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Using acoustic telemetry to monitor the effects of crowding and delousing procedures on farmed Atlantic salmon (*Salmo salar*)

M. Føre^{a,b,*}, E. Svendsen^a, J.A. Alfredsen^b, I. Uglem^c, N. Bloecher^a, H. Sveier^d, L.M. Sunde^a, K. Frank^a

^a SINTEF Ocean, 7465 Trondheim, Norway

^b NTNU Department of Engineering Cybernetics, 7491 Trondheim, Norway

^c Norwegian Institute for Nature Research, 7485 Trondheim, Norway

^d Lerøy Seafood Group ASA, Bontelabo 2, 5003 Bergen, Norway

ABSTRACT

The aim of this study was to demonstrate the feasibility of acoustic telemetry for monitoring fish during farm operations and gather knowledge about Atlantic salmon responses during crowding and delousing events in a commercial sea-cage. 21 fish were equipped with a novel transmitter tag type using data from pressure sensors and accelerometers to compute swimming depth and swimming activity of individual fish. The fish were monitored over four months, during which they were subjected to three thermal delousing events. In the periods before and after delousing, the fish generally exhibited a circadian rhythm in both swimming activity and depth, with high activity and deep swimming during daytime and low activity and shallow swimming during night. Swimming activity recorded during crowding and delousing events was significantly higher than background swimming activity levels registered a day before and after delousing. Although activity levels differed significantly between the three events and between the different stages within each event, the highest activity levels were consistently measured during thermal treatment. Swimming depth differed significantly between delousing events and was strongly influenced by daylight. In summary, crowding and delousing induced increased movement in the fish, while swimming depth appeared to be less sensitive to these operations. The conclusion of the study is that acoustic telemetry is a suitable tool for monitoring fish during challenging operations such as crowding and delousing, as well as during normal cage management. Moreover, this study provides new knowledge on how the behaviour of Atlantic salmon may be affected by delousing.

1. Introduction

Modern aquaculture sea-cages may have internal volumes as large as $60,000-130,000 \text{ m}^3$ (50 m deep and circumference 160 m/25-30 mdeep and 240 m circumference, Huon aquaculture, Tasmania) and contain up to 200,000 individual fish. Although online monitoring of physiological, behavioural and welfare-related fish states is still a major technical challenge (Føre et al., 2018), the acquired data may be of crucial importance for the optimisation of farm management, fish handling and farm operations (Huntingford et al., 2006; Noble et al., 2018). Development of new technological tools that provide farmers with new data types to improve decision support is therefore an essential element in preparing the fish farming industry for sustainable future growth (Føre et al., 2018). The proper conduct of work operations associated with high risks for fish welfare and survival is one area where such tools may prove particularly valuable. Many of the most challenging work operations used by the industry today are connected to sea-lice infestations (*Lepeophtheirus salmonis*) and their management (Erikson et al., 2016).

1.1. Sea lice in commercial salmon production

Although sea lice have always been a component in Atlantic salmon (*Salmo salar*) ecology, infestation levels at commercial salmon farms have increased dramatically over the last decades, making sea lice one of the main challenges facing the Norwegian and global salmon industry today (Igboeli et al., 2014). In addition to impairing both welfare and health of the salmon (Finstad et al., 2000), the transmission of sea lice from farmed fish to wild salmonids may lead to negative environmental impacts (Bjørn et al., 2001). Moreover, the economic expenses associated with sea lice (e.g. louse assessments, delousing operations and mortality during delousing) increase directly or indirectly with

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^{*} Corresponding author at: SINTEF Ocean, 7465 Trondheim, Norway. *E-mail address:* martin.fore@sintef.no (M. Føre).

infestation level and represent a significant proportion of the total production costs of salmon today (Iversen et al., 2013). The incentives for controlling the sea lice problem in Atlantic salmon farming are therefore founded in three key aspects of modern cage-based farming; fish welfare, environmental sustainability and economy.

The most common sea lice treatment methods are medicinal feeds, or exposure to anti-louse pharmaceuticals in closed or semi-closed baths (Shao, 2001). However, due to increased resistance against pharmaceuticals (Aaen et al., 2015), the industry is now increasingly replacing such methods with non-pharmaceutical treatments that remove lice from the fish through e.g. immersion in fresh water (Powell et al., 2015), or by mechanical or thermal means (Lekang et al., 2016). Since freshwater bathing is often conducted in well boats or tarpaulin-lined cages and mechanical/thermal treatment systems are usually placed at barges or ships near the farm, the fish need to be pumped into these systems. To achieve the desired pumping efficiency, the fish then need to be crowded to higher than usual concentrations (Erikson et al., 2016).

1.2. Crowding operations during delousing procedures

Crowding processes are usually conducted by first raising the net wall in gradual steps, and then applying smaller crowding nets to facilitate the final increase in fish density. This may affect fish welfare in several ways, including: 1) abrupt reductions of available volume require the fish to relate to a larger number of conspecifics which may increase the stress level of the fish (Larsen et al., 2015); and 2) reduction of the cage volume will increase the chance of fish colliding/hitting other fish or cage components (e.g. the net wall or bottom), potentially leading to fish suffering mechanical damage (e.g. wounds and abrasions). Reduced fish welfare may in turn result in health issues or even trigger mortality events in salmon populations (Erikson et al., 2016). Being able to improve or control crowding processes to the extent that one may avoid such incidents should therefore be an overarching aim from both ethical and economic perspectives in both research and industry alike.

1.3. Monitoring fish during crowding with acoustic telemetry

One of the first steps in asserting better control over crowding operations is to establish methods for monitoring values or trends in fish states (i.e. quantifiable behavioural or physiological status) that may indicate if the fish are suffering mechanical, physiological or behavioural stress that in time may result in impaired welfare. This harmonises with the principles of Precision Livestock Farming (PLF), where continuous monitoring of animal states in commercial farms is a central aspect of developing new methods for terrestrial farming (Berckmans, 2004). In PLF-based methods, monitoring data is used for decision support with the aim of improving animal health and welfare while increasing productivity, yield and environmental sustainability (Berckmans, 2014). Although animal monitoring data from sea cages could be similarly applied to achieve better control over crowding processes in salmon farming, this requires knowledge on which animal states to monitor (Føre et al., 2018). At present, there is little scientific knowledge on the behavioural or physiological responses of salmon towards stressors such as delousing events, mainly because fish are more difficult to monitor when kept at higher than normal densities, and that stationary sensor systems are difficult to deploy in cages during the different physical operations (e.g. net manipulation, crowding, pumping). Subjective observations made by fish farmers suggest that Atlantic salmon sometimes dive towards the deeper layers of the cage once the net is released post-crowding. Moreover, crowding and net handling are commonly believed to affect the swimming activity levels of salmon, the expression of which may range from lowered activity due to lack of movement space to increased activity due to agitation and stress. Although these behavioural traits have not yet been scientifically documented and quantified and are thus based on anecdotal evidence, monitoring the spatial behaviour of the salmon could result in information that may be used to determine the fish response before, during and after delousing (Føre et al., 2018).

