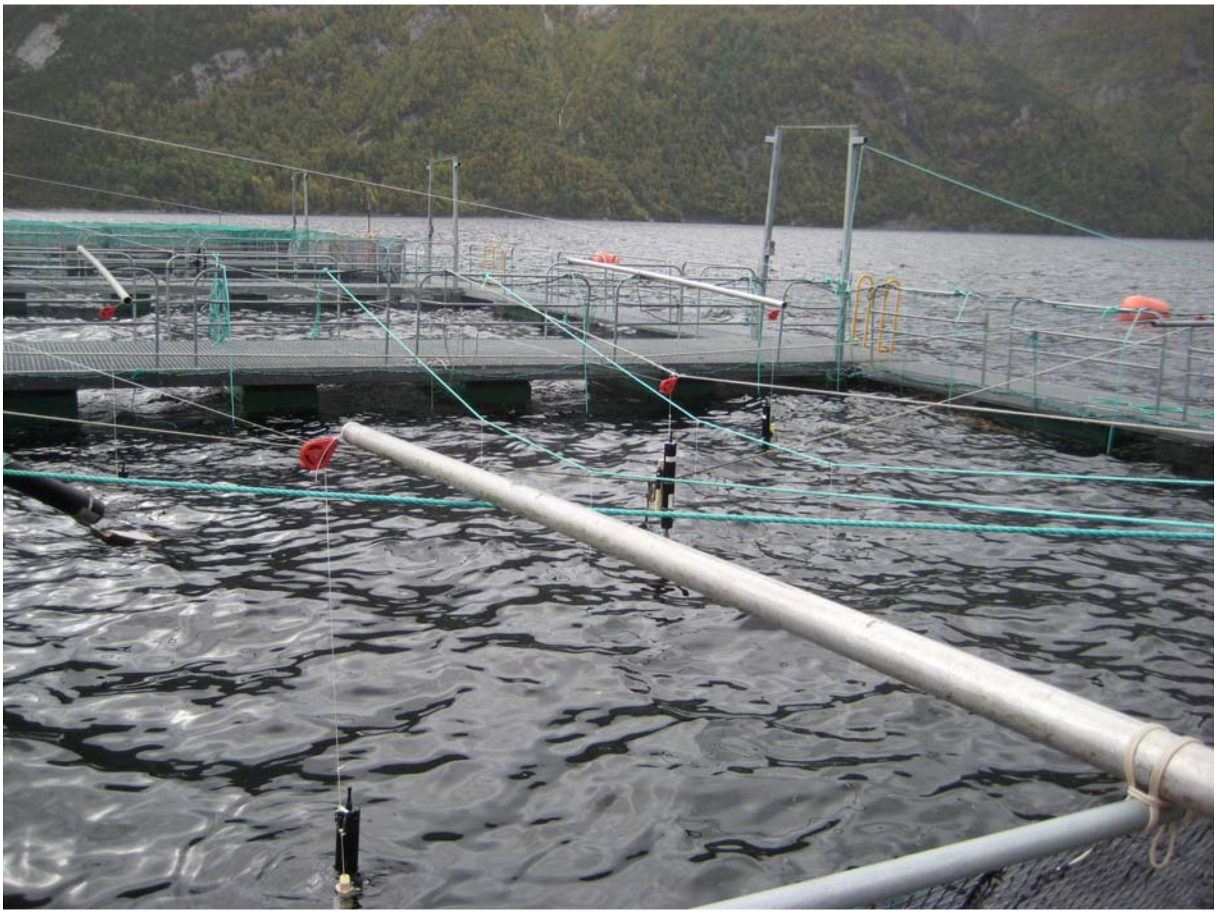
Oxygen variation within a seacage



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Abstract

In recent years, fish welfare during aquaculture production has received increasing attention, and it has been suggested that welfare is threatened as larger seacages are developed. Larger seacages with higher stocking densities are harder to control, thus knowledge of the physical chemical and biological processes that affect water quality is vital in order to ensure fish welfare. Information about the behaviour of the fish in relation to the environmental dynamics in various production systems is also essential. This thesis looks at the variation, particular to oxygen levels within a seacage and in relation to a reference point outside. The behaviour of Atlantic salmon was also investigated.

