmon health and welfare in sea-cages. To better understand cage-site conditions and aspects of salmon behaviour and physiology during the winter, we fitted Atlantic salmon in commercial size sea-cages in Newfoundland (Canada) for two consecutive years with internal and external data storage tags (DSTs) that recorded depth, temperature, heart rate (f_H) and 3D-acceleration (swimming activity). Tags were surgically attached / implanted in late October / early November when water temperatures were 8–10 °C, and the DSTs were collected at the time of harvest. Although tag retrieval was limited due to some early mortality, challenges due to Covid-19 and with fish identification during harvest, the data collected for both years were comparable.

Water temperature decreased at a rate of 0.35–0.57 °C week^{-1} from October / November to March, and the coolest average weekly temperature experienced by the fish was 1.10 °C in early March of both years. Average f_H decreased with temperature starting in the fall, and the fish primarily occupied the upper 5 m of the cage for the duration of this study, despite the fact that temperatures were generally homogeneous with depth. Nonetheless, vertical migrations to deeper depths were observed during some periods (e.g., at night during the coldest months), and thus, the average depth of the fish was greater during these times.

These data reveal that temperatures in sea-cages in Newfoundland remain below 5 °C for ~5 months and are below 2 °C for ~1.5 months. Thus, understanding how cold temperatures affect various aspects of salmon biology, and monitoring these fish during this period, is critical to the sustainability and future of this industry.

1. Introduction

With the stagnation of global fisheries landings, the aquaculture industry currently provides approximately half of the world's seafood (FAO, 2022). Further, the global demand for seafood is rapidly rising, and the aquaculture sector will need to increase production levels considerably to meet consumer needs (Cai and Leung, 2017). The Atlantic salmon (*Salmo salar*) is amongst the top five most economically important aquaculture finfish species worldwide (FAO, 2022), and is the main species produced by the Canadian aquaculture industry. This production is primarily in British Columbia, New Brunswick, and Newfoundland and Labrador.

In Newfoundland (Canada), production was anticipated to more than double from ~20,000 metric tonnes (MT) to 50,000 MT by 2030 ("Support Growth of the Aquaculture Industry to 50,000 MT Annually for Salmon and 10,750 MT Annually for Mussels – The Way Forward", 2018). This was largely due to the significant expansion of the existing industry (Northern Harvest Sea Farms / MOWI Canada East and Cold

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Ocean Salmon / Cooke Aquaculture Inc.), but also the arrival of Grieg Seafood NL Ltd. in the province. Despite this, production has declined since its peak in 2013 (Government of Newfoundland, 2022) due to a number of challenges that are common across the salmon aquaculture sector including sea lice, viral and bacterial pathogens, and unfavourable environmental conditions such as extreme seasonal temperatures (Barange et al., 2018; Burke et al., 2020; Calado et al., 2021; Falconer et al., 2020, 2022; Gagné and Leblanc, 2018; Islam et al., 2022; Reid et al., 2019).

There has been significant attention devoted to understanding the consequences of climate change on salmon aquaculture and assessing strategies to mitigate these impacts, with the primary foci being rising average sea temperatures, hypoxia (reductions in water oxygen levels), and marine heat waves (Anttila et al., 2015; Beemelmanns et al., 2021a, 2021b; Gamperl et al., 2020, 2021; Ignatz et al., 2023; Stehfest et al., 2017). Surprisingly, however, there has been little effort to understand the impacts of cold temperatures (< 5 °C) on salmon physiology until recently (Liu et al., 2020; Porter et al., 2022: Porter and Gamperl, 2023; Tang et al., 2022; Vadboncoeur et al., 2023a, 2023b). This is despite the fact that winter storms are predicted to increase in frequency and intensity (IPCC, 2022), and these storms can lead to episodes where deeper waters mix with cold surface waters resulting in rapid reductions in temperature (Johnson et al., 2018; Szekeres et al., 2016; U.S. Global Change Research Program, 2017). Further, Atlantic Canada's salmon aquaculture industry has observed several recent 'winter chill' mortality events (i.e., in 2014, 2015, 2019). In the past it was presumed that 'winter chill' mortality is associated with temperatures below 0 °C which cause blood and tissues to freeze, however, other factors such as disease, stress and overcrowding may also be contributing factors (Huffman, 2019; CBC News, 2020; Pennell, 2014; The Canadian Press, 2015; Círíc, 2020; Vadboncoeur et al., 2023a, 2023b).

Monitoring fish health, welfare and behaviour at aquaculture sites, particularly in winter, can be challenging given the number of fish in a cage, sea ice cover, rough seas and winter storm events. However, valuable insights can be gained from the long-term, continuous, monitoring of animals that are exposed to natural and aquaculture-related stressors. Recent advancements in the development of bio-loggers [also known as data storage tags (DSTs)] have allowed for the monitoring of a variety of environmental and physiological parameters in aquaculture-reared salmonids including depth, temperature, heart rate and acceleration / activity (Føre et al., 2018; Gamperl et al., 2021), and provided valuable information on the stress and physiological responses induced by various aquaculture procedures (e.g., crowding, brailing, transport, euthanasia; Brijs et al., 2018, 2019; Føre et al., 2021; Hvas et al., 2020) and their behavioural and physiological responses to extremes in summer water temperatures (Gamperl et al., 2021). However, to date, there have been no investigations on specifically how winter conditions in the North Atlantic affect the physiology and behaviour of salmon reared at commercial scale sea-cages. This research has recently been made more feasible by the development of DSTs that can record ECGs for longer durations (e.g., at 100 Hz for 15 s; https://www.star-oddi.com; Garðabær, Iceland), and thus, are capable of accurately determining heart rate (f_H) at cold temperatures (i.e., down to ~10 beats min^{-1}). In this study, we implanted salmon with Star-Oddi HRT-ACT [that measure heart rate, 3-D acceleration (swimming activity) and temperature] DSTs and externally attached milli-TD (that measure temperature and depth) DSTs at two commercial sea-cage sites in Newfoundland, with the goals of: 1) documenting what temperatures sea-caged salmon actually experience (and potentially avoid) during this period; and 2) better understanding their physiology, distribution and behaviour when they are exposed to the coldest temperatures (< 5 °C) of the year.

2. Methods

This study was approved by the Animal Care Committee of Memorial University of Newfoundland and Labrador (protocol #20–03-KG), and experimental procedures were performed in accordance with the Canadian Council on Animal Care Guidelines on the 'Care and Use of Fish in Research, Teaching and Testing' (https://ccac.ca/Documents/Standards/Guidelines/Fish.pdf).