To avoid interfering with the execution of the procedure, fish monitoring during operations should be based on automated solutions rather than direct human observation. Acoustic telemetry is a monitoring method that may be used for this purpose and that entails equipping individual animals with embedded electronic transmitters containing sensors, processing units, batteries and an acoustic modem for wireless communication in a miniature package (see Føre et al., 2011 for more on the components of acoustic transmitter tags). The transmitters periodically emit acoustic signals (or sound signals) encoding data and/or information. These signals are picked up by submerged acoustic receivers, which are dedicated electronic units that demodulate and decode the acoustic signals into physical values and store them in internal memory. Acoustic receivers are typically placed such that the user may access them directly to retrieve data offline, or attached to communication systems or solutions enabling real time data transfer and monitoring. Historically, this method has primarily been used to study wild fish movement, ecology and conservation (e.g. Thorstad et al., 2008; Plantalech Manel-La et al., 2009; Jensen et al., 2014; Hussey et al., 2015), but more recent research efforts have also applied telemetry in aquaculture settings (e.g. Rillahan et al., 2009; Ward et al., 2012; Kolarevic et al., 2016; Føre et al., 2017). Although the data provided by acoustic transmitter tags mainly depend on which sensor(s) are included in the tag, the output format is determined by the algorithm running on the CPU within the tag and may range from raw instantaneous data values (e.g. Skilbrei et al., 2009) to compound data values (e.g. Føre et al., 2011; Kolarevic et al., 2016). Acoustic telemetry has previously been used to monitor swimming activity (e.g. Føre et al., 2011; Kolarevic et al., 2016) and depth dynamics (e.g. Skilbrei et al., 2009; Føre et al., 2011) of salmon, albeit not during operations such as delousing.

1.4. Aims of this study

Atlantic salmon in a commercial fish farm were monitored using a novel type of acoustic telemetry tag designed to monitor the swimming activity and depth of the fish over a period of five months, during which the fish were subjected to three delousing operations. The primary aim was to 1) demonstrate and validate the functionality of a technological tool for monitoring fish during critical operations, and 2) gather new knowledge about behavioural responses towards delousing and crowding procedures. The main research questions in this study were:

- i) Can an acoustic telemetry system be used to collect continuous data during farm work operations?
- ii) May activity and depth values acquired with acoustic telemetry be used to describe the behavioural responses of the fish?
- iii) What values and trends in the monitored fish states describe the normal behavioural patterns of salmon in commercial net cages?
- iv) How will a delousing operation affect these behavioural patterns?

2. Materials and methods

2.1. Animal ethics

All fish handling and surgery were made in compliance with the Norwegian animal welfare act and was approved by the Norwegian Animal Research Authority (permit no. 9595).

2.2. Experimental site and delousing operations

The experiment was conducted from October 10, 2016 to February 28, 2017, at a SalMar Farming AS/SINTEF ACE site in Nord-Trøndelag,

Norway (64.60°N, 11.27°E). There were in total six stocked cages at the site during the experiments, each containing 393 t of salmon on average. The fish were fed during the daylight hours.

During the experimental period, the fish were deloused three times, using thermal delousing (Thermolicer, Steinsvik AS). In this operation, the fish were first crowded and then pumped from the net cage into a treatment chamber aboard a barge moored to the cage. Here, the fish were immersed in seawater warmed to 30-34 °C for about 20 s with the intent of killing and detaching the sea lice. After treatment, the fish were pumped into an empty cage. Crowding was conducted as a twostage process where the cage net wall was first raised to 7 m depth, kept there for approximately 1 h, and then raised to 1 m depth followed by another pause of about 1 h. Although this greatly reduced the available cage volume, the fish were, in addition, actively crowded from the top using large crowding nets to achieve sufficient densities to enable efficient pumping. The final stage of the process (i.e. active crowding, pumping and treatment) was therefore conducted as a sequence of several smaller operations where the fish stock was treated in groups rather than in a single operation including all the fish at once. As a result, this stage lasted between 5 and 9 h in total, with groups of individual fish being treated and transferred at different times.

Delousing events took place on 31.10.2016, 07.11.2016 and 06.12.2016. The first delousing event was conducted during daytime (11:00–18:35), while the second and third delousing event were conducted after sunset (21:00–06:05 and 19:00–09:35 respectively). All fish were starved prior to and during the delousing events (delousing 1 and 2: 18 days, 25.10.2016–12.11.2016; delousing 3: 8 days, 30.11.2016–08.12.2016). Approximately one month prior to this experiment, the fish had been subjected to a mechanical delousing event, however, they had never experienced thermal delousing.

2.3. Tagging of experimental fish

To record the activity levels and swimming depth of the salmon during the experiment, 21 individual fish (average weight $3.0 \text{ kg} \pm$ 0.6 kg std. dev., average length $61.9 \text{ cm} \pm 3.6 \text{ cm}$ std. dev.) were equipped with acoustic tags. To collect the specimens, a group of fish in the cage was attracted by feed and captured in a large pull net (2 m diameter, 2 m depth). Individual fish were subsequently caught by using knotless dip nets. Fish tagging was conducted between 09:00 and 16:00 on October 3rd, with a mean air temperature of 8.7 °C and a mean water temperature of 12.3 °C. Selected fish were anaesthetised by immersion in a 1001 bath containing 300 mg/l metacaine (tricaine mesylate) until they lost buoyancy equilibrium and ceased all movements except respiration (mean immersion time 4 min). The fish were then placed with the abdominal area facing upwards in a cradle lined with wet tissue. A small incision (approximately 12-15 mm) was made in the abdominal wall through which an acoustic tag (Thelma Biotel AADT-LP-13, Thelma Biotel AS, Trondheim, Norway, 13 mm diameter and 42 mm length, 5.6 g in water) was inserted. In addition, a PIT tag (HPT 12, Biomark inc., 2.12 mm diameter and 12.5 mm length) was inserted with the intent of identifying and sorting out all tagged fish on the slaughter line. The incision was closed with two or three independent silk sutures (1/0 Ethicon) before fish length and weight were measured. The fish were then released into a 1001 bath containing constantly refreshed seawater for recovery from anaesthesia. Fish were assumed recovered when they regained their buoyancy equilibrium (average recovery time of 4 min) and were thereafter released back into the cage.