Both a seacage in the cage environment laboratory at the Institute of Marine Research and a commercial salmon farm to obtain “real-life conditions” applicable to the farming industry were investigated. In addition to oxygen, temperature, salinity and current velocity were recorded. Fish behaviour, such as swimming depth, swimming speed and ventilation frequency was also investigated. An experimental setup was also done, where skirts were put around a seacage at Solheim, to study oxygen levels and fish behaviour during delousing treatment.

The results demonstrate that salmon in an aquaculture situation are exposed to a highly variable environment, both physically and chemically, with large spatial and temporal variations of the environmental factors. Different levels of environmental stratification could be explained by the location of the farm (fjord site or a coastal site). The levels of oxygen within the seacages were related to the degree of stratification, water currents, stocking density, fouling and time of day. The interaction between the behaviour of the fish and environmental variation was demonstrated, such as the variations in natural light levels lead to a cyclic pattern in swimming depth, while feed attracted fish to the surface. In the skirt experiment, increased swimming speed and ventilation frequency was observed with decreasing dissolved oxygen levels, and was more pronounced when delousing treatment was added to the system, indicating that the treatment itself had an effect on the fish.

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1. Introduction

1.1. Background

The aquaculture industry is now the fastest growing sector of food production worldwide (Lymbery, 2002; Stevenson, 2007). In 2006, the Norwegian export of trout and salmon exceeded 18.5 billion NOK (Dahl et al., 2007), and the value of cultivated salmon was, for the first time, higher than wild caught salmon. About 630 000 metric tonnes of Atlantic salmon were produced in 2006 compared to around 298 000 metric tonnes in 1996 (Dahl et al., 2007). One of the reasons for the success of the aquaculture industry is the simple and inexpensive technology of the seacages. Floating marine net-cages are the major on-growing system used in salmon aquaculture, and hold virtually all of the biomass in the Norwegian aquaculture (Kristiansen et al., 2007). In recent years, bigger seacages have become more common; a normal sized cage in the 1980s was between 500-1 000 m^3, while cages today have an average size of 15 000-20 000 m^3 (Kristiansen et al., 2007). As cage size increases it would be assumed that the fish would have a greater volume of water to move around in. This is however not the case; stocking densities in larger seacages are still the same, and sometimes even higher (Lymbery, 2002). The biggest seacages in use today are 80 000 m^3 with a depth of 40 m and can hold up to 1 000 tonnes of fish (Kristiansen et al., 2007). With increasing size of seacages and a larger number of fish in each cage, it has become harder to control what happens in the system. At the same time, welfare of farmed fish, which is defined as "an individual's subjective experience of its mental and physical state as regards its attempt to cope with its environment" (Braastad et al., 2006, pg.8) has received increasing attention (Ellis et al, 2002; Turnbull et al., 2005), and it has been suggested that the current farming practices might compromise fish welfare (Lymbery, 1992, 2002).

1.2. The cage environment

The cage environment is a complex system in which the environmental conditions fluctuate both temporally and spatially. Oxygen levels, salinity, and temperature can all vary on a daily basis and often do so in conjunction with changes in tidal flow, heavy rain etc (Turnbull et al., 2005). Even though the majority of salmon are reared in seacages, very little is known about the dynamics inside the cage with regards to environmental factors, nor are there any specific requirements for the environment inside a seacage today in relation to fish welfare (Johansson et al., 2004).

The fish farmer can to some extent influence the environment in the seacages by controlling the stocking density, feeding regimes (Juell et al., 1994), artificial lighting regimes (Oppedal et al., 2001; Juell et al., 2003; Juell and Fosseidengen, 2004; Oppedal et al., 2007), and the frequency of maintenance such as fouling and changing nets (Johansson et al., 2004). The environment in which the fish are held captive is to some extent determined by the location of seacages in terms of latitude, topography and the degree of exposure. Furthermore, environmental factors at the specific site, such as temperature, oxygen, water current, salinity and light will vary over time, both short term (hours) and long term (season), as well as with depth. All these sources of natural variation are out of control of the fish farmer. The development of models describing the dynamic features of the highly complex fish cage environment is essential to be able to predict the environment inside the cage and the surroundings in the future and to identify periods where fish are exposed to health threatening conditions.

