Waves and currents decrease the available space in a salmon cage

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Abstract

Due to increasing demand for salmon and environmental barriers preventing expansion in established sites, salmon farmers seek to move or expand their production to more exposed sites. In this study we investigate the effects of strong currents and waves on the behaviour of salmon and how they choose to use the space available to them. Using video cameras and echo sounders, we show that fish prefer to use the entire water column, narrowing their range only as a response to cage deformation, waves, or daylight. Conversely, fish show strong horizontal preference, mostly occupying the portions of the cage exposed to currents. Additionally, waves cause salmon to move away from the sides of the cage. Even when strong currents and waves decrease the amount of available space, salmon choose to occupy the more exposed part of the cage. This indicates that at least with good water exchange, the high biomass caused by limited vertical space is not so aversive that salmon choose to move to less desirable areas of the cage. However, the dispersal throughout the entire available water column indicates that keeping the cone portion of the cage available in strong currents would be beneficial to salmon welfare.

Introduction

Aquaculture is a major provider of fin fish protein consumed globally, accounting for approximately 52% of all fish produced for human consumption [1]. In aquaculture, Atlantic Salmon accounts for only 4.5% of production in weight, but 19% in value, largely due to the popularity of salmon sushi. While aquaculture production is increasing globally, salmon production in the Atlantic is stagnating. The causes mainly relate to complete exploitation of available farming sites, with pollution and parasite infestations being the major factors limiting expansion in near-shore sites [2].

Salmon lice (*Lepeophtheirus salmonis*) are a major parasite in Atlantic salmon farming. They spend their parasitic life stages on the salmon where they consume mucous, blood, and skin, which leads to sores and in extreme cases, mortality [3,4]. Even sub-lethally, salmon lice are a cause of poor welfare due to the stress and pain caused both by the parasites themselves and the removal methods [5,6].

Because of the ever escalating challenges posed by salmon lice and the limitations put on biomass in near shore sites, the salmon aquaculture industry is making 1

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investments in adapting current farming methods. One such adaptation is to move farms out to more exposed locations where higher water exchange can mitigate pollution and possibly dilute infectious sea lice [7,8]. At the current rate of development, salmon will experience substantially larger waves in substantially different farm constructions than those being used in industry for the last 20 years [9].

Due to the forthcoming changes in salmon aquaculture, much work has been carried out in order to determine how well salmon are able to cope with the currently most extreme conditions [8]. From these studies, some information is available on swimming speed capacity [10], sensitivity to variation in temperature and oxygen saturation [11–14], swimming energy expenditure, and how a variety of these factors affect growth and feed conversion [15–17].

Recently, work has also been carried out on how behaviour is affected by waves, mostly investigating vertical preference and swimming effort [18, 19]. Data on how salmon behaviour and welfare is affected by cage deformation, are still limited, however. Furthermore, the combination of waves and currents and their effect on behaviour has not yet been thoroughly investigated.

In addition to increasing demand for salmon driving industry to innovate, there is also an increased awareness of fish welfare considerations [20, 21]. This means that there is growing consumer pressure for not only environmental certifications such as ASC, but also for assurances that the farms can deliver a minimum welfare standard [22]. Being able to farm fish in exposed locations without compromising on welfare requires extensive knowledge of how these new conditions will affect the fish. While most salmon farmers have intimate knowledge of already established sites, it is still necessary to be able to generalise such knowledge to new and more exposed sites. This study is an attempt at detailing how salmon are affected by a combination of many environmental factors and how they interact, particularly the combination of currents and waves.

Here, we monitor fish in a cage exposed to both currents and waves throughout the winter months of 2019/2020.

We predict that currents cause fish to move upwards in the water column, and that this is at least partially caused by the cage bottom being pushed upwards by the current.

We predict that daylight and waves will cause the salmon to move downwards in the water column, and that situations where large waves and strong currents coincide is where salmon have the most limited space available to them.

Materials and methods

Field site

Work was carried out at Hiddenfjord's "Velbastaður" salmon farm on the Faroe Islands, 51 which is a site that is exposed to strong tidal currents as well as large waves in winter. The cages are arranged in a straight line along the coast, which is oriented close to a 53 Northwest-Southeast axis (Fig 1). A small island ("Hestur") west of the farm creates a 54 strait through which tidal currents move, alternating between northbound and southbound currents. Due to the hydrodynamic conditions at the site, the side of the 56 farm nearer the shore is more sheltered than the outer side. Depending on wind 57 direction, waves enter the strait either from the south or north of Hestur, so either the 58 southernmost or the northernmost cage will receive a larger portion of the wave energy.

Fig 1. Study site. The map shows precise close up location of the farm and study cage with 5 m depth contours as well as zoomed out maps of general location in relation to surrounding islands with 10 m depth contours.

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For the purposes of this study, the southernmost cage was selected for observation. Being located at one end of the row of cages, it was highly exposed to currents, especially from the south. Additionally, the cage was expected to be exposed to waves entering the strait from either side of Hestur.

The cage was stocked with 112 thousand salmon with a mean body length of 54.0 ± 4.1 cm, weighing 2.16 ± 0.6 kg, which amounted to an approximate biomass of 15 kg m³-1. Additionally, the cage housed approximately 10 thousand lumpfish (*Cyclopterus lumpus*). The fish were fed using air driven surface feed spreaders regulated using a feed camera, which detected uneaten pellets.