2.4. Acoustic telemetry system

Variations in values and trends in swimming activity and depth dynamics may be measured by accelerometers and pressure sensors, respectively. The AADT-LP-13 tag type contained a 3-axis accelerometer and a pressure sensor, and had a power output of 150 dB re



Fig. 1. a) action sequence describing how the interval (220 to 380 s) between two consecutive transmissions (T_n and T_{n+1}) is divided between sensor sampling periods and data processing/idle periods; b) activity byte encoding the RMS-acceleration (0–255) for the dataset collected in the acceleration measurement interval (30 s); c) depth byte 1 encoding the max (0–15) and min (0–15) depths registered in the depth sensing interval (150 s); d) depth byte 2 encoding the average (0–15) and standard deviation (0–15) of the depth dataset (150 s).

1µPa at 1 m. The tags were set to transmit data at randomised intervals of between 220 and 380 s, with the first 150 s of each inter-message interval being used to collect depth data at 1 Hz, followed by a 30 s period collecting accelerometer data at 5 Hz (Fig. 1a). Mean, standard deviation, minimum and maximum values were derived from the depth dataset, while the total Root Mean Square (RMS) value for all three axes was computed from the acceleration dataset and summed, being a proxy for the effective activity level of the fish over the period when acceleration data was collected (Kolarevic et al., 2016). The effects of gravity introduce a large constant vertical component on the raw data registered by an accelerometer. To compensate for this, the data used to compute the RMS value was high pass filtered using the same method as Føre et al. (2011). The resulting value thus reflected the acceleration components caused by fish movement in m s⁻².

These five values were transmitted as three separate data bytes, with the first data byte (Fig. 1a) containing the RMS acceleration $(0-255 \text{ representing } 0.014 \text{ m s}^{-2})$ per increment yielding a range $0-3.465 \text{ m s}^{-2}$). The second and third bytes were split into two four-bit values (0-15) to encompass two data values each, the second byte (Fig. 1b) describing the max and min depth values (0-15 representing 1 m depth bins from 0 to 15 m, i.e. 0-1 m, 1-2 m, ..., > 15 m), and the third byte (Fig. 1c) containing average depth (0-15 with same conversion as max and min values) and standard deviation in depth $(0-15, 15 \text{ representing the variation that would be caused by an instantaneous step from 0 to <math>15 \text{ m depth}$).

The high fish density during crowding could have an impact on the transmission conditions in the cage as the fish may attenuate the acoustic signals, and hence potentially cause increased data loss during delousing operations, compromising the objective of the study. Furthermore, acoustic reception is impossible when the fish are removed from the water while within the treatment system. Depending on the treatment duration, this could cause additional loss of data during the most relevant periods. To prevent these factors from affecting the data describing fish responses during crowding/treatment, the transmitter tags were set up with a transmission time delay of 12 h, meaning that the data generated during these processes was buffered in the tag and transmitted 12 h after the delousing rather than being sent while the fish were undergoing crowding/treatment.

When several acoustic transmitter tags use the same acoustic carrier frequency, there is a risk that two or more tags will try to transmit in overlapping time windows. This may cause acoustic interference or signal collisions, meaning that the acoustic signals that are sent simultaneously are not possible to separate, and hence that the data



Fig. 2. Experimental setup indicating receiver placement relative to cage components (cage collar, bridles) and tagged fish within the cage volume. The number on each receiver provides the monitored acoustic frequency of the receiver, i.e. 69 or 71 kHz.

contained therein is lost (Heupel et al., 2006). This has previously been found to be an important source for data loss in systems where many fish are monitored at the same time using acoustic telemetry (Heupel et al., 2006; Føre et al., 2017). The impact on the resulting dataset depends on the number of transmitters used, and the time intervals between transmissions. To counter this effect, transmission intervals were randomised such that systematic data loss due to clock drift was minimised (Føre et al., 2017), and by dividing the tags between two carrier frequencies (12 at 69 kHz, 9 at 71 kHz).

Eight acoustic receivers were used in the experiment (TBR700 from Thelma Biotel AS), with four receivers monitoring each of the chosen communication frequencies (69 kHz and 71 kHz). To minimise the chance of the receivers coming in conflict with net operations (e.g. during crowding), they were mounted outside the net cage in pairs (one 69 kHz unit and one 71 kHz unit) at each of the bridle attachment points at the floating collar, as boats and crew usually avoid bridles when manipulating the net (Fig. 2). This receiver distribution pattern also ensured a homogeneity in the geometric coverage of the cage cross section for both acoustic frequencies, increasing the likelihood of achieving beneficial reception conditions in larger parts of the cage. In addition, the TBR700 units used multi-threshold signal detection that enabled them to untangle overlapping transmissions when these were received with different signal strengths. Since the strength of an acoustic signal depends strongly on the distance between source and receiver, the signal with the highest power will often originate from the transmitter closest to the receiver unit (granted that all transmitters are sending with approximately equal acoustic power). With the even geometric distribution of the receivers, this may further reduce the loss of data due to acoustic interference.

In addition to providing good coverage and redundancy in data storage during the experiments, the receiver configuration also led to a duplicity in data points when single transmissions were detected by two or more receivers. This was handled by merging data points in the full dataset that had identical ID and data values, and timestamps that were too close to represent consecutive transmissions. The software for downloading data from receivers (Thelma Biotel AS) removed all data points that were the result of erroneous receptions (e.g. due to wrong checksum) as these data were likely to be flawed and hence should not be used in the analyses.