1.3. Fish in an aquaculture situation

In an aquaculture situation a fish is removed from its natural environment and introduced to a new environment to which it has to adapt. This environment may or may not represent optimal conditions for the fish. The fish is restricted to the environment that exists in that particular enclosed volume, and will only be able to choose microhabitats within this unit. Thus, the fish will often not be able to choose its environment of preference and the risk that health and welfare of the fish will be hampered is therefore higher in an aquaculture situation than in the wild.

All animals are adapted to a particular ecological niche in which the biological, chemical, physical, nutritional and social environment enables it to function properly (Staurnes et al., 1998). These locations can be very specific for fish, especially with regard to oxygen concentration and temperature. Threshold levels for carp was found to be ~31 % dissolved oxygen (DO), while sockeye salmon had a threshold level of ~64 % saturation (Davis, 1975). Brett (1952) investigated temperature tolerance ranges for five different types of salmonids and found that sockeye salmon was held at a maximum acclimation of 23 ^{o}C, but showed an inherent tolerance when temperature levels rose to 24 ^{o}C. He also found that the preferred temperature was between 11 to 14 ^{o}C in a vertical gradient. Sigholt and Finstad (1990) found and increased survival with increasing temperatures, with a preferred temperature above 6 ^{o}C. Any changes in one or more of the environmental factors may lead to stress. Stress results in reallocation of an individual’s energy resources in order to compensate for the changes. (Iwama et al., 1997; Iwama et al., 2004). Continual stress is not preferable, and often results in a reduction of the animal’s welfare and consequently a lowered production. If the animal is kept outside its preference area for too long; normal development, health and life of the animal may be in danger (Elliott, 1991; Iwama et al., 1997; Bevelhimer and Bennett, 2000; Iwama et al., 2004).

1.4. Oxygen levels and fish welfare

The oxygen level in the water is one of the key environmental factors affecting the welfare and development of fish (van Raaij et al., 1996; Staurnes et al., 1998; Ellis et al., 2002). Despite having been thoroughly investigated in land-based systems (Kutty and Saunders, 1973; Guinea and Fernandez, 1997), few studies have been conducted regarding the complex mechanisms that control oxygen levels in commercial seacages.

The levels of DO normally vary a great deal, and are often unpredictable, in the marine cage environment. Environmental factors such as light, tidal current and wind influence water flow and mixing of oxygen, and this will determine how much oxygen is available (Beveridge, 2004; Bergheim et al., 2005). The primary sources of oxygen in the water are the mixing of atmospheric oxygen, and photosynthesis (Fig. 1.1) (Davis, 1975; Kvamme et al., 2008). The extent to which this oxygen can be dissolved depends on temperature, salinity and barometric pressure (Beer, 1997). When there is an increase in temperature or salinity, less oxygen will be dissolved, whilst an increase in barometric pressure results in an increase in the amount of oxygen dissolved. Hence, physical factors influence the amount of oxygen dissolved in water at a certain place and time. Oxygen produced by photosynthesis is not adequate to meet the oxygen demands of fish in marine farms with the high biomass in the cages today (Wildish et al., 1993). Mixing from surface is high under wavy conditions and low with small or no waves and only takes place in the surface layers. Physical transport of water (water current) is thus the most important factor for the oxygen supply to the fish (Wildish et al., 1993; Kvamme et al., 2008).