Equipment setup

To monitor waves and currents, two Acoustic Doppler Current Profilers (ADCPs) were 70 deployed: one AWAC directly north of the northernmost cage and one Sentinel V 71 directly south of the study cage. Both profilers were set up to collect hourly wave data 72 and current data every ten minutes. To monitor vertical distribution of fish within the 73 cage, two echo sounders were attached to the cage bottom, both positioned half way 74 between the centre and side of the cage at opposite sides parallel to the coast line. The 75 echo sounders were suspended from the bottom of the cage looking up, thereby 76 recording distance to the surface as well as any fish within the echo sounder beam. This 77 allowed us to measure the depth of the cage as well as which parts of the water column 78 were occupied by fish. The echo sounders were equipped with sensors measuring tilt and 79 pressure. These were used to detect any instances where deviations from vertical would 80 invalidate distance data and to validate the distance to the surface measured by the 81 echo sounders. The echo sounders were set up to ping once every four seconds and tilt 82 sensors recorded tilt every five seconds. In addition to the echo sounders, six pressure 83 sensors were attached to the cage in order to properly account for any cage deformation 84 that may occur. These were set up to record pressure every five seconds. To monitor fish behaviour such as swimming effort, shoal cohesion, and swimming direction as well 86 as collisions with the cage netting and jumping, five video cameras were set up within 87 the cage. In the centre of the cage was a camera used by the farmers for feed 88 monitoring ("Feed camera"). Three cameras were at the bottom looking up located approximately equidistantly around the edge of the cage, one towards the south where 90 northbound tidal currents entered the cage ("South"), one towards the north where 91 southbound tidal currents entered the cage ("North") and one towards the east, which 92 was the most sheltered location in the cage ("East"). One camera was placed on the 93 side of the cage at five metres depth looking inward ("Inwards") near the "South" 94 camera (Fig S2). Camera "North" and "South" were positioned such that they would 95 capture current related swimming behaviour, such as maintaining position against the 96 current as well as any potential changes caused by waves. The more sheltered camera 97 was used to record fish avoiding currents or waves and whether consistent swimming 98 behaviour (for example circling the cage) persisted throughout the cage. The camera 99 looking inwards was used to capture close up video of fish either orienting towards the 100 current or swimming alongside the edge of the cage as well as capturing fish near the 101 surface of the water. Finally, the feed camera was used to capture feeding, jumping, and 102 presence within the centre of the cage outside of feeding times. Details about the 103 instruments can be found in Table 1. 104

Fig 2. Layout of equipment. Aerial and side on view of the study cage with the location of echo sounders, pressure sensors and video cameras. Camera viewing angles are approximate. The camera with diagonal stripes is the feed camera, which was nearer the surface than the bottom mounted cameras.

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Table 1. Equipment deployed.		
Type	Manufacturer	Specifications
ADCP	Teledyne	RDI Sentinel V 500 kHz with 50m range
ADCP	Nortek	AWAC 600 kHz with 50m range
Echo sounder	Simrad	EK 15 200 kHz 26° viewing angle
Tilt sensor	Star-Oddi	Starmon Tilt; tilt, pressure, and temperature logger calibrated to 50m
Pressure sensor	RBR	RBRSolo 3 D; Depth logger, range 1700m, calibrated to 50m
Video camera	JT Electric	

Table 1. Equipment deployed.

Location of equipment in the cage can be seen in Figure S2.

Data collection

Data collection was carried out from the first of November 2019 to the 15th of February 2020 in order to capture as much as possible of both bad weather events as well as different tidal conditions.

Video cameras were remotely controlled using iSpy [23] and scheduled to record for five minutes each once per week. In addition to these baseline recordings, alternative schedules were enacted for bad weather events to record 3-4 times each day to capture behaviours in large wave conditions as well as different current conditions. At the end of the trial, videos to extract behaviours from were chosen based on current and wave data from ADCPs to represent a range in conditions.

Echo data was recorded continuously on a local hard drive and then uploaded remotely to a cloud server. Current and wave data was recorded locally and downloaded when the ADCPs were recovered. Tilt and pressure sensors stored data locally and data were downloaded when the sensors were recovered.

During the sampling period, Operational Welfare Indicators (OWIs) were recorded 119 every two weeks when weather allowed (Table 2). Prior to this, welfare indicators were 120 collected on a more ad-hoc basis, and finally again at harvest. The large gap in data 121 from March until harvest is due to the COVID-19 pandemic preventing fieldwork. The 122 OWIs were collected from 10 fish from each cage in connection with routine louse 123 counting. The fish were caught using a dip net, anaesthetised in Finquel (MS-222) and 124 lice numbers and gill condition were recorded before OWIs were recorded. After 125 regaining consciousness in fresh seawater, they were released back into the cages. 126

Fins Sclera Type Pupil Snout Skin 0 A little wear Black White No injury No injury 1 White spot 10% black Slightly worn < 2.5 cmDamaged $\overline{2}$ Missing fins Big white spot 25% black Wound $> 2.5 \,\,\mathrm{cm}$ 3 Bleeding > 50% black Bleeding

 Table 2. Operational welfare scores recorded.

Each fish was scored on their overall condition, so both eyes and all fins were checked and the greatest score recorded for each. 105 106

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Data processing

Behaviours extracted from videos depended on the location of the camera. The cameras 128 that were near the edge of the cage looking up were used to record collisions with the 129 net while the cameras that were nearer the surface ("Inwards and "Feed") were used to 130 record jumping behaviour, feeding and presence of fish near the surface. All cameras 131 were used to record swimming effort determined as the time taken to beat with the tail 132 three times (and hence converted into tail beats per second "tbps"). Additionally, a 133 qualitative measure of number of fish present was recorded; "No fish"; fewer than 5 fish 134 visible, "Few fish"; Fewer than 50 fish visible, "Many fish"; More than 50 fish visible. 135 Finally, general swimming direction, in cases where more than 80% of the fish were 136 swimming in the same direction, and whether the fish were shoaling was recorded from 137 all locations. Behaviours were extracted using BORIS [24] and swimming effort was 138 recorded using VLC [25] with the "Time" extension [26]. 139

Echo sounder data was extracted from the raw data files using the "oce" package in R [27] and exported for further processing in Python [28] (github). First, the water surface was found. Second, data above the surface was removed, and depth adjusted to the surface rather than the distance from the echo sounder. Third, the data were binned into 5 minute intervals and 16.5 cm depths and S_v (acoustic back scattering strength) averages were exported. Once data had been exported, the exported files were read into R, where the surface and the lowest 4.5 metres (below the cage bottom) were removed.