The fish were moved to a new cage after each delousing event, and the receiver setup was therefore moved to the new cage after the procedure to maximise acoustic coverage of the fish group containing the tagged fish throughout the experiment. Receiver relocation was always done < 12 h after a delousing event to ensure that receiver configuration was optimal when data collected during the crowding/ delousing were transmitted with the 12 h delay.

2.5. Data processing

To study how the fish responded to different phases in the delousing treatment, the time series of collected data streams were harmonised to UTC time. This was done by subtracting 12 h from the timestamps of all telemetry data points and converting the operational time series (i.e. delousing schedules) to UTC.

To attribute specific reaction patterns to individual operational aspects of the crowding/delousing process, the procedure was divided into 6 individual phases:

- 1. "Day before": background activity level and swimming depth before start of the operation, recorded at the same time of day, one day before the operation. This was done to avoid an eventual effect of ongoing preparations for the delousing operation (e.g. increased boat traffic, preparation of net for crowding) on fish behaviour.
- 2. "Net at 7m": first crowding phase where the net was elevated to 7 m depth.
- 3. "Net at 1m": second crowding phase where the net was elevated to 1 m depth.
- 4. "Thermal treatment": delousing of the fish by pumping it through the thermal treatment chamber and releasing them again.
- 5. "After treatment": when the fish had been released into the net cage just after the conclusion of the delousing treatment.
- 6. "Day after": fish behaviour measured at the same time of day, one day later, to test for return to background levels.

Of these six phases, phases 2–5, where the fish were crowded and treated, were considered "active treatment" phases, while the other two phases (1 and 6) measured background levels or recovery after treatment.

2.6. Statistical analysis

Of the 21 tagged fish, 15 fish that gathered data during all three delousing treatment were included in the statistical analysis. For each fish, the data collected in a 40-min time window in the middle of the respective period for each individual delousing operation phase was selected. The only exception was phase 4, "Thermal treatment" where data from a time window of 25 min was used to reflect the comparatively short time it takes the fish to pass through the treatment chamber. Since the average operational time span for the thermal treatment of the entire population was 7 h, and the tagged fish were processed at different times during this time span, the time window for data used in the analyses pertaining to phase 4 was manually selected. The selection was based on the group data showing uniform behaviour patterns with high and distinct activity peaks during the period, as well as the following assumption: crowding and treatment affect the swimming activity of salmon, and the transfer to an un-manipulated cage without depth restriction would likely lead to rapid changes in swimming depth and trends in activity. Consequently, with the net wall of the original cage raised to 1 m at the time of treatment, any point during the final stage at which the fish abruptly increased swimming depths was likely to indicate transfer to the new full-depth cage. Assumed individual moments of treatment and subsequent transfer were therefore identified by finding times where the fish exhibited abrupt changes in activity and/or sudden increases in swimming depth. Data was collected from a period of 20 min before and 5 min after this marked peak in activity or change in swimming depth.

To test for differences in activity level and swimming depth during

the six operational phases of delousing treatments, permutational analysis of variance (PERMANOVA, PRIMER v7) was used. The analysis involved a repeated measures model that incorporated two factors -'delousing event' (fixed, 3 levels) and a temporal factor 'delousing operational phase' (fixed, 6 or 3 levels - see below). Euclidian distance matrices were constructed for the two univariate variables ('activity levels', i.e. RMS of acceleration caused by fish movement over 30s periods [m s⁻²], and 'swimming depth', i.e. mean swimming depths over 150 s periods [m]) and analysed using 9999 permutations of residuals under a reduced model. For the analysis of 'activity levels', all six operational phases were included, while the analysis of swimming depth was limited to the three phases where depth was unrestricted ("Day before", "After treatment" and "Day after" phases). The variances of the differences between the three delousing events across delousing operation phases were not homogenous (Levene's test; P < .05). However, the analysis was carried out nonetheless as repeated measures models in PERMANOVA do not strictly require data sphericity (Anderson et al., 2008). Pairwise comparisons were used to examine differences, where main or interaction terms associated with the tested factors were significant. For all analyses, a significance level of 5% was used. Detailed results of the statistical analyses can be found in Appendix 1.

3. Results

3.1. Fish survival, health and tag recovery

Three transmitter tags ceased transmitting early in the experimental period and were excluded from all analyses. Another five tags started consistently transmitting maximum depth values (implying a depth ≥ 15 m) and zero activity values at later stages. This is an indicator that the fish carrying the tag has died or that the tag has been expelled through the abdominal wall (Moore et al., 1990; Føre et al., 2017). These five tags were therefore excluded from the analyses from the moment their output started transmitting such values.

The standard deviation values reported by the transmitter tags were generally low, implying that the individual fish did not exhibit very rapid changes in swimming depth in the depth sensing periods. Furthermore, the minimum and maximum depths (with a 1 m resolution) were often identical to the mean swimming depth, suggesting that the fish mostly stayed in a depth range spanning 1 m between transmissions. Due to these observations, the analyses were focused on mean swimming depths and RMS acceleration values.

3.2. Background levels of activity and swimming depth

Before the first delousing event, the mean activity of the tagged fish followed a circadian rhythm where registered activity levels were higher during daytime than at night, with values ranging between 0.14 and 0.7 ms^{-2} (Fig. 3). Similarly, there was a daily rhythm in mean swimming depth, with deeper swimming at daytime than during night (ca. 8 m vs. 4 m). This cyclical pattern was also observed in the periods between the delousing operations, and in the period after the final treatment, although with less pronounced circadian activity patterns immediately after operations 1 and 2 (Fig. 3).

3.3. Behaviour during delousing

Synchronisation of the individual data series around their assumed treatment/transfer times allowed for a direct comparison between individual responses toward the thermal treatment and transfer process (Fig. 4).

Activity levels measured in the six delousing operation phases during the three delousing events differed significantly between phases and delousing events (Event x Delousing operation Phase; f_{10} , $_{217} = 5.143$; p < .001). In all three delousing events, average activity

levels measured in fish undergoing the "Thermal treatment" phase were significantly higher than during any of the other five delousing operation phases ("Thermal treatment": 1.24–1.74, other phases: 0.25–1.09; pairwise comparisons, p < .05, Fig. 5). Activity levels during "Thermal treatment" were significantly higher in the third delousing event (pairwise comparison, p < .05; 1.74 \pm 0.14 SE) than during the first (1.3 \pm 0.13) and second event (1.24 \pm 0.14). However, with exception of the "Thermal treatment" and the "After treatment" recovery phase, activity levels were generally higher in fish during the first delousing event conducted at daytime than in the following two events conducted without daylight (pairwise comparisons, p < .05).