2.1. Location and fish husbandry

Farmed Atlantic salmon (*Salmo salar*), originally of Saint John River Stock (New Brunswick, Canada), were reared in commercial sea-cages ~2 km apart on either side of a fjord in the Bay D'Espoir (Site #1: 2020–2021 and Site #2: 2021–2022; Supplemental Fig. 1) on the south coast of Newfoundland, Canada. These fish were reared using typical aquaculture protocols and stocking density in circular sea-cages [150 m circumference, 20 m depth (with extended conical bottom to 30 m)] and fed to satiation daily using a surface mounted automated (pneumatic) feeding system. Mortality dives were conducted weekly by the company. This research was conducted in collaboration with Cold Ocean Salmon, a subsidiary of Cooke Aquaculture Inc. (CAI).

2.2. Data storage tags

2.2.1. DST specifications

The externally attached milli-TD DSTs (weight in air, 12 g; diameter, 13 mm; length, 39.4 mm) record temperature (−3 to 40 °C; accurate to ±0.1 °C and depth (0 to 100 m; accurate to 0.6 %). The internally implanted milli-HRT ACT DSTs (weight in air, 12 g; diameter, 13 mm; length, 39.5 mm) record ECGs (for 15 s) and f_H, tri-axial acceleration (resolution ±2 m-g) and temperature (0 to 45 °C; accurate to 0.2 °C). Custom ordered milli-HRT ACT DSTs were used at Site #1. These DSTs had centi-HRT housings (larger casing: weight in air, 19 g; diameter, 15 mm; length, 46 mm) and battery, and this increased the battery life of the DST, the manufacturer later released these loggers as DST centi-HRT ACT G2. Time recorded from both tags is accurate to ±1-min $month^{-1}$. All tags were produced by Star-Oddi, and combined, did not exceed 2.2 % of the salmon's body weight.

2.2.2. DST programming and preparation

Prior to implantation, the tags were inserted into Star-Oddi's communication interface (COM-BOX) and connected to a computer. Sea Star (v. 8.55) and Mercury (v. 5.59) (Star-Oddi) software were then used to program the milli-TD and milli-HRT ACT DSTs, respectively. The start date, sampling time intervals and frequencies were set using this software. Mercury (v. 5.63) was used to calculate sampling intervals for the milli-HRT ACT-custom DSTs using centi-HRT ACT G2 as the selected recorder type. The DSTs were set to begin recording on October 27th, 2020 (Site #1) and November 1st, 2021 (Site #2) at 12:00:00 AM Newfoundland Standard Time (UTC-3:30). The milli-TD tags were set to record depth and temperature at 5-min intervals. The milli-HRT ACT custom tags (used at Site #1) were set to record heart rate (f_H) (100 Hz for 15 s: saving the raw ECG every 6 h), temperature and acceleration (10 Hz for 600 s, saving raw acceleration data every 42 h) every 1 h, whereas the milli-HRT tags (used at Site #2) were set to record f_H (100 Hz for 15 s: saving the raw ECG every 6 h), temperature and acceleration (1 Hz for 60 s, saving raw acceleration data every 42 h) every 2 h.

The milli-HRT ACT DSTs were prepared for implantation by tying two 30 cm pieces of non-sterile 2–0 silk suture around the tag, with the knots secured and stationed directly over the front sensor and directly behind the back sensor so that the loose ends were approximately the same length. The milli-TD DSTs were prepared using the tag holder kit provided by Star-Oddi which includes two plastic molds and two silicone pads. The milli-TD DSTs were prepared for attachment by: looping two pre-sterilized pieces of 30 cm stainless steel (1/8 hard T316L, 0.02″ diameter, Malin Co., Brookpark, OH) wire over the tag, and passing the ends of the wire through one of the kit's silicone pads and the pre-drilled holes in the kit's plastic mold; and by attaching the DST to one of the

plastic molds (which has a cut-out for the tag) using stainless steel wire (see Zrini and Gamperl, 2021). All DSTs were sterilized with 70 % ethanol, and the milli-HRT ACT DSTs with attached silk suture were soaked in sterile seawater prior to implantation.

2.2.3. Surgical implantation / attachment

On October 26th, 2020, twenty-three pre-adult Atlantic salmon in two sea-cages at Site #1 [average mass of 1.68 ± 0.07 kg (range 1.15 to 2.36 kg) and a fork length of 52.35 ± 0.53 cm (range 47.4 to 57.2 cm)] were implanted with an external DST ($n = 5$) or internal and external DSTs ($n = 18$). On November 1st, 2021, twelve Atlantic salmon in one sea-cage at Site #2 [average mass of 4.66 ± 0.26 kg (range 3.2 to 6.04 kg) and a fork length of 69.63 ± 2.01 cm (range 50.5 to 76 cm)] were implanted with an external DST ($n = 2$) or internal and external DSTs ($n = 10$). Tagging occurred when surface temperatures at the cage-site were ~ 8–10 °C.

A box seine (~1.5 m long x 3.5 m wide x 1.5 m deep) attached to the inside border of the sea-cage was used to aid in the netting of fish for tagging and for holding tagged fish for up to 24 h post-surgery. Fish were individually netted from the box seine into a fish tote (~1.5 m long x 1.5 m wide x 1.5 m deep) supplied with a continuous flow of seawater. Individual fish were then netted and anesthetized in seawater containing 0.2 g L^{-1} tricaine methanesulfonate (Syncaine TMS, Syndel Laboratories Canada, Nanaimo, BC, Canada), had their mass and fork length recorded after loss of equilibrium, and were immediately transferred to a surgical table where they were placed in a supine (ventral side up) position on a wetted sponge. Throughout the surgery, the salmon's gills were irrigated with seawater containing 0.1 g L^{-1} TMS delivered from an oxygenated reservoir. To begin surgery, lidocaine hydrochloride (Hospira Healthcare Corp. Kirkland, QC, Canada) was administered subcutaneously (1 mg kg^{-1}) along the location of the intended incision (dose divided between 3 and 4 injections). A short mid-ventral incision (~2–3 cm), at the posterior limit of the base of the pectoral fins, was made in the fish's body wall using a scalpel, and cotton swabs were used to stop any bleeding at the incision site. A milli-HRT ACT DST was then inserted, blunt end first, towards the posterior of the fish, and then pulled forward using the attached sutures to within 0.5 cm of the pericardium. A ½ circle, 28 mm, cutting edge needle (SE-MH 28, Mani Surgical Needles, Japan) was then used to pass the silk sutures through the body wall at the front and back of the incision to secure the tag and to start to close the incision. Finally, the incision was closed using 3–0 Prolene® suture (with 24 mm cutting needle) (8684G, J&J Ethicon Suture, San Lorenzo, Puerto Rico) and 4–7 interrupted stitches depending on the incision length. Vaseline® was applied to the incision to prevent water from entering the wound during initial recovery / healing.