Data analysis

Analysis was carried out in R [29] and tidyverse [30] using the packages lubridate [31] and circular [32] for data cleanup, lme4 [33] and lmerTest [34] for statistical inference, and ggplot2 [35] with colorspace [36] was used for plotting . 150

For video data, the following methods were used; to analyse swimming mode, a general linearised mixed effects model was used with a binomial (log link) family specified where each video was classified as most fish being in either swimming mode, with current strength, current direction, and wave height as predictors, and with camera as the random intercept term. The effects of environmental conditions on swimming effort was analysed using linear models. Nearness to camera was analysed using a general linearised mixed effects model with wave height (Hm0) and period (Tp) as predictors and cameras as random intercept term.

Linear models were used to estimate the effects of environmental variables on the 159 "evenness" of fish dispersal within the cage using raw S_v as a proxy for relative fish 160 density. The residuals from these models indicated how variable S_v was, so large 161 residuals indicated "clumping" and small residuals indicated evenly dispersed fish. We 162 also used linear models to how estimate how environmental variables affected where in 163 the water column the salmon were, weighing the depth variable by S_v . While it is 164 possible to estimate real biomass from the back scatter [37], we did not calibrate gain to 165 do this, as we were more interested in relative changes rather than biomass estimation. 166

Ethics statement

This study was not a manipulative experiment. However, we did install video cameras within the cage as well as echo sounders underneath it. We do not have reason to believe that these affected the salmon, but they were a deviation from the regular routines on the farm. We also handled the fish in order to perform OWI monitoring, but this was already part of the management routine at Hiddenfjord farms, so didn't deviate from normal practices. Regardless, ethical approval was still applied for and given by Fiskaaling's Ethical Board (Approval number 007).

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Results

Environmental conditions

During the monitoring period, currents at the north of the farm ranged from 0.00 to 0.49 m s^{-1} with a mean current of 0.10 m s⁻¹. At the south of the farm, conditions were similar with a range between 0.06 and 0.51 m s⁻¹, and with stronger currents on average (0.16 m s^{-1}) (Fig 3). Flow direction was mostly bimodal switching between a north-westerly current and a south-easterly current, hereafter referred to as Northbound and Southbound current (Fig 3). Due to the difference in particularly current direction between the two ADCPs, the Sentinel V or a tidal analysis built on the data from the Sentinel V were used for further data analysis using current as a predictor.

Fig 3. Current and wave directions from two current profilers. Wind roses of the currents and waves measured by the two profilers. Currents are towards the indicated directions, waves travel from the indicated directions

The maximum significant wave height (Hm0) measured north of the farm was 3.02 185 m. South of the farm it measured (Hs) 3.24 m (Fig 4). Wave period (Tp) ranged from 186 2.07 to 22.55 seconds. Low and high wave heights were recorded at the same time in 187 both ADCPs, indicating that they were exposed to similar wave heights, though wave 188 directions differed between the two locations, with waves coming from the south rarely 189 being measured in the Sentinel V (Fig 3). Even though wave directions differed between 190 the two ADCPs, the wave data from the AWAC was used in analyses going forward due 191 to the longer measurement period. 192

Fig 4. Wave height measured by two current profilers. The wave heights measured throughout the monitoring period. The Sentinel V was located south of the study cage whereas the AWAC was located north of the farm.

Cage deformation

The bottom of the cage moved up from almost -20 m up to -6 m depth. The sides of the 194 cage did not move as much, varying approximately three metres in depth between -9 m 195 and -6 m (Fig 5). The direction of current affected how the pressure sensors moved with 196 oncoming current causing the bottom of the net to move up farther than current from 197 the lee side of the cage. In other words, in a northbound current, the bottom of the 198 south side of the cage moved up more whereas in a southbound current, the bottom of 199 the north side of the cage moved up more. The southern side of the cage was 200 particularly affected in a northbound current, as there were no cages south of the study 201 cage to shelter it. 202

Fig 5. Depth measured by pressure sensors. Pressure sensors were located in eight locations at the bottom of the cage. Four sensors were located at the bottom of the side net (Side- west, south, east, and north) and four were half way from the side to the centre (Bottom- west, south, east, and north)

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Video observations

Swimming mode

There was a connection between current speed and swimming mode. The number of videos where the most prevalent swimming mode observed was keeping place against the current increased with current speed. This effect was decreased in southbound current (Current speed; z = 3.643, residual df = 151, P < 0.001, Flow direction; z = -3.683, residual df = 151, P < 0.001, Fig 6), which is consistent with the indication from the pressure sensors that northbound current affected the cage more than southbound current.

Fig 6. Proportion of time spent by the majority of the fish in frame

keeping against the current. Points are proportion of time where the majority of the fish were keeping place against the current in a video and lines are model predictions of the probability of a video having fish keeping place against the current a majority of the time. Lighter colour signifies a northward current direction whereas a darker colour signifies a southward current direction

Swimming effort

Because fish recorded for swimming effort were more likely to be fish that spent a longer time in frame than those who spent a short time in frame, there are likely to be differences between these fish and the general population within the cage.