During the first and third delousing event, there were significantly higher activity levels when crowding to 1 m than when crowding to 7 m, while the second delousing event featured higher activity levels when crowding to 7 m than to 1 m (pairwise comparisons, P < .05; Fig. 5). In all delousing events, activity levels during active operation (crowding and thermal treatment) were significantly higher than background levels measured a day before or a day after the event (pairwise comparisons, P < .05; Fig. 5). During the second and third event, activity levels measured in the "After treatment" recovery phase were equally high as when crowding to 7 m (delousing events 2 and 3) and 1 m (delousing event 3; pairwise comparisons, P < .05; Fig. 5). Contrastingly, activity levels in this phase were lower than during crowding and did not differ from background values taken the day before or the day after during delousing event 1. Background values (i.e. "Day before" and "Day after") were similar before and after the second delousing event, but higher a day before than a day after treatment for the first and third delousing events (pairwise comparisons, P < .05; Fig. 5).

Swimming depth did not differ significantly between the three delousing operation phases where cage depth was unrestricted ("Day before", "After treatment" and "Day after"; Delousing operation phase: $f_{2, 110} = 0.616$; p = .543). It did, however, differ significantly between delousing events (Event; $f_{2, 110} = 6.148$; p = .004), with fish swimming markedly deeper during the first delousing event conducted in daylight (7.3 ± 1 m) than during the second and third delousing events conducted at night (5.0 ± 0.7 m and 4.1 ± 0.8 m, respectively; pairwise comparisons, p < .05).

4. Discussion

4.1. Technical system performance

The results demonstrate the feasibility of using acoustic telemetry to monitor fish in commercial aquaculture. Although delousing treatment operation was chosen as a specific case for this study, the technology is also applicable as a tool for monitoring fish during other potentially critical and demanding operations such as net cleaning, and during everyday management routines such as feeding. The acoustic system was able to collect data throughout the experimental period, except when the receivers were moved between cages after the fish had been transferred. As there exists no reported knowledge in the literature describing individual responses of salmon to crowding, pumping and treatment operations during delousing, this illustrates how the use of technological tools such as acoustic telemetry can generate knowledge previously unavailable through conventional means of fish observation.

Since the RMS-acceleration was compensated for the effects of gravity, the activity value was probably dominated by accelerations caused by the tail-beat motion of the fish, transient changes in swimming direction/orientation/attitude and linear accelerations (Føre et al., 2011). The swimming speed of salmon is a function of tail beat rate and amplitude (Bainbridge, 1958). Increased measured activity values therefore imply that the fish had increased its swimming speed and/or was displaying more rapid changes in swimming direction (primarily pitch/tilt and roll, see Fig. 5 in Føre et al., 2011). However, also passive movement induced upon the fish during pumping and



Fig. 3. Time series plot of mean values based on data from all tagged individuals, with activity/RMS-acceleration in the top plot and mean swimming depth in the bottom plot of each figure. Topmost figure: long-term data (October 10–December 22) covering all three delousing events and periods before, between and after these (averaging interval 60 min., dark grey fields: delousing events). Lower part of the figure: detailed data series for the periods before delousing event 1, between delousing events 2 and 3, and after delousing event 3 (averaging interval 60 min.).

treatment in the treatment chamber of the delousing unit may be registered as activity.

Although the use of acoustic telemetry involves fish handling and surgical implantation of transmitter tags, which requires special competence, is expensive and may permanently affect the fish if not conducted properly (Moore et al., 1990), this is the only extant method for obtaining online true individual based information. Online operation is a necessity if the system is to be used for decision support during such operations. The potential of using this method in operational decision support could be further improved by increasing the time resolution of the data. This would provide a higher detail level, which would enable a closer study of individual variations, especially around short-time events such as treatment and transfer to a new cage. Possible ways to achieve this include spreading the transmitters over more transmission frequencies or developing an acoustic transmission protocol with higher data throughput.

4.2. Salmon responses to delousing operations

While the fish were not undergoing treatment, they showed a consistent swimming pattern of high activity at deeper water during day, and low activity at shallower depths during the night. This is in accordance with depth dynamics (Fernö et al., 1995; Johansson et al., 2006; Oppedal et al., 2011) and activity patterns (Juell and Westerberg, 1993; Andrew et al., 2002; Føre et al., 2011) seen in previous studies, and probably due to day versus night time light intensity and feeding. Interestingly, the diurnal pattern was also present during the starvation periods around the delousing events, indicating that light was the dominating factor for the recorded behaviour. The effect of light was also apparent when comparing the delousing events, as the fish swam deeper and had higher activity values during delousing 1 that was conducted at daytime than in the other two events that were conducted at night.



Under the assumption that the background activity levels displayed before and after the delousing events were the preferred swimming

Fig. 4. Time series plot for all individual fish (coloured lines) during the three delousing events. Individual time series have been synchronised around the highest peak in activity occurring in individual datasets during the treatment and transfer phase under the assumption that this marks the point in time where the fish were pumped into the delousing system and transferred. The thick black line represents the mean values of all individuals (10 min averaging interval) after time series synchronisation, while the red dashed line marks the assumed point at which the fish are subjected to treatment and transfer.



Fig. 5. Mean activity and swimming depth of fish during three delousing events (Delousing 1–3), shown for the six phases that were included in the analysis: "Day before" delousing, crowding to "7 m", crowding to "1 m", thermal "Treatment", "After" treatment and "Day after" treatment.

modes of the fish, the increased activity levels during the operations may indicate that they experienced these as stressful. While the maximum peak values in activity during the treatment phase could have been caused by mechanical manipulation due to pumping and thermal treatment, the elevated activity levels observed during crowding could only be a result of changes in the fish behaviour. Although activity levels were significantly higher during active operation phases for all delousing events, the differences in activity level between the events also implies that this response to delousing is sensitive to other external factors (e.g. time of day, differences in personnel/execution of operations, weather conditions and sea state). Conversely, the depth dynamics of the fish did not appear to be affected by delousing procedures as the only differences in swimming depth when the cage was unrestricted could be ascribed to day/night light variations. The shallower swimming during the active operation phases was an expected result of the decrease in cage depth during crowding, as this physically limited the vertical range available to the fish.