Immediately following implantation of the milli-HRT ACT, the fish was turned over, and four pre-sterilized stainless steel hypodermic needles (15 gauge, 3.5″ long) were passed through the skin and muscle below the dorsal fin to allow the stainless-steel wire of the prepared milli-TD DST to be guided through the fish. Then, the hypodermic needles were removed and the 4 wires exiting the muscle were passed through the kit's other silicone pad and plastic mold. These wires were then twisted together to secure the DST to the fish (see Zrini and Gamperl, 2021).

Following tag insertion and attachment, all fish received an intraperitoneal injection of the antibiotic enrofloxacin (Baytril, Bayer; 10 mg kg^{-1}), and were recovered in a fish tote with aerated flowing seawater. This antibiotic was administered prophylactically to prevent bacterial infections at the site of the incision. The surgeries and associated procedures took ~15 min per fish, and the salmon were closely monitored until they began to swim freely and were then returned to the box seine inside the cage. After 24 h, the box seine was carefully lowered so that the fish could enter the main area of the sea-cage. There were no mortalities in the box seine (i.e., within 24 h post-surgery).

2.2.4. Tag retrieval and analysis

Weekly mortality dives were conducted by the cage-site staff. Cages at Site #1 were harvested in June and October of 2021, and Site #2 was harvested in March of 2022. The external milli-TD DSTs were used to identify experimental animals during harvest and mortality dives.

Data from the milli-HRT ACT and milli-TD tags were downloaded by putting them into a COM-BOX and using a computer with associated Star-Oddi software. Manual calculations of f_H and heart rate variability (HRV) were performed using the saved ECGs. To calculate f_H, the time between R wave peaks was measured (in seconds), averaged, and then 60 was divided by the average to obtain the fish's f_H in beats $minute^{-1}$ (bpm). HRV was calculated as the standard deviation of the time between successive R wave peaks (in ms). The milli-HRT ACT tag records when the sensor is measuring acceleration above standard gravity and the software calculates external acceleration (EA) as a vectoral sum dynamic of body acceleration, or VeDBA, (measured in m-g at 1 Hz for 60 s, where g is the acceleration of gravity or 9.8 m s^{-2}), which is then averaged over 1 min. In addition, the software performs a 360-degree static calibration on each DST for each of the axes. The Mercury software reports minimum, maximum and average EA values recorded over the 1-min sampling period. VAR is the variance in EA calculated as the standard deviation squared over a set sampling period (measured in m-g^2 at 1 Hz for 60 s). Values of VAR greater than 222 m-g^2 were used to identify when the fish were not constantly swimming, [i.e., they were engaged in burst-coast swimming (Zrini and Gamperl, 2021) or potentially struggling, etc.]

Graphing and statistical analyses were performed using Prism 10 (GraphPad Software Inc., San Diego, CA, USA). The depth and temperature recordings from the milli-TD were graphed both for each individual as well as the mean for each site. Weekly temperatures were calculated based on the milli-TD recordings at each site, and a linear regression between week and temperature was calculated until the lowest weekly temperature for each site was recorded. Daily temperature recordings for the depths of 1, 5, 10 and 15 m were provided by Cold Ocean Salmon (Cooke Aquaculture Inc.), and these data were plotted following the completion of each study. These daily recordings were also used to calculate weekly temperatures from the week of tagging until the lowest recorded temperatures, and linear regressions were fit to each depth. Average values of temperature, heart rate, HRV, EA and the percentage of non-steady swimming were calculated for each day and night. At each site, relationships between heart rate, HRV and EA versus temperature were calculated using linear regressions. Relationships between heart rate and external acceleration were also calculated at each site using the linear regressions.

3. Results

3.1. Fish recovery and tag retrieval

At Site #1 a total of 23 salmon were implanted with tags. A mortality dive conducted 10 days post-tagging recovered 3 fish with both milli-HRT ACT and milli-TD tags, and 15 days post-tagging an additional 2 fish were retrieved. However, the milli-HRT ACT tags were missing in these fish (Supplemental Table 1). Fish / tags were recovered by commercial divers so limited information on incision and fish condition were available. Additional fish were recovered ~1 month ($n = 2$) and ~ 2 months ($n = 1$) post-tagging with both tags recovered (Supplemental Table 1), leaving 15 tagged fish (65 % of those initially implanted) in the cages. The data for the salmon that died after 1 and 2 months in the cages were analyzed, and the f_H, activity, distribution and temperatures occupied did not differ to that obtained for the surviving fish for much of the time they were in the sea-cage. However, large vertical migrations, followed by a major drop in f_H, were observed in the days prior to the last viable f_H (Supplemental Fig. 2). No mortalities (fish or tags) were recovered during weekly dives at Site #2 (Supplemental Table 1), and thus, 12 tags could have potentially been recovered.

Harvest occurred in June and October 2021 at Site #1 and 3 fish (1 milli-HRT ACT and 3 milli-TD tags) and 1 fish (1 milli-TD and milli-HRT ACT tag missing) were recovered, respectively (Supplemental Table 1). Harvest at Site #2 occurred in March 2022 and 2 milli-HRT ACT and 1 milli-TD tags from 3 fish were recovered (1 tag was missing for each fish, Supplemental Table 1).

3.2. Data analysis and quality

Data of harvested fish was analyzed from the tag start time (October 27th, 2020 at 12:00 am NST) to April 1st, 2021 for Site #1 (156 days) and from November 1st, 2021 to March 24th, 2022 for Site #2 (142.5 days). During these periods 3744 and 1711 f_H measurements, and 534 and 497 associated ECG tracings, were recorded for Site #1 and Site #2, respectively. The quality of the f_H measurements were $QI_0 = 71.4 \pm 7.3$ %, $QI_1 = 27.7 \pm 7.6$ %, $QI_2 = 0.13 \pm 0.08$ %; $QI_3 = 0.84 \pm 0.4$ %. All saved ECGs had identifiable PQRS intervals, and therefore, could be used to manually calculate and validate f_H values determined by the software. Less than 1.5 % of f_H values were deemed outliers and removed (i.e., values <10 beats min^{-1} or > 200 beats min^{-1} or with a QI_2 or QI_3 indicating that the PQRS complex could not be identified by the software).