Swimming mode significantly affected tail beats per second with fish beating faster 216 with their tails when not swimming against the current ($F_{1.445} = 28.34$, P < 0.001). 217 Because of this change in swimming effort related to swimming mode, data were 218 analysed with swimming mode as a random predictor in a linear mixed effects model. 219 Swimming effort increased with current speed in northbound current, but this 220 connection was not present in southbound current (t = -2.358, df = 440, P = 0.019, 221 Fig 7). Wave length interacted with current speed in such a way that in weak current, 222 fish had slower tail beats in shorter waves, but in stronger currents, they had faster tail 223 beats in longer waves (t = 2.309, DF = 440, P = 0.021, Fig 7). 224

Fig 7. Swimming effort measured in tail beats per second (tbps) over

current. Swimming effort in fish keeping place against the current in northbound and southbound currents. Shading indicates wave length less than 12 seconds (lighter colour) and more than 12 seconds (darker colour).

Cage perimeter interactions

Fish showed great horizontal preference ($F_{4,160} = 8.641$, P < 0.001) with the "South" 226 camera recording "Many" fish 36% of the time compared to the "East" camera, which 227 only recorded "Many" fish 4.5 % of the time. The amount of time where "Many" fish 228 were recorded in cameras generally decreased in large waves (both high Hm0 and Tp) 229 $(F_{3.161} = 3.398, P = 0.019, residual df = 159)$, indicating movement away from the sides 230 of the cage, and in case of the feed camera, the surface. However, in taller waves the 231 amount of fish seen in the "East" camera increased, with the proportion of time when 232 any ("Some", "Many", or "Shoal") fish were visible in the "East" camera increasing 233 from 50% in waves smaller than 1 m to almost 100% in waves larger than 1 m (F_{4,155} = 234 7.545, P < 0.001). 235

Collisions with the net decreased in larger waves, but less so if current was strong too (z = 2.431, DF = 41, P < 0.015).

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Shoal position

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Fish avoided the surface during the day (Fig 8) and this pattern persisted regardless of hydrodynamic conditions.

Fig 8. Depth and dispersal of fish seen in the south echo sounder over hour in the day when current is weak. Back scatter strength (S_v) indicates fish density, with higher values (-70) indicating many fish and lower values (-100) indicating fewer fish. Data presenting current stronger than 0.11 m s⁻¹ is not included for simplicity.

As current increased, the fish narrowed their vertical distribution within the water column resulting in stronger localised S_v (South echo sounder; $F_{3,250864} = 2993$, P < 242 0.001, North echo sounder; $F_{3,239438} = 1836$, P < 0.001) and greater residuals (South echo sounder; $F_{3,250864} = 759.1$, P < 0.001, North echo sounder; $F_{3,239438} = 1265$, P < 244 0.001) as opposed to a lower signal with more even dispersal in weaker currents (Fig 9). 245

Fish moved upwards in the water column in stronger current. The side of the cage and direction of current affected the degree to which the shoals moved up (South echo sounder; $F_{3,218622} = 8665$, P < 0.001, North echo sounder; $F_{3,206399} = 7170$, P < 0.001, Fig 9). They still avoided the surface during the day, resulting in a greater concentration of fish below 5m depth (Fig 9).

Fig 9. Depth and dispersal of fish over current. The upper and lower panels indicate the two echo sounders, and the left and right panels the direction of current. Back scatter strength (S_v) indicates fish density, with higher values (-70) indicating many fish and lower values (-100) indicating fewer fish. Data presenting shoal depth during the night is not included for simplicity.

In an effect similar to that of daylight, waves caused fish to move away from the surface (South echo sounder; $F_{4,218621} = 6307$, P < 0.001, North echo sounder; $F_{3,206399} = 6026$, P < 0.001). However, at the side of the cage where current entered, fish moved upward, countering the effect of waves (Fig 10).

Fig 10. Depth and dispersal of fish over wave height (Hm0) in weak

current. The left and right panels are the south and north echo sounder. Data where current exceeded 0.11 m s⁻¹ are excluded. Signal strength (S_v) indicates fish density with higher values (-70) indicating many fish and lower values (-100) indicating fewer fish. Data presenting shoal depth during the day not included for simplicity.

Welfare

While injury scores were low throughout the entire production cycle with 90% of fish 256 scoring three or lower in injuries most of the time, there is a period in January and February where more than 25% of the fish have a score of four or higher. In late June, when the fish were harvested, higher scoring fish had decreased again to less than 20%259 (Fig 11). 260

Fig 11. Distribution of welfare scores over time Proportion of fish with summed welfare scores between 0 and 9. A score of zero indicates that the fish had no injury at all and higher scores are more injuries.

Discussion

At the study site, currents caused the bottom of the salmon cage to move upwards from 262 almost 20 metres up to almost 5 metres in extremes. The majority of the deformation is 263 in the cone part of the cage, which is not included in biomass calculations for stocking 264 purposes. Therefore, this deformation does not cause a lack of space in the cage in 265 terms of biomass limitations, but rather displaces salmon that might otherwise choose 266 to occupy that space.