Observed individual activity patterns resembled observations that have been reported by industry, with activity peaks associated with the thermal treatment and transfer of the fish. This also harmonises with previous studies that imply that thermal stress may induce increased activity and panic behaviour in salmon (Elliott, 1991; Elliott and Elliott, 1995; Mangor-Jensen et al., 2017). In contrast, the data on swimming depth could not confirm reported observations of salmon reverting to markedly deeper waters after release into an unrestricted cage after treatment. Instead, recorded swimming depth equalled background levels measured on the days before and after treatment. This implies that the activity level of the fish may be more susceptible to disruption than swimming depth and consequently a more appropriate indicator for the responses of salmon towards delousing events, other potentially stressful operations, and cage management routines such as feeding.

4.3. Potential industrial applications

One apparent industrial application for the telemetry system used in this study could be as a component in an early warning system during crowding and delousing operations (Føre et al., 2018). Online continuous data series describing the activity dynamics of individual sentinel fish could then represent input to a Decision Support System (DSS, see Rose et al., 2016 for examples of DSS applications in agriculture) aimed at a crowding process. The DSS could then use fish activity levels combined with water temperature and light intensity to recommend whether a crowding operation should be continued, paused or terminated. This would require that activity levels are more directly linked to the health/welfare status of the fish, indicating if good welfare is provided or not. Such links could be identified through focused calibration studies where measured activity levels are correlated with data series on fish physiology and stress levels, e.g. through combined physiological-behavioural approaches (Gilmour et al., 2005). In addition, other biological and physical factors (e.g. diseases, water temperature, oxygen levels) can act as additional stressors that may lower the ability of the fish to recover from sustained high activity levels (Iversen et al., 2005) and should therefore be identified and fed into the DSS. This application would also be relevant for other operations and procedures that include crowding, such as well-boat operations for transport, or sorting of fish.

The telemetry system could also be a potential component in future systems for real-time monitoring of fish under production. For instance, the maximum or prevailing mean currents salmon may endure without risking impaired welfare/health effects have recently been identified (Remen et al., 2016; Hvas and Oppedal, 2017; Hvas et al., 2017a). When combined with knowledge on how salmon behaviour changes in response to such conditions (e.g. Johansson et al., 2014; Hvas et al., 2017b), this knowledge could shed light on the well-being of fish when exposed to changing current velocities. The telemetry system could probably detect such behavioural changes, and hence be a base component in future systems for online assessment of fish welfare in relation to current speed. This could be an increasingly relevant application as the salmon industry is presently moving farming operations further from shore, primarily due to the lack of nearshore sites (Bjelland et al., 2015). These more exposed sites often feature harsher weather conditions, larger waves and stronger currents than conventional sites, and would thus benefit from automated monitoring solutions.

To stimulate a more rapid technological development in the aquaculture industry, the Norwegian government has recently started a license arrangement with so-called development permits for producing salmon. To address the main challenges of salmon farming (e.g. sea lice, escapes or environmental impacts), many proposed concepts feature production units that differ in size, shape and/or general design from the present industrial standard (i.e. open flexible cages), with the already operative Ocean Farm 1, which is a rigid structure of 250.000 m³, being a notable example. Due to the novelty of these concepts, there is no knowledge on how fish behaviour will be affected. Acoustic telemetry could be useful for studying fish and their response to such new systems, as the maximum detection range of acoustic telemetry systems (typically up to 1 km) is sufficient to cover also substantially larger volumes of novel designs. The technology could also be used to study fish in new concepts featuring closed production units, but this would require further research on the feasibility of using acoustic telemetry in closed systems similar to that of Kolarevic et al. (2016).

4.4. Future technological improvements and research

The minimum and maximum depth and the standard deviation in depth did not yield equally interesting data as the RMS-activity and mean depth. Removing these output values from the communication scheme would relinquish more acoustic bandwidth to communicating RMS-activity and depth, leading to better density on these datatypes in the resulting dataset. Alternatively, the outputs could be exchanged with other data values from the accelerometer, such as the acceleration components representing gravity or only lateral dynamics (Kolarevic et al., 2016). Through post processing, these values could be used to gain information on the orientation and tail beat rate of the fish, respectively. New data values could also be obtained by equipping the tags with other sensors, such as magnetic sensors. By placing magnets at the inlet and outlet of the pump system used during delousing treatment, this could allow a much more precise determination of when the fish is subjected to treatment and transferred to a new cage than what was possible in this study.

Since telemetry tags are located within or on the fish, one very interesting path for new tag development could be sensors that measure physiological properties in the fish. Examples of variables that could be relevant include heart rate, respiration frequency and muscle activity. Physiological indicators could prove more sensitive towards detecting the effects of external stimuli such as environmental variations, management routines and operations. Although tags containing physiological sensors have previously been tested under laboratory conditions, e.g. in measuring muscle activity in trout (Cooke et al., 2004), and heart rate in pike (Lucas et al., 1991) and sockeye salmon (Prystay et al., 2017), inventing technology that is sufficiently robust to handle the conditions at a commercial fish farm would be both a research and engineering challenge.

5. Conclusion

This study represents an example of Precision Fish farming which is a concept where Precision Livestock Farming (PLF, Berckmans, 2004, 2014) principles are applied to commercial fish farming (Føre et al., 2018). By using a novel type of acoustic transmitter tags, data was automatically collected from the fish during all stages of several delousing events, exemplifying how this technology can be used to monitor fish during challenging operations and daily management routines at fish farms. This study generated new knowledge on the typical behaviour of Atlantic salmon and their responses towards delousing and found that salmon activity levels increased during crowding and peaked during thermal treatment. This may imply that the fish are stressed by the operation, and hence change their swimming patterns. The ability to collect such information on fish responses during operations may be vital for the development of the farming methods of the future.

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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.2018.06.060.