Annual variation in primary production coupled with variable water currents may result in extensive fluctuations of DO available in seacages (Johansson et al., 2004; Johansson et al., 2007; Kvamme et al., 2008). Large variations in oxygen saturation between day and night have been observed, especially in periods when primary production has been high (Treasurer, 2003). Inside seacages, the oxygen conditions are further influenced by the respiration of the fish (Johansson et al., 2006), and is expected to vary with feed intake and activity. It has been shown that Atlantic salmon show large temporal and spatial variation in stocking density (Fernö et al., 1995; Juell and Fosseidengen, 2004; Johansson et al., 2006; Oppedal et al., 2007). Thus, the amount of oxygen consumed with depth will differ, leading to lower oxygen in areas with higher fish densities.

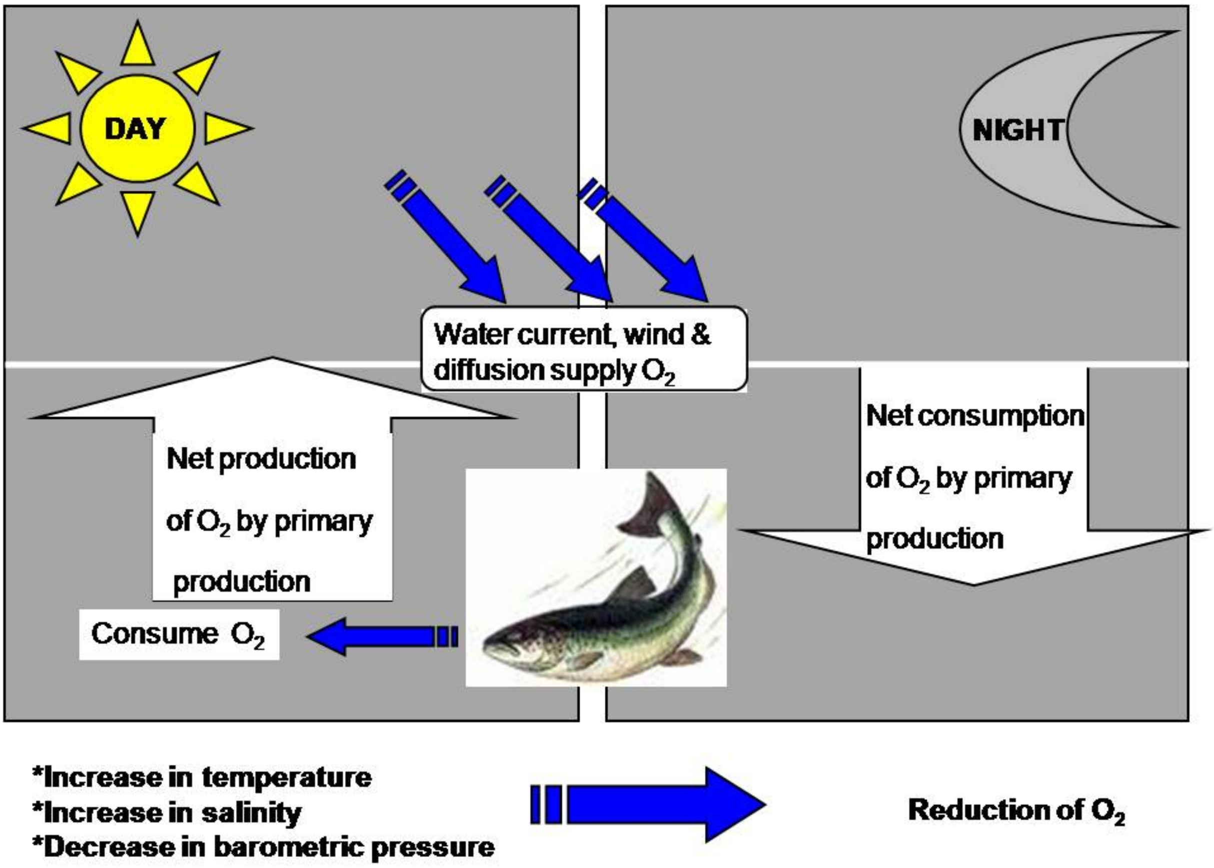

Figure 1.1: The most important factors determining oxygen levels in sea water (Adapted from Johansson et al., 2004).