Salmon at this study site, did prefer to occupy the cone portion of the cage during 268 the day, while they occupied the entire water column during the night. This caused a 269 concentration of fish above the cone (upwards of 10m) in stronger currents, and an even 270 tighter concentration of fish between 5-10 metres during the day. 27

In addition to the effect of daylight and current, waves also affected vertical shoal 272 positioning. At night, salmon avoided the surface in tall waves similarly to how they 273 respond to daylight. However, due to the effect of cage deformation, this preference was 274 not so clear on the side of the cage affected by oncoming current, as surface aversion 275 due to waves was weaker than that caused by daylight. 276

As expected, salmon swimming mode was affected by current speed with a majority 277 of fish changing from swimming freely to maintaining their position against the current 278 once current speed reached 0.2 ms⁻¹. Northbound current more strongly affected 279 swimming effort, most likely due to the lee effect of the adjacent cages in a southbound 280 current. Additionally, longer waves increased salmon swimming effort. 281

Taken together, the results indicate that salmon prefer to use the entire water 282 column available to them, and only move upwards in the water column due to cage 283 deformation and downwards due to waves and daylight. However, the data suggest that 284 they do not use all of the horizontal space available to them. There are a few potential 285 explanations for this. Two likely candidates are; 1) water quality is undesirable in the more sheltered areas of the cage, 2) salmon prefer to occupy a space with current. We 287 have no reason to suspect poor water quality in the sheltered parts of the cage, 288 particularly as this study was carried out in the winter months with a lot of mixing in 289 the water column and good general water exchange, even in the sheltered areas. 290 Therefore, the more likely explanation is that the salmon actively choose the more 291 exposed side of the cage rather than avoid the sheltered side. 292

As opposed to our previous paper [18], swimming effort did not decrease in larger 293 waves, but rather increased. However, this effect was most apparent in stronger currents, 294 which were not present at the previous study site. Additionally, in our previous paper, 295 wave data did not coincide with video data, so it is possible that what looks like large 296 waves on camera is not the equivalent of large measured waves. Particularly shorter 297 waves may look more extreme than long waves due to the more rapid vertical movement. 298

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In the current study, salmon increasingly avoid the surface as the wave height increases. 299 While we only had good data up to 2 m wave height (Hm0), the trend indicates that 300 salmon will dive further down in even larger waves. When combining cage deformation 301 due to currents and surface and side avoidance due to waves, the available space decreases dramatically when all these conditions affect the fish at the same time. 303

In our previous paper, it was not clear whether the change in vertical position 304 caused by current was related to cage deformation or a choice by the salmon. In this 305 paper, we show that the bottom of the shoal moves upwards almost exactly as the 306 bottom of the cage. Therefore, there is no evidence to suggest that the salmon move 307 away from the bottom of the cage at any time, rather that they adjust to the change in 308 space available to them. However, there was horizontal preference in this study related 309 to current with fish preferring areas within the cage exposed to more current to areas 310 with little to no current. Therefore, given zero cage deformation, the factors affecting 311 vertical distribution of salmon within a cage are surface related (such as waves and 312 daylight) and factors affecting horizontal distribution within a cage are current and 313 wave related with fish preferring to swim in more current, but moving inwards away 314 from the net in large waves. This move away from the sides was probably the reason for 315 why observed collisions with the net decreased in larger waves. However, there appears 316 to be an effect of weather on welfare indicators with fish scoring higher in the 317 examinations carried out after large wave events in January and February 2020 318 compared to late 2019. As fewer collisions were seen, the causes of these injuries must 319 happen off-camera, such as elsewhere in the cage or at night. However, during the large 320 wave events, the cameras lost power, which resulted in limited footage from the most 321 extreme conditioned at the farm. It is possible that the fish were injured during these 322 periods, though it is impossible to say for certain. 323

Conclusion

The strongest effects that currents and waves have on salmon relate to how they 325 decrease the space available to the fish. Salmon actively choose to occupy areas in the 326 cage exposed to stronger currents, but avoid the surface and sides in large waves. For 327 farming in new sites exposed to strong currents and potentially also in currently used 328 sites, one ought to consider making the cone portion of the cage available to the fish 329 even in stronger currents, as this will provide more space for them. This is particularly 330 relevant during the day, when waves are large, and if the biomass is high, for example 331 close to harvest. It is important to consider that unlike the effect of daylight, which 332 only decreases the vertical availability of space, waves decrease the effective diameter of 333 the cage, greatly reducing the volume of the cage. 334

Supporting information

We would like to thank Hiddenfjord for cooperating with us in this project. Without 336 access to their farm and the help of their staff on site, this work would not be possible. 337

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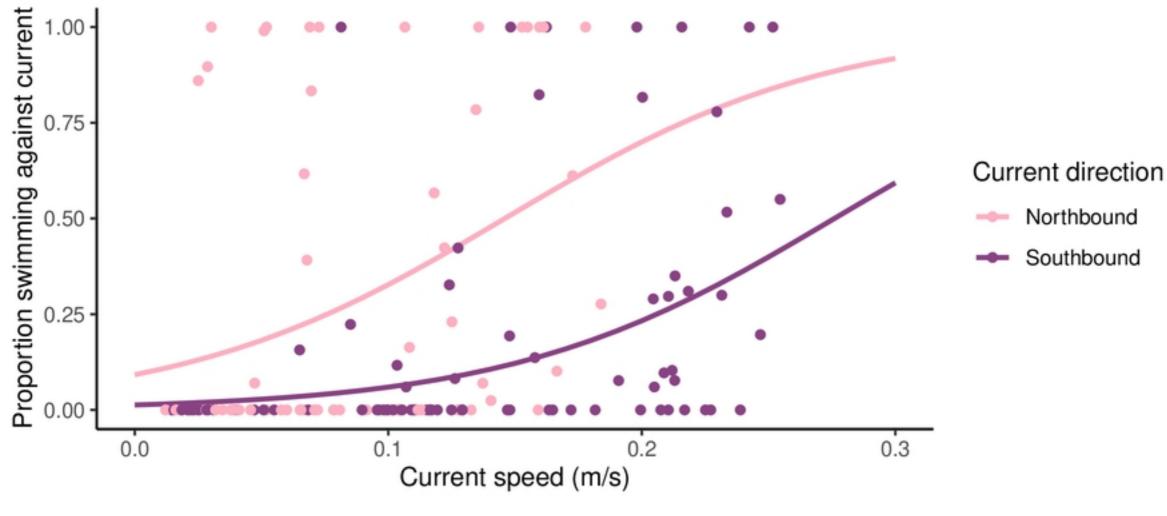
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North echosounder