3.3. Temperatures and distribution

Temperature and depth were recorded by the externally attached milli-TD tags every 5 min for the duration of the study and totaled 44,928 and 41,040 measurements per fish at Site #1 ($n = 4$) and Site #2 ($n = 1$), respectively (Fig. 1, Supplemental Fig. 3). Water temperatures at tagging were ~ 8–10 °C, but decreased steadily following tagging. This temperature decrease averaged 0.35 and 0.57 °C $week^{-1}$ for Sites #1 and #2, respectively, until the lowest weekly temperature of 1.10 °C occurred in early March for both years (Fig. 2). Analysis of the data provided by Cold Ocean Salmon revealed a weekly decrease in temperature of 0.29–0.35 and 0.55–0.57 °C (depending on depth) for Site #1 and Site #2. On average, the temperature difference between 5 and 15 m was 0.36 ± 0.03 and 0.40 ± 0.03 °C at the two sites, respectively, while the difference between the temperature at these depths and at the surface (i.e., at 1 m) was 0.66 ± 0.05 and 1.08 ± 0.08 °C, respectively. The maximum daily difference recorded between depths was ~3.6 °C, with the temperature at the surface being colder (Fig. 3). Following the coolest temperature recorded in early March to the end of the analyzed period (April 1st / March 24th for Site #1 and Site #2, respectively), temperatures increased slightly, however they averaged ~1.7 °C (Figs. 2, Fig. 3, Supplemental Fig. 3). Collectively, these data reveal that temperatures at any depth within the sea-cages studied remained below 2 °C for ~1.5 months and below 5 °C for ~5 months (December to May;

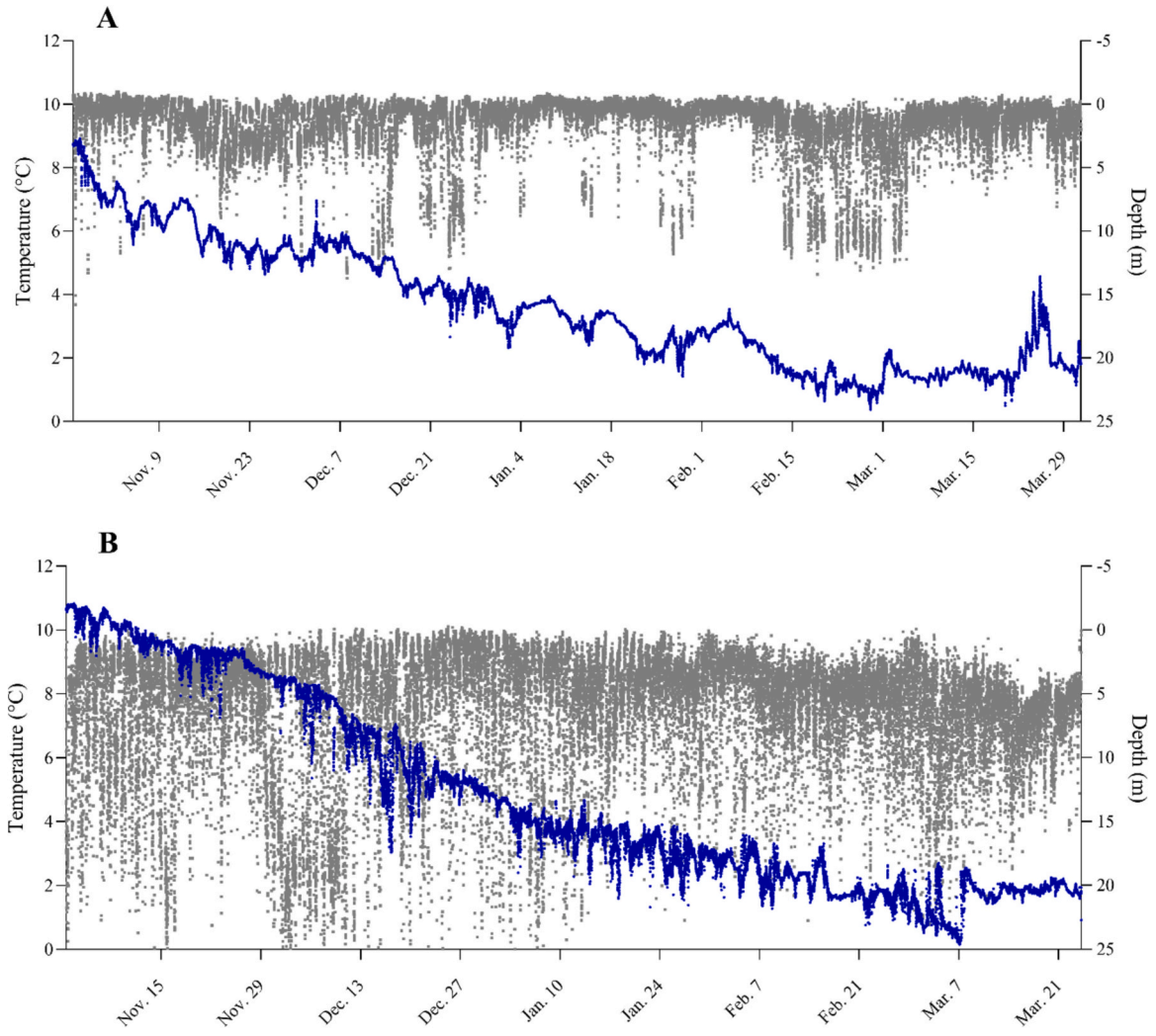

Fig. 1. Mean depth (gray) and temperature (blue) measured every 5 min in four fish (A) at Site #1 and one fish (B) at Site #2 fitted with milli-TD tags over the duration of the study. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

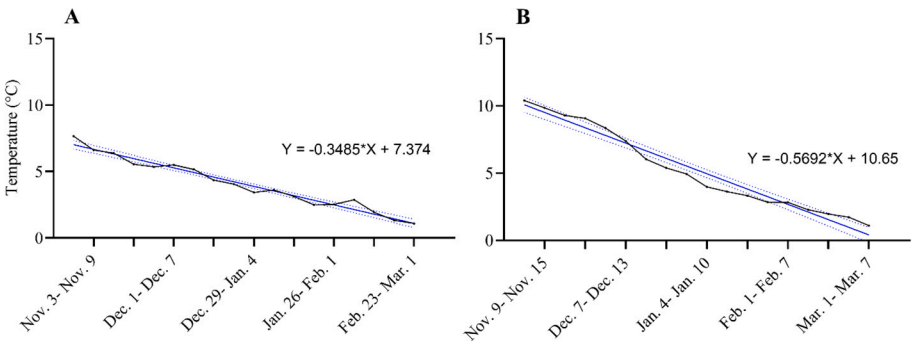

Fig. 2. Mean weekly cage-site temperatures recorded by milli-TD tags attached to (A) four fish at Site #1 and (B) one fish at Site #2 until the lowest weekly temperature. Linear regressions were calculated based on these data to determine the average weekly rate of temperature decline.