References

- Aaen, S.M., Helgesen, K.O., Bakke, M.J., Kaur, K., Horsberg, T.E., 2015. Drug resistance in sea lice: a threat to salmonid aquaculture. Trends Parasitol. 31 (2), 72–81.
- Anderson, M., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA + for PRIMER: Guide to Software and Statistical Methods Plymouth. PRIMER-E, UK.
- Andrew, J.E., Noble, C., Kadri, S., Jewell, H., Huntingford, F.A., 2002. The effect of demand feeding on swimming speed and feeding responses in Atlantic salmon Salmo salar L., gilthead sea bream Sparus aurata L. and European sea bass Dicentrarchus labrax L. in sea cages. Aquac. Res. 33 (7), 501–507.
- Bainbridge, R., 1958. The speed of swimming of fish as related to size and to the frequency and amplitude of the tail beat. J. Exp. Biol. 35 (1), 109–133.
- Berckmans, D., 2004. Automatic on-line monitoring of animals by precision livestock farming. In: Proceedings of the ISAH Conference on Animal Production in Europe: The Way Forward in a Changing World. vol. 1. pp. 27–31 Saint-Malo, France, October 11–13.
- Berckmans, D., 2014. Precision livestock farming technologies for welfare management in intensive livestock systems. Sci. Tech. Rev. Office Int. des Epizooties 33 (1), 189–196.

- Bjelland, H.V., Føre, M., Lader, P., Kristiansen, D., Holmen, I.M., Fredheim, A., Grøtli, E.I., Fathi, D.E., Oppedal, F., Utne, I.B., Schjølberg, I., 2015, October. Exposed aquaculture in Norway. In: OCEANS'15 MTS/IEEE. IEEE, Washington, pp. 1–10.
- Bjørn, P.A., Finstad, B., Kristoffersen, R., 2001. Salmon lice infection of wild sea trout and Arctic char in marine and freshwaters: the effects of salmon farms. Aquac. Res. 32 (12), 947–962.
- Cooke, S.J., Thorstad, E.B., Hinch, S.G., 2004. Activity and energetics of free-swimming fish: insights from electromyogram telemetry. Fish Fisheries 5 (1), 21–52 (78, 163-172).
- Elliott, J.M., 1991. Tolerance and resistance to thermal stress in juvenile Atlantic salmon, Salmo salar. Freshw. Biol. 25 (1), 61–70.
- Elliott, J.M., Elliott, J.A., 1995. The effect of the rate of temperature increase on the critical thermal maximum for parr of Atlantic salmon and brown trout. J. Fish Biol. 47 (5), 917–919.
- Erikson, U., Gansel, L., Frank, K., Svendsen, E., Digre, H., 2016. Crowding of Atlantic salmon in net-pen before slaughter. Aquaculture 465, 395–400.
- Fernö, A., Huse, I., Juell, J.E., Bjordal, Å., 1995. Vertical distribution of Atlantic salmon (Salmo salar L.) in net pens: trade-off between surface light avoidance and food attraction. Aquaculture 132 (3), 285–296.
- Finstad, B., Bjørn, P.A., Grimnes, A., Hvidsten, N.A., 2000. Laboratory and field investigations of salmon lice [*Lepeophtheirus salmonis* (Krøyer)] infestation on Atlantic salmon (*Salmo salar* L.) post-smolts. Aquac. Res. 31 (11), 795–803.
- Føre, M., Alfredsen, J.A., Gronningsater, A., 2011. Development of two telemetry-based systems for monitoring the feeding behaviour of Atlantic salmon (*Salmo salar L.*) in aquaculture sea-cages. Comput. Electron. Agric. 76 (2), 240–251.
- Føre, M., Frank, K., Dempster, T., Alfredsen, J.A., Høy, E., 2017. Biomonitoring using tagged sentinel fish and acoustic telemetry in commercial salmon aquaculture: a feasibility study. Aquac. Eng. 78, 163–172.
- Føre, M., Frank, K., Norton, T., Svendsen, E., Alfredsen, J.A., Dempster, T., Eguiraun, H., Watson, W., Stahl, A., Sunde, L.M., Schellewald, C., 2018. Precision fish farming: a new framework to improve production in aquaculture. Biosyst. Eng (In press).
- Gilmour, K.M., Wilson, R.W., Sloman, K.A., 2005. The integration of behaviour into comparative physiology. Physiol. Biochem. Zool. 78 (5), 669–678.
- Heupel, M.R., Semmens, J.M., Hobday, A.J., 2006. Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. Mar. Freshw. Res. 57 (1), 1–13.
- Huntingford, F.A., Adams, C., Braithwaite, V.A., Kadri, S., Pottinger, T.G., Sandøe, P., Turnbull, J.F., 2006. Current issues in fish welfare. J. Fish Biol. 68 (2), 332–372.
- Hussey, N.E., Kessel, S.T., Aarestrup, K., Cooke, S.J., Cowley, P.D., Fisk, A.T., Harcourt, R.G., Holland, K.N., Iverson, S.J., Kocik, J.F., Flemming, J.E.M., 2015. Aquatic animal telemetry: a panoramic window into the underwater world. Science 348 (6240), 1255642.
- Hvas, M., Oppedal, F., 2017. Sustained swimming capacity of Atlantic salmon. Aquacult. Environ. Interact. 9, 361–369.
- Hvas, M., Folkedal, O., Imsland, A., Oppedal, F., 2017a. The effect of thermal acclimation on aerobic scope and critical swimming speed in Atlantic salmon, *Salmo salar*. J. Exp. Biol. 220 (15), 2757–2764.
- Hvas, M., Folkedal, O., Solstorm, D., Vågseth, T., Fosse, J.O., Gansel, L.C., Oppedal, F., 2017b. Assessing swimming capacity and schooling behaviour in farmed Atlantic salmon Salmo salar with experimental push-cases. Aquaculture 473, 423–429.
- Igboeli, O.O., Burka, J.F., Fast, M.D., 2014. Lepeophtheirus salmonis: a persisting challenge for salmon aquaculture. Anim. Front. 4 (1), 22–32.
- Iversen, M., Finstad, B., McKinley, R.S., Eliassen, R.A., Carlsen, K.T., Evjen, T., 2005. Stress responses in Atlantic salmon (*Salmo salar* L.) smolts during commercial well boat transports, and effects on survival after transfer to sea. Aquaculture 243 (1–4), 373–382.
- Iversen, A., Andreassen, O., Hermansen, Ø., Larsen, T.A., Terjesen, B.F., 2013. Oppdrettsteknologi og konkurranseposisjon. Nofima report 32/2013.
- Jensen, J.L.A., Rikardsen, A.H., Thorstad, E.B., Suhr, A.H., Davidsen, J.G., Primicerio, R., 2014. Water temperatures influence the marine area use of *Salvelinus alpinus* and *Salmo trutta*. J. Fish Biol. 84 (6), 1640–1653.
- Johansson, D., Ruohonen, K., Kiessling, A., Oppedal, F., Stiansen, J.E., Kelly, M., Juell, J.E., 2006. Effect of environmental factors on swimming depth preferences of Atlantic salmon (*Salmo salar* L.) and temporal and spatial variations in oxygen levels in sea cages at a fjord site. Aquaculture 254 (1), 594–605.
- Johansson, D., Laursen, F., Fernö, A., Fosseidengen, J.E., Klebert, P., Stien, L.H., Vågseth, T., Oppedal, F., 2014. The interaction between water currents and salmon swimming behaviour in sea cages. PloS one 9 (5), e97635.
- Juell, J.E., Westerberg, H., 1993. An ultrasonic telemetric system for automatic positioning of individual fish used to track Atlantic salmon (*Salmo salar* L.) in a sea cage. Aquac. Eng. 12 (1), 1–18.
- Kolarevic, J., Aas-Hansen, Ø., Espmark, Å., Baeverfjord, G., Terjesen, B.F., Damsgård, B., 2016. The use of acoustic acceleration transmitter tags for monitoring of Atlantic salmon swimming activity in recirculating aquaculture systems (RAS). Aquac. Eng. 72, 30–39.
- Larsen, M.H., Johnsson, J.I., Näslund, J., Thomassen, S.T., Aarestrup, K., 2015. Reduced rearing density increases postrelease migration success of Atlantic salmon (Salmo salar) smolts. Can. J. Fish. Aquat. Sci. 73 (5), 804–810.
- Lekang, O.I., Salas-Bringas, C., Bostock, J.C., 2016. Challenges and emerging technical solutions in on-growing salmon farming. Aquac. Int. 24 (3), 757–766.
- Lucas, M.C., Priede, I.G., Armstrong, J.D., Gindy, A.N.Z., Vera, L., 1991. Direct measurements of metabolism, activity and feeding behaviour of pike, *Esox lucius* L., in the wild, by the use of heart rate telemetry. J. Fish Biol. 39 (3), 325–345.
- Mangor-Jensen, A., Stien, L.H., Fosseidengen, J.E., Mangor-Jensen, R., 2017. Varmebehandling av laks i forbindelse med avlusing. Institute of Marine Research report, pp. 7/2017 (In Norwegian).