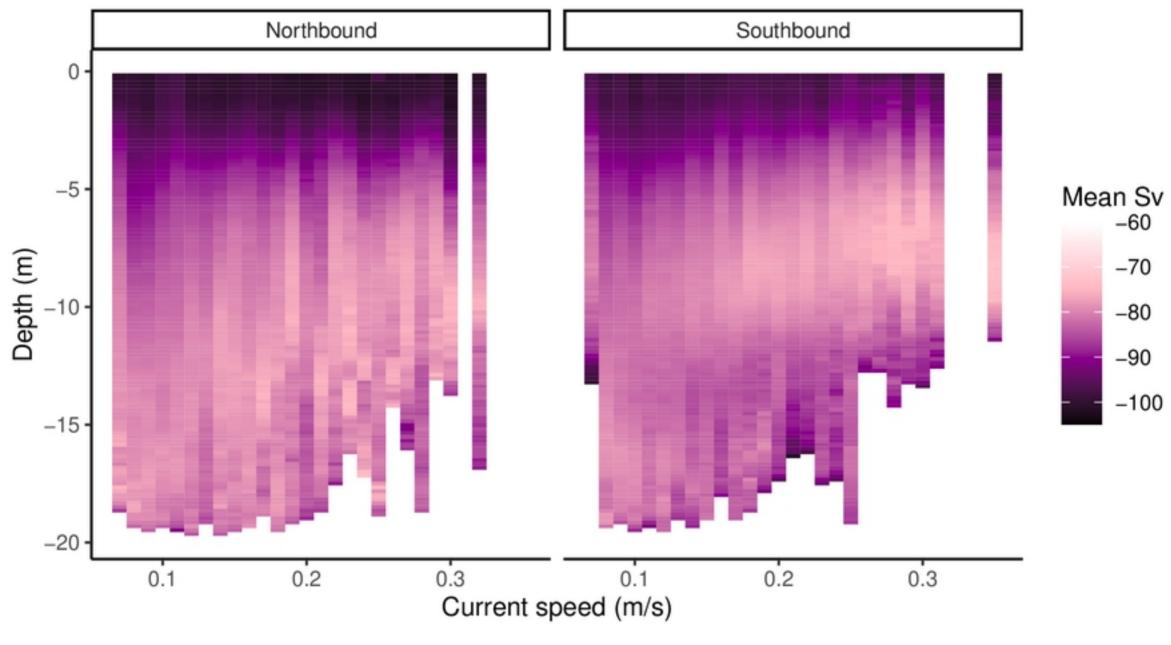
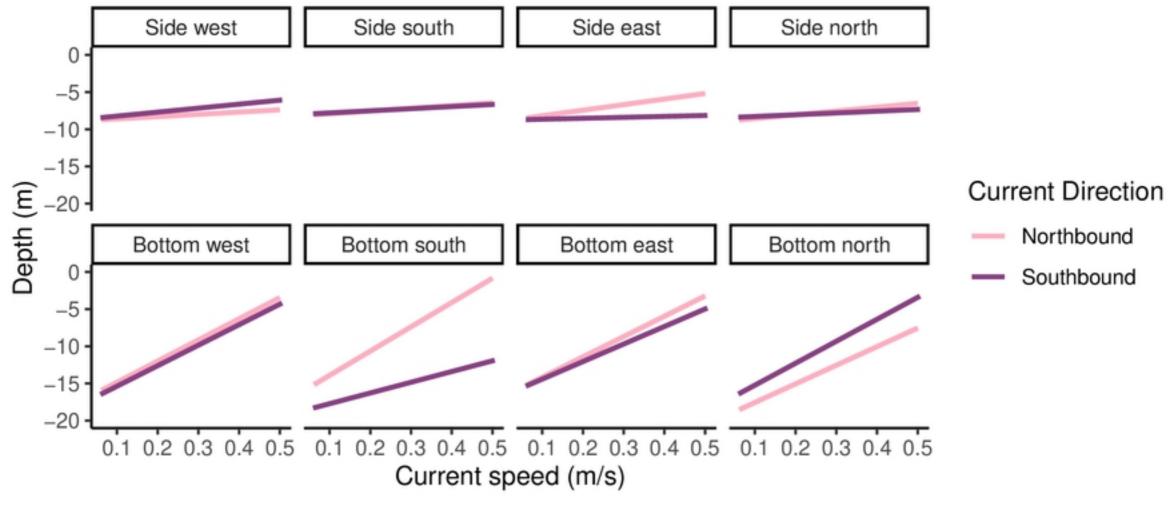