Fig. 3. Daily temperatures at 1, 5, 10 and 15 m at (A) Site #1 (2020/2021) and (B) Site #2 (2021/2022), as recorded by our industrial partner (Cold Ocean Salmon / Cooke Aquaculture Inc.).

see Supplemental Fig. 3 for data on sea-cage temperatures).

Although temperature steadily decreased over much of the experimental period, the salmon generally remained in the upper ~5 m of the sea-cage (Fig. 1, Fig. 4, Supplemental Fig. 3) at both Sites #1 and #2. While, on average, fish remained in the upper part of the sea-cage, they continued to frequent all depths throughout the study (Figs. 1 and 4, Supplemental Fig. 3). For several of the fish, this appeared to be at particular intervals / times [i.e., in November / December and when cage temperatures were ~ 2 °C (March – April)], but for the one fish that data was obtained for at Site #2, it was evident that it made excursions to the bottom of the cage throughout the study period (Fig. 1B). Feeding data provided by the company revealed that there were 10 days at Site #1 (Fig. 4) and 16 days at Site #2 (data not shown) where fish were not fed due to weather/operational challenges. These days did not have a clear impact on the fish's depth distribution. However, the salmon's overall depth preference had a diurnal pattern, with the tagged fish occupying deeper depths during the night and shallower depths during the day. This pattern was particularly evident in early March, when temperatures were the lowest, with the mean depth of the fish ~5 m deeper during the night (Fig. 4).

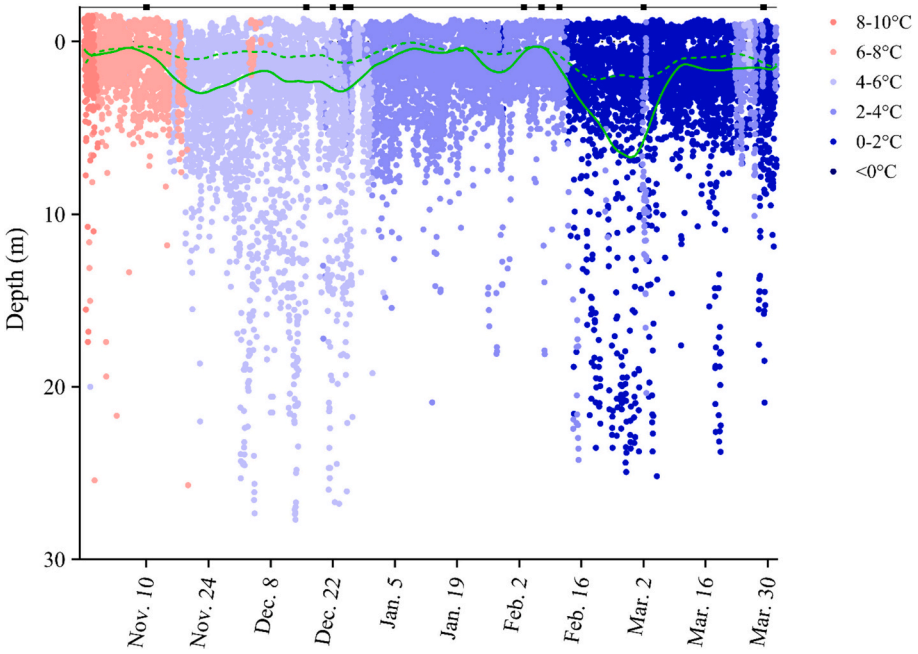

Fig. 4. Cage-site temperature at various depths over the duration of the study. The data were obtained from milli-TD tags that were attached to four Atlantic salmon at Site #1 (2020/2021). The Lowess curves (green) show the mean depth occupied by the salmon during the day (broken line) and night (solid line). The days fish were not fed due to weather/operational challenges are shown as black squares at the top of the figure. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.4. Heart rate and activity

At the beginning of this study, water temperatures were ~ 8 and 10 °C at Site #1 and Site #2, respectively, and f_H was ~50 beats minute^{-1}. Thereafter, the average heart rate closely followed the decrease in temperature. Heart rate was ~40 beats minute^{-1} when temperatures were ~ 5 °C and ~ 20 beats minute^{-1} at ~1–2 °C (Fig. 5). Indeed, the f_H and temperature relationships were highly significant when the data for all retrieved tags were combined (Fig. 6). While statistical analysis did not identify a diurnal pattern in f_H over the duration of this study, overall, heart rates were higher during the day-time in comparison with night-time values (Fig. 5, Supplemental Table 2). Although higher heart rate variability values (HRV) were observed at the beginning of the study, an overall relationship between HRV and temperature was not clearly identified (Fig. 6). External acceleration remained constant, between ~10 and 15 m-g, for the majority of the study. Finally, while a clear relationship was not identified between non-steady swimming and temperature, it appears that the fish regularly engaged in 'burst-coast swimming' and that this was more prevalent during the day-time (Fig. 5).

4. Discussion

The finfish aquaculture industry will continue to be impacted by climate change given the predicted increase in average seawater temperatures, and in the frequency and severity of storms and weather events. Year-round production in sea-cages in the North Atlantic means that temperature-related challenges are not confined to the warm summer waters, but also occur in the winter. Thus, additional knowledge and understanding of cage-site conditions during the winter is critical if the industry is to implement management strategies to mitigate issues with decreased production, and fish health and welfare.

4.1. Mortality and tag retrieval

In the immediate two weeks following surgery, a mortality rate of 22 % (based on retrieved mortalities) was observed at Site #1 (Supplemental Table 1), with an overall mortality of 35 %. This may be attributed to several factors. First, we had purchased 'centi-sized' HRT-ACT tags to take advantage of the additional battery capacity, and they were intended to be implanted into fish that were ~ 2.3 kg and larger. However, the fish available for this study were considerably smaller. We believe the size of the tags, combined with poor healing (i.e., due to the cool temperatures) and the limited recovery period (24 h), resulted in the loss of a number of internal tags and associated mortality. Further, tag attachment / surgery is associated with significant stress (Hvas et al., 2020; Macaulay et al., 2021; Wright et al., 2019), and elevated heart rates in free-swimming fish can be observed for up to 3 weeks post-surgery / implantation of DSTs (Føre et al., 2021; Hvas et al., 2020; Yousaf et al., 2022; Zrini and Gamperl, 2021).