- Moore, A., Russell, I.C., Potter, E.C.E., 1990. The effects of intraperitoneally implanted dummy acoustic transmitters on the behaviour and physiology of juvenile Atlantic salmon, Salmo salar L. J. Fish Biol. 37 (5), 713–721.
- Noble, C., Nilsson, J., Stien, L.H., Iversen, M.H., Kolarevic, J., Gismervik, K., 2018. Velferdsindikatorer for oppdrettslaks: Hvordan vurdere og dokumentere fiskevelferd. (In Norwegian).
- Oppedal, F., Dempster, T., Stien, L.H., 2011. Environmental drivers of Atlantic salmon behaviour in sea-cages: a review. Aquaculture 311 (1), 1–18.
- Plantalech Manel-La, N., Thorstad, E.B., Davidsen, J.G., Økland, F., Sivertsgård, R., McKinley, R.S., Finstad, B., 2009. Vertical movements of Atlantic salmon post-smolts relative to measures of salinity and water temperature during the first phase of the marine migration. Fish. Manag. Ecol. 16 (2), 147–154.
- Powell, M.D., Reynolds, P., Kristensen, T., 2015. Freshwater treatment of amoebic gill disease and sea-lice in seawater salmon production: considerations of water chemistry and fish welfare in Norway. Aquaculture 448, 18–28.
- Prystay, T.S., Eliason, E.J., Lawrence, M.J., Dick, M., Brownscombe, J.W., Patterson, D.A., Crossin, G.T., Hinch, S.G., Cooke, S.J., 2017. The influence of water temperature on sockeye salmon heart rate recovery following simulated fisheries interactions. Conserv. Physiol. 5 (1).

Remen, M., Solstorm, F., Bui, S., Klebert, P., Vågseth, T., Solstorm, D., Hvas, M., Oppedal,

- F., 2016. Critical swimming speed in groups of Atlantic salmon Salmo salar. Aquacult. Environ. Interact. 8, 659–664.
- Rillahan, C., Chambers, M., Howell, W.H., Watson, W.H., 2009. A self-contained system for observing and quantifying the behavior of Atlantic cod, *Gadus morhua*, in an offshore aquaculture cage. Aquaculture 293 (1), 49–56.
- Rose, D.C., Sutherland, W.J., Parker, C., Lobley, M., Winter, M., Morris, C., Twining, S., Ffoulkes, C., Amano, T., Dicks, L.V., 2016. Decision support tools for agriculture: towards effective design and delivery. Agric. Syst. 149, 165–174.
- Shao, Z.J., 2001. Aquaculture pharmaceuticals and biologicals: current perspectives and future possibilities. Adv. Drug Deliv. Rev. 50 (3), 229–243.
- Skilbrei, O.T., Holst, J.C., Asplin, L., Holm, M., 2009. Vertical movements of "escaped" farmed Atlantic salmon (Salmo salar L.)—a simulation study in a western Norwegian fjord. ICES J. Mar. Sci. 66 (2), 278–288.
- Thorstad, E.B., Økland, F., Aarestrup, K., Heggberget, T.G., 2008. Factors affecting the within-river spawning migration of Atlantic salmon, with emphasis on human impacts. Rev. Fish Biol. Fish. 18 (4), 345–371.
- Ward, D., Føre, M., Howell, W.H., Watson, W., 2012. The influence of stocking density on the swimming behavior of adult Atlantic cod, *Gadus morhua*, in a near shore net pen. J. World Aquacult. Soc. 43 (5), 621–634.