Fish use oxygen in the production of energy needed for food digestion and activity. Low oxygen levels may result in a range of problems; at first, fish are able to compensate by increased heart beat, stroke volume, ventilation frequency, ram ventilation, or by seeking other water bodies containing higher levels of DO. When this compensation is no longer possible the fish will reduce, and under severe hypoxia, stop feeding, and there will be an accordingly reduction in growth (Jobling, 1995).

Previous studies have shown that oxygen measured in a reference point outside the aquaculture facilities can differ greatly from oxygen levels measured within a seacage (Johansson et al., 2006; Johansson et al., 2007). Johansson et al. (2007) measured oxygen levels in a reference point of > 100 % saturation, while ~60 % saturation was found inside the cage at the same time. With larger seacages, it is also likely that oxygen levels vary greatly within a single seacage, and not only between cages and the surroundings. Water flows through the cage and the oxygen is consumed by the fish. Theoretically, the oxygen level would be reduced along the water current axis. This fact has not been measured/tested in seacages.

How fish behaviour is altered due to long term variations in the environment like season, light and temperature has been described earlier (Rimmer and Paim, 1990; Huse and Holm, 1993; Fernö et al., 1995; Oppedal et al., 2001; Oppedal et al., 2007). However, short term observations (days) of variation in the oxygen environment within a seacage and how this affects the behaviour of the fish, is lacking.

1.5. Seacage farming and sea lice

Considering the increased seacage sizes followed by an increase in total biomass at the farm, concerns about fish health has arised. Intensive farming has led to increased infestations with parasitic sea lice that in many areas have become the greatest single problem for the farming of salmon (Lymbery, 2002). Sea lice infestation is a serious welfare problem and if left untreated, it can cause great suffering and death in affected fish (Johnson et al., 2004; Ashley, 2007). A number of different species of parasitic copepods, referred to as sea lice feed on the host salmon eventually causing skin and scale loss, and can also act as a vector of other disease (Johnson et al., 2004). In an economic perspective, losses due to sea lice in salmonid aquaculture have been estimated to be more than 100 million US dollars a year (Johnson et al., 2004).

The most common method of delousing salmon is bath treatments, exposing the fish to a substance which aims to remove the sea lice without affecting the fish in any way. When this is performed, “skirts” are placed around the seacages, leaving them as partly closed systems resulting in a reduction in the flushing of water and a reduced supply of oxygen within the seacages. As a result of this, oxygen concentration within the seacage drops drastically. There is little information about the environment within these systems and how fish respond to the treatments.

1.6. Aims

The primary aim of this project is to describe the short term variation of oxygen within a single seacage, and compared to outside, in both small and large seacages. Further, influence of the natural variations in environment on the behaviour of the fish, with regards to fish density, swimming behaviour and group structure, will be studied.

A secondary aim is to describe the short term variation of oxygen within a semi closed seacage using skirts. Focus will be on how oxygen is consumed and how this will affect the fish behaviourally. Delousing treatment will also be added to see if this has any effect on the fish. The effect of variations in oxygen on the behaviour of the fish will be studied.

More specifically, questions to be raised are 1) will variations in DO levels be greater at fish farms with larger seacages and more biomass?, 2) are the fish responsible for the variations?, and 3) how will the fish respond to the variations?.

2. Materials and Methods

The experiments were conducted between September 11 and October 10, 2007 at two marine cage farms stocked with Atlantic salmon on the west coast of Norway. Both farms had the same basic rectangular floating steel structure, holding two parallel rows of net cages. Water characteristics (temperature, salinity, oxygen and current velocity) and swimming behaviour were recorded in one sea cage at each farm. A reference point, assumed to be uninfluenced by the facility, was chosen based on information supplied by the fish farmer of the main current direction at the farm site, and the same parameters as measured inside the sea cages were recorded here.