No mortalities were retrieved at Site #2, and tags from only 3 out of the 12 tagged fish were retrieved at harvest. Similarly, there were 11 fish with tags not retrieved at Site #1. The missing fish / tags may not have been retrieved during the harvest (processing of the cages) as a result of lack of dentification of experimental fish and/or expelled tags. Also, there were health / environmental issues at both sites that resulted in significant mortalities, and at Site #2 these fish were 'pumped' out of the cage with limited opportunity for inspection of fish for DSTs. Finally, the tags were intended to be deployed for approximately 4–5 months, instead it took 238 and 363 days to completely harvest the cages at Site #1, and 142 days at Site #2. This extended period of deployment could have led to the loss of the external (milli-TD) tags, and thus, precluded the identification of tagged fish at harvest. This hypothesis would fit with Macaulay et al. (2021), who reported that while the mortality of tagged fish in sea-cages can be quite variable, their model predicted that mortality of tagged fish would be approximately 36 % at 100 days post-surgery. Collectively, the above highlights the difficulties that can arise from working in commercial sea-cages in the winter and deploying tags for extended periods of time. Further, it provides several insights that can be used to improve tag retrieval in the future.

4.2. Temperature

The tagging at Sites #1 and #2 occurred almost exactly one year

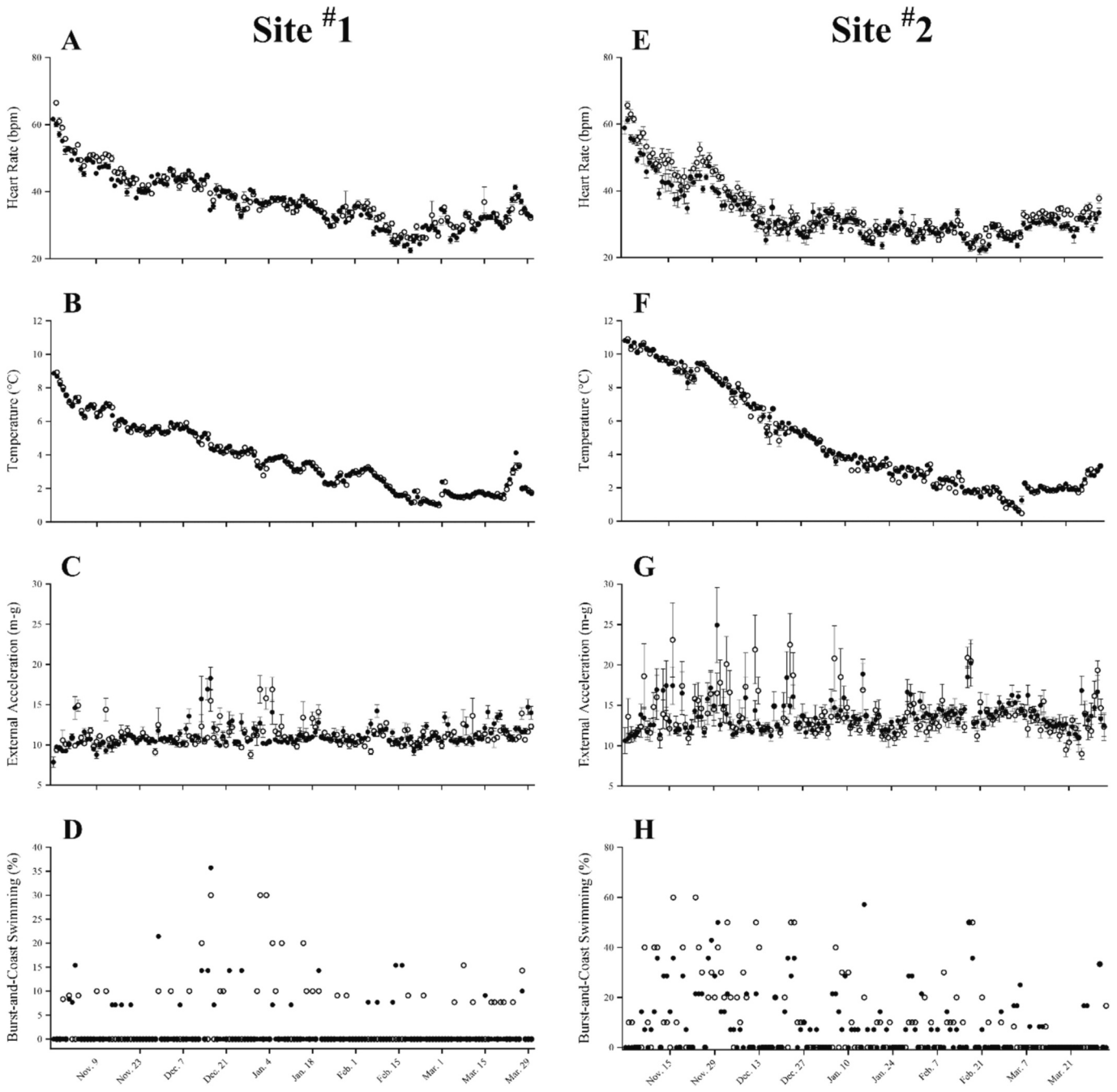

Fig. 5. Average day-time (open circles) and night-time (closed circles) values for heart rate (A, E), temperature (B, F), external acceleration (C, G) and the percentage of non-steady swimming (D, H) measured for (A) one fish at Site #1 and (B) two fish at Site #2.

apart. Temperatures at the time of tag implantation were quite comparable (8 °C vs. 10 °C), and a very similar decline in weekly mean temperatures occurred between November and March. These values were 0.35 and 0.57 °C week^{-1} based on the data obtained from milli-TD DSTs, and this was very similar to that obtained based on the aquaculture company's temperature logs. Overall, this study revealed that sea-cage temperatures are less than 5 °C for nearly half of a year's production cycle, and below 2 °C for approximately 1.5 months. Thus, in Newfoundland, these cool / cold water temperatures can have significant impacts on fish health and production, and the time that the salmon must remain in the cages prior to harvest. For example, Vadboncoeur et al. (2023a) recently performed a lab-based study on post-smolt salmon from these same stocks that mimicked the fall/early winter temperatures experienced in this study (a decrease in temperature from 8 to 1 °C over 8 weeks, with an additional week at 1 °C). These fish began to reduce feed intake at 6 °C and stopped feeding by ~2 °C, and this was associated with a reduction in growth of 58 % over the experimental period. In addition, a number of differences as compared to fish held at a constant temperature of 8 °C were reported. At 4–5 °C, cellular stress (as evidenced by increased liver hsp70 and hsp90 transcript expression) and an osmoregulatory disturbance were first noted, and these became progressively worse. Finally, plasma cortisol levels were elevated at 2 and 1 °C, and at 1 °C the fish were found to have enlarged livers (i.e., an increased hepatosomatic index, HSI) and early signs of fin rot and skin erosion/ulceration of the head.