Figure 9



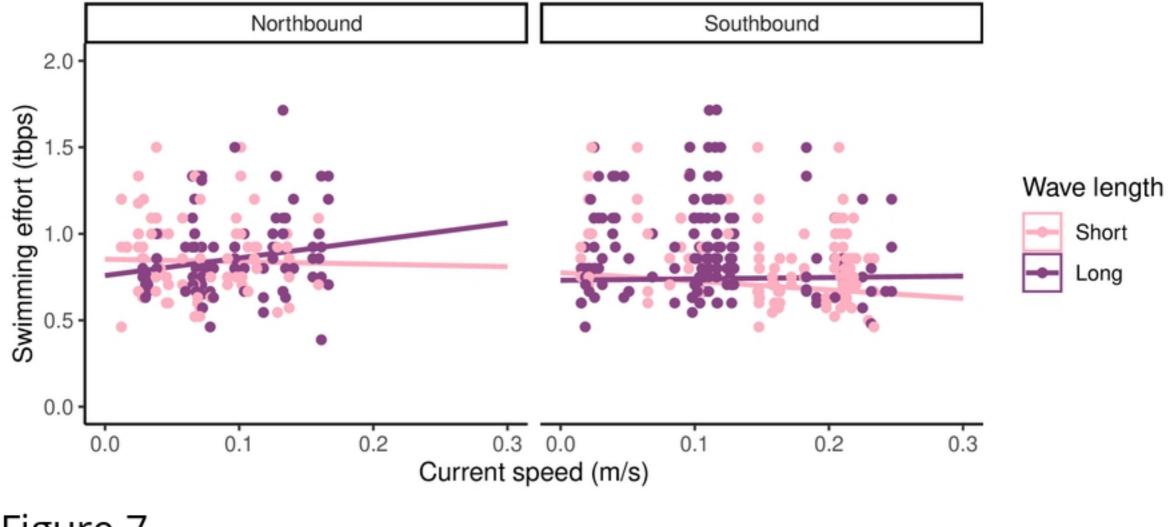


Figure 7

South echo sounder

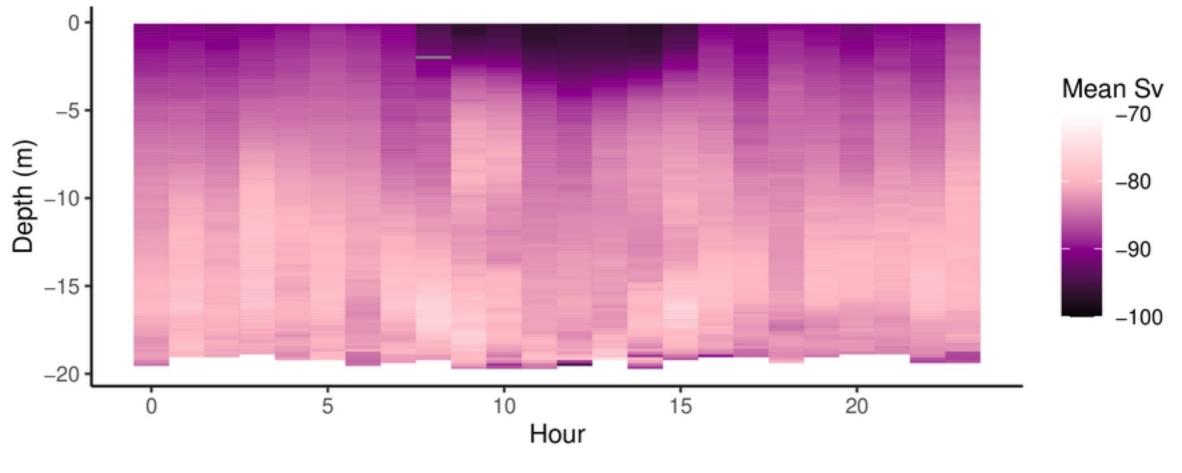
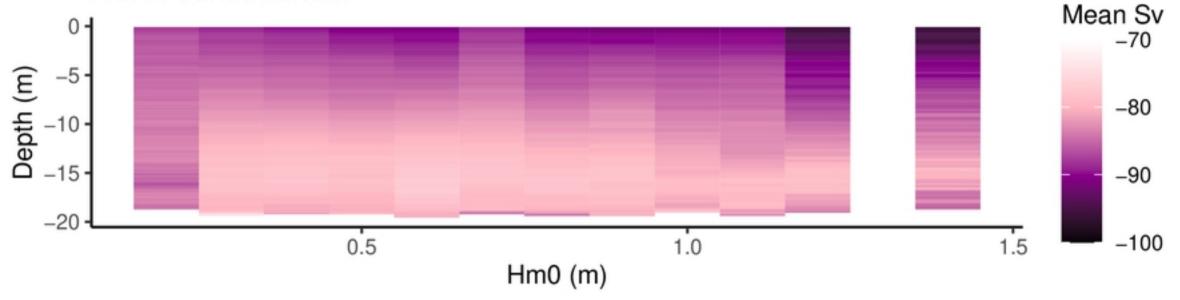
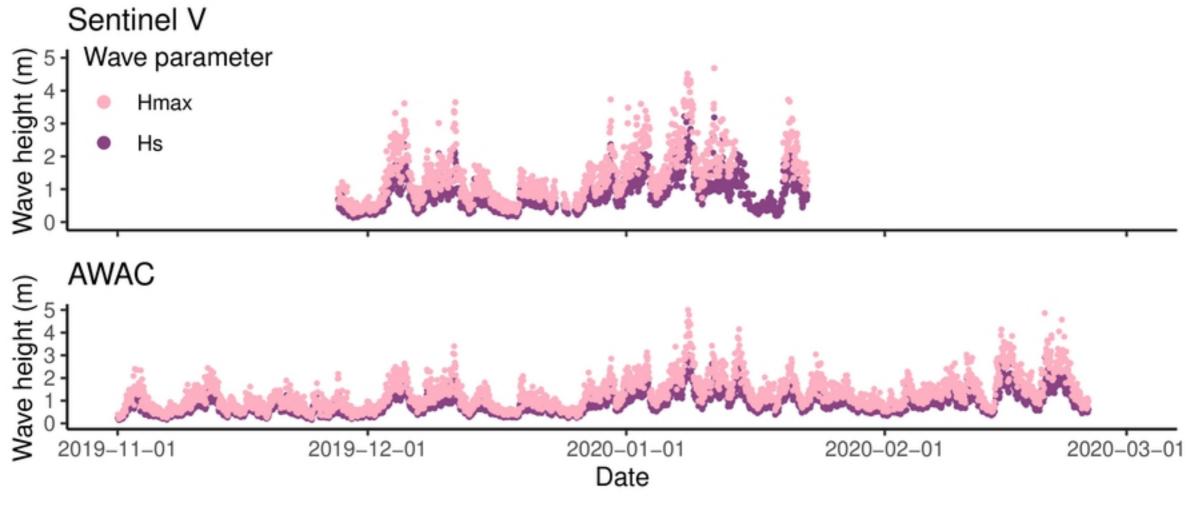
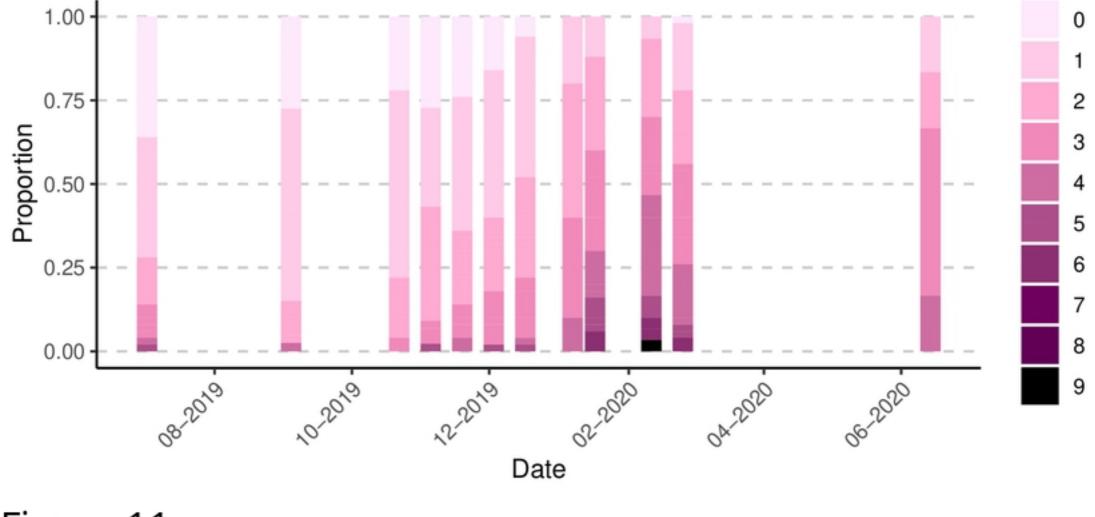