2.1. General site description

Solheim cage- laboratory site of the Institute of Marine Research was located approximately 2/3 of the way into a fjord (Masfjorden) in Hordaland on the west coast of Norway (Fig. 2.1.a). It was regarded as a typical fjord site with a constant supply of freshwater. The farm had ten cages which measured 12 m x 12 m wide and 14 m deep, and the depths under the cages site varied from 40 - 90 m. Total biomass at the fish farm was about 37 tonnes and the seacage used in this study had a biomass of ~17.5 tonnes, which gives a stocking density of 8.7 kg m^{-3}. A new net was used so that biofouling would not be an issue. Fish were fed with a centralised automatic feeding system twice daily to satiation, at 09.00 h and again at 14.00 h.

The commercial marine farm site was located in Hordaland, on the west coast of Norway and was regarded as a coastal site with more homogenous environmental conditions and limited input of freshwater (Fig. 2.1.b). It was also located in an area with strong tidal influence. The farm had 8 seacages each measuring 24 m x 24 m wide and with varying depths. The seacage used in this study had a maximum depth of 20 m, with the bottom line at around 15 m. The depths below the cages were approximately 70 m and the farm had a total biomass of ~446 tonnes. The fish were fed with a centralised automatic feeding system from 0800 h to 1630 h.

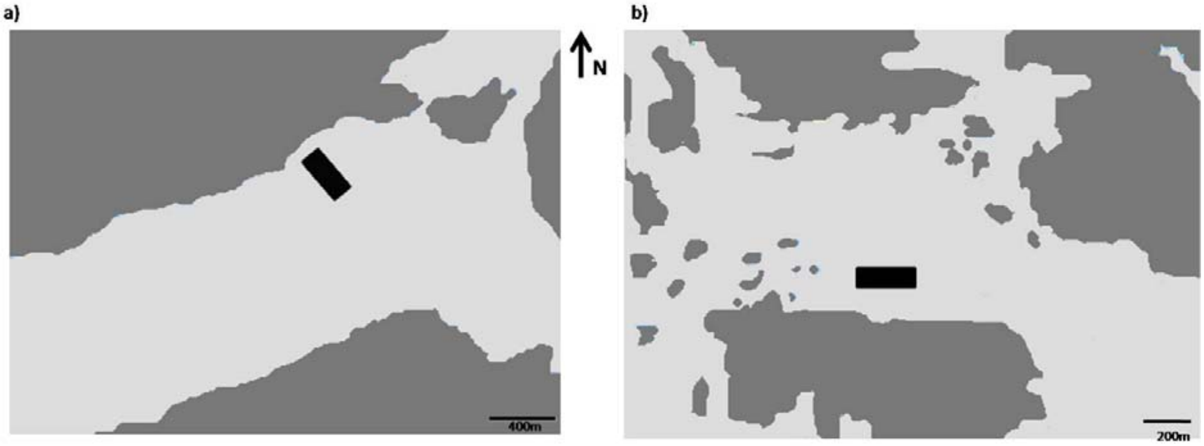

Figure 2.1: Geographical location and the placement of the salmon farms, **a)** Solheim cage laboratory site and **b)** commercial marine farm. Black boxes indicate the orientation of the farms.

2.2. Data sampling

2.2.1. Temperature, salinity, dissolved oxygen and current velocity

Vertical depth profiles of DO (% DO), temperature (^{o}C) and salinity (ppt) were sampled using a SAIV SD204 CTD (Conductivity, Temperature, Depth) (SAIV A/S www.saivas.no). All CTDs were equipped with an oxygen sensor (Oxyguard Ocean probe, www.oxyguard.dk). To each of the CTDs (except for the reference CTD), a single point acoustic based current meter Vector (Nortek, Oslo, Norway, www.nortek.no) that measured water current speed and direction was attached. The Vector Current Meter measures water speed using the Doppler Effect, by transmitting a short pulse of sound, listening to its echo and measuring the change in pitch or frequency of the echo (Vector Current Meter user manual, www.nortek.no). The instruments were simultaneously hauled up and down the water column with approximately 1 cm s^{-1} using an automatic winch (HF5000, Belitronics, Sweden). The CTDs sampled once every 5 seconds and Vectors every second, restricted by the memory and battery capacity of the instruments and the requirement of high resolution. Water current outside the sea cages was monitored using three Acoustic Doppler Current Profilers (Aquadopp 0,6M Hz, Nortek, Norway, www.nortek.no). Two of the profilers were located upstream and downstream of the sea cages, in relation to the believe direction of the main current, and the third one was used as a reference point. The instruments were placed on the surface resulting in a dead zone close to the instrument (about 1 m) where the current could not be measured, pointing downwards and measuring water current in 1 m depth intervals from 1 m to approximately 25 m (depend on the amount of scattering particles). Current profilers operate by transmitting short acoustic pulses from two or more acoustic beams, measuring the change in pitch or frequency of the echo (www.nortek.no).