In general, temperatures throughout the sea-cage were relatively homogeneous over the study period; although there were times that temperatures at the surface (1 m) were 2–4 °C lower than in the rest of

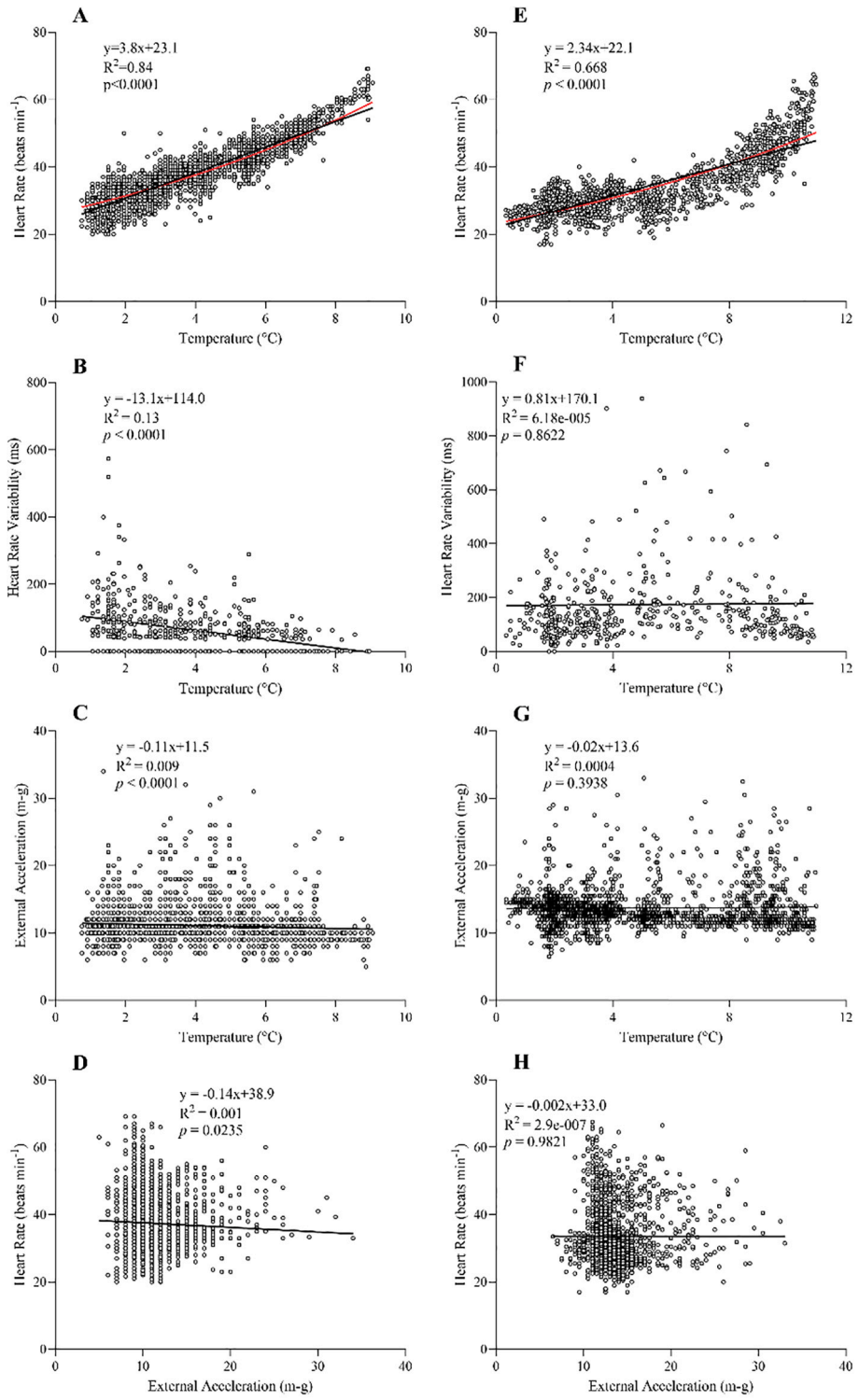

Fig. 6. Relationships between recorded temperature and heart rate (A, E), heart rate variability (B, F) and external acceleration (C, G), and between heart rate and acceleration (D, H). Panels A-D shows data retrieved from one fish from Site #1 and *E*-H is the average data from two fish at Site #2. Linear regression equations are shown in each panel. Note: an exponential equation (red line) was also fit for heart rate (A, E); $R^2 = 0.835$ and 0.701, respectively.

the water column. This limited temperature variability is in stark contrast to what has been observed during the warmest summer months at salmon sea-cages. For example, Stehfest et al. (2017) reported a major crowding event which resulted from water temperature stratification and a subsequent hypoxic squeeze that occurred at a sea-cage in Tasmania, Australia. Further, temperatures at the surface of sea-cages during the Newfoundland heat wave of 2019 were often approximately 10–12 °C above those measured at 15–20 m depth (Burke et al., 2020; Gamperl et al., 2021). While the latter has also led to changes in management practices / protocols (i.e., deeper nets, submersible cages, and additional aeration / oxygenation etc.) to ultimately mitigate the challenge of summer temperatures, it does not appear that similar efforts would be of benefit to salmon in the winter.

4.3. Cage use and fish distribution

While there was some individual variation in cage use by the fish, overall, the fish had remarkably similar movement patterns. In the days immediately following tagging, fish predominately occupied the upper 5 m of the cage with occasional migrations to deeper depths (e.g., see Supplemental Fig. 3). This pattern in depth distribution continued for much of the study, however, there were periods where they would use the deeper depths of the cage quite regularly. For example, many of the fish made more frequent migrations to the deeper parts of the cage in November / December, and again when temperatures reached ~2 °C. This was particularly during the night-time in this latter period, which is comparable to observations made by Korus et al. (2024) for this species. Interestingly, this is the opposite to what has been observed during warm temperatures in summer (Gamperl et al., 2021; Korus et al., 2024; Stehfest et al., 2017) and salmon in Norwegian cages in February/March where temperature was uniformly ~10.5 °C with depth (Johannesen et al., 2020). In these studies, the fish avoided the surface waters during the day and returned to shallower depths at night. As temperatures within the sea-cage during this study remained relatively homogenous with depth, it is unlikely that temperature explains the fish's diurnal change in depth distribution. This behaviour could be related to feeding which only occurred during daylight hours at the surface using pneumatic feeders. For example, while the salmon continued to be fed to apparent satiation throughout the winter months (until ~1 °C), feeding behaviour and overall feed consumption decrease as metabolic demands are reduced (Ibarz et al., 2007; Porter et al., 2022). For example, a recent study by Vadboncoeur et al. (2023b) reported a substantial decrease in salmon feed consumption (and behaviour) during a seasonal decline (~1 °C week^{-1}) in temperature. Feeding / appetite began to decrease at 6 °C, with complete loss of appetite by 1–2 °C. Similarly, Liu et al. (2020) reported that Atlantic salmon stopped feeding below 2 °C. Thus, it is likely that the tagged fish within this study also decreased and/or stopped feeding at these low temperatures, and this was reflected in their cage-site depth distribution.