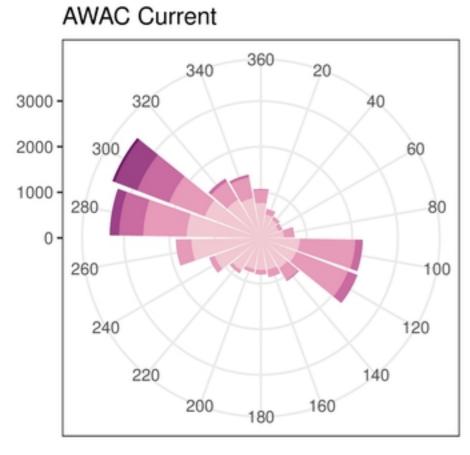
Figure 8

North echosounder

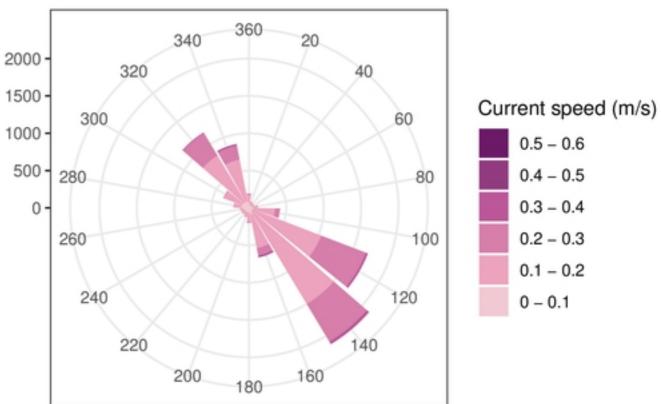




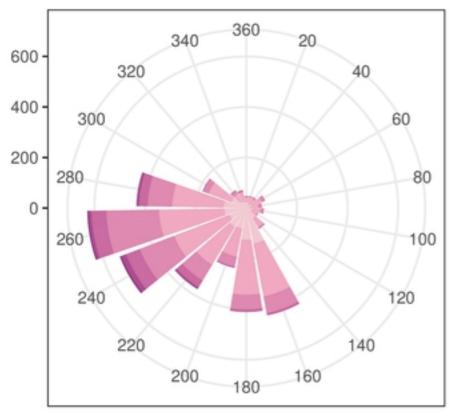




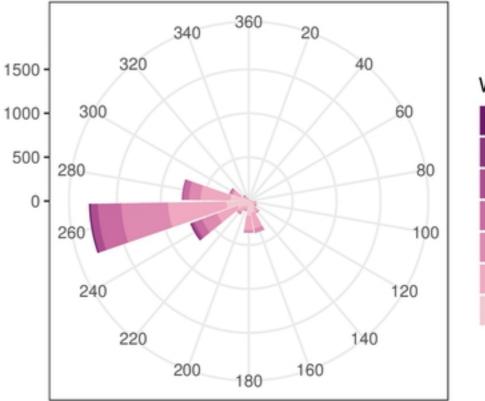
Sentinel V Current



AWAC Waves



Sentinel V Waves



Wave height (m)