4.4. Heart rate and acceleration

Heart rates at the beginning of this study, at temperatures between 8 and 10 °C, were ~ 50 beats min^{-1}. This is very similar to values reported by other studies (Gamperl et al., 2021; Sandrelli and Gamperl, 2023; Warren-Myers et al., 2021; Yousaf et al., 2022). Given that temperatures began to decline shortly after the fish were returned to the cage, a recovery period characterized by stable f_H values (i.e., no further decrease in f_H) was not seen. Instead, f_H was observed to closely follow the seasonal decline in temperatures (Figs. 5 and 6), with the lowest average heart rates (20–25 beats min^{-1}) recorded at temperatures below 2 °C. A diurnal effect on f_H was not found to be statistically significant, likely due to the small sample size. This, however, may also be due to the fact temperatures were < 5 °C for a large proportion of this study and were relatively homogeneous from the surface to the bottom of the cage. For example, while diurnal changes in f_H of ~5 beats min^{-1} have been reported at water temperatures of ~5 °C (Føre et al., 2021; Svendsen et al., 2021), these are much lower than the ~25 beats min^{-1} that Brijs et al. (2018) found at 15 °C.

External acceleration was more variable from October to January (i.e., at temperatures >4 °C) compared to January to March / April, with values often ranging between 15 and 25 m-g. However, this pattern of activity ended as the temperature fell further, and very little variation in activity (external acceleration) was observed over the rest of the winter (Fig. 5). While it is difficult to draw firm conclusions from these data given the small sample size, they are consistent with lab-based studies on the effects of cold temperatures on salmon swimming performance. Lab-based studies on fish acclimated to control (8–11 °C) vs. cool/cold (1–4 °C) temperatures report decreases of 20–35 % in the critical swimming speed of salmon due to factors independent of metabolic capacity (Porter and Gamperl, 2023; Riseth et al., 2020; Taylor et al., 1996).

5. Conclusions and perspectives

Farmed aquatic animals are an important, and arguably, a critical source of protein and food for the growing human population. As with wild fish populations, the aquaculture industry faces a number of climate change-related challenges (Cheung and Frölicher, 2020; Cheung et al., 2021; Falconer et al., 2020; Genin et al., 2020; Islam et al., 2022; Perry et al., 2005; Reid et al., 2019; Szekeres et al., 2016). While the main focus has been on addressing the effects of high temperatures, it is clear based on recent losses of fish in the winter that research needs to be conducted on the effects of temperatures as low as 0 °C on salmon health and welfare (Reid et al., 2022; Szekeres et al., 2016).

We fitted Atlantic salmon with DSTs that could record temperature, heart rate, acceleration and depth to further understand how temperatures in sea-cages in Newfoundland change seasonally, and how they might affect fish activity, physiology and distribution. Although aquaculture companies monitor water temperature and oxygen, and feeding behaviour, quite closely, their observations can be limited particularly during the winter months as sea ice cover, limited day-light hours and storms can hinder cage-site monitoring. Although, there are now several publications on how temperatures down to 1 °C affect the physiology (i.e., stress hormones, heat shock protein levels, ion regulation, and cardiac function) and swimming performance of Atlantic salmon (Porter et al., 2022: Porter and Gamperl, 2023; Reid et al., 2022; Vadboncoeur et al., 2023a, 2023b), these data have all been collected in lab-based settings where the fish are highly manipulated and confined. Further, the literature provides several caveats with regard to directly comparing lab-based studies to those on free-swimming fishes (Mignucci et al., 2021; Sandrelli and Gamperl, 2023).

In this study, we were able to successfully record f_H, temperature, depth and swimming activity from Atlantic salmon in commercial sea-cages in the fall / winter in Newfoundland. In addition, we were able to show that: 1) water temperatures fell by 0.35 and 0.57 °C week^{-1} until early March when temperatures were ~ 1 °C, and the decrease in f_H closely followed temperature; 2) temperatures remained below 5 °C for five months, and while often lower at the surface, they were generally homogenous from 5 to 20 m; and 3) while fish mainly occupied the upper 5 m of the cage, there were some excursions to deeper depths at night and during the lowest temperatures. However, we also learned several valuable lessons with regard to the implantation / use of these tags for long-term studies at cold temperatures. First, although the DSTs used at Site #1 had larger batteries, which made frequent and long-term recordings possible, these tags were considerably larger and likely more invasive to the fish. This, combined with the effects of cold temperatures on wound healing, probably led to the loss of a number of tags / mortalities. Second, retrieving DSTs from tagged fish placed in commercial cages (150 m circumference, with 50,000–60,000 other fish) for periods in excess of 6 months, and having tagged fish identified on a processing line, is not easy and leads to a poor rate of tag recovery. Finally, the recent increase in maximum recording time for ECGs (from 6 to 15 s at 100 Hz) allows for very accurate measurements at low water temperatures. For example, at temperatures <2 °C, we had <10 f_H values that were QI = 3 (i.e., the PQRS interval could not be identified) of the hundreds that were recorded. It is this technological advancement, and the fact that acoustic HRT DSTs tested in Newfoundland under cage-site conditions will soon be commercially available, that should allow such technology to be incorporated into real-time aquaculture monitoring systems. Real-time monitoring of f_H, activity and depth could be an important addition, and enable the industry to remotely identify, and respond quicker, when issues threaten fish health and welfare.

CRediT authorship contribution statement

Rebeccah M. Sandrelli: Writing – original draft, Investigation, Formal analysis, Data curation, Conceptualization. **Émile Vadboncoeur:** Writing – review & editing, Investigation. **Sheldon George:** Resources, Investigation. **Eric H. Ignatz:** Writing – review & editing, Investigation. **Andrew K. Swanson:** Writing – review & editing, Resources, Conceptualization. **A. Kurt Gamperl:** Writing – review & editing, Supervision, Resources, Project administration, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.aquaculture.2024.741777.

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