2.2.2. Fish density and behaviour

A PC based echo-sounder (Merdøye, Lindem Data Acquisition, Oslo, Norway) recorded swimming depth and fish density from the surface and down beyond the bottom of the sea cage, described by Bjordal et al. (1993). It was connected to upward facing transducters with a 42^o acoustic beam suspended at approximately 17 m. Echo intensity, which is directly proportional to fish density, was recorded at 0.5 m depth intervals from 0 – 14 m and converted to relative echo intensity (ER) in each depth interval. The mean of the observations (60 pings per minute) was recorded. Observed fish density (OFD) in kg m^{-3} was estimated based on these measurements as $\mathrm{OFD}_n = B\ \mathrm{ER}_n\ V_n^{-1}$, where B is total biomass in the cage, ER is the relative echo intensity and V is the volume of the one meter depth interval.

Three cameras (Orbit 3000, www.orbitaquacam.no) positioned in the middle of the sea cages, at different depths were used to observe the fish and their swimming behaviour (anti-clockwise or clockwise, swimming with the current or against, swimming or "standing still" on the current etc.), group structure (structured as in all fish doing the same i.e. swimming in a "donut shape" or unstructured as in no specific pattern amongst the fish). Group structure was categorized into 4 categories based on the proportion of fish doing the same thing. Swimming speed was also recorded. Four ropes were placed 2 m from the cameras, in four directions facing the corners of the seacage. Swimming speed was measured on individual fish as the time used by the fish to swim one body length (from when the snout passed the rope till the tail passed). A criteria used for these measurements were that all fish measured should be approximately the same distance from the camera as this would provide a more correct picture. In some cases ventilation frequency was also recorded, which is the frequency of gill movements per second. Individual fish was monitored using cameras. The time in which the fish remained visible to the camera was recorded using a stop clock, and the number of gill movements done by the fish during this period was counted. Two of the cameras were equipped with infrared lights, permitting observations at night. The infrared lights only reached 1.2 meters away and hence only a part of the fish could be observed at night.

2.3. Pilot survey

CTDs require a minimum current velocity of 1 cm s^{-1} to produce accurate data. Vectors are used to measure water current speed and direction, and it is preferred to let them hang still in the water column during recording to get high accuracy. Therefore, prior to the survey, a pilot survey was conducted in order to determine which methods were most suitable, and how the best and most accurate data would be obtained. The same profiling setup had to be used for both CTDs and Vectors as they were attached to one another. This would also give more comparable data. Pilot measurements were recorded (from 1 - 10 m depth) both by continuously profiling and with a 3 minute stop every second meter. Six instruments (3 x CTDs, 3 x Vectors) were used and they were all placed on a straight line inside a salmon cage. The conclusion from this trial was that continuous measurements (about 1 cm s^{-1}) gave good data for both the CTDs and the Vectors, and this profiling setup was therefore used in the survey.

Another goal for the pilot surveys was to check if all instruments were working properly, with no differences in the readings amongst them. Five set of instruments (one set containing 1 x CTD and 1 x Vector) + the reference CTD from the reference point were placed on a straight line attached to a steel pipe about 80 cm apart and profiled twice from 1 - 10 m depth. The steel pipe was placed across the main direction of the current so that the instruments would not influence each other. Any discrepancies between instruments were sorted out prior to the main experiment.

2.4. Solheim cage- laboratory site of the Institute of Marine Research, Matre, Norway

The pilot experiments and the first part of the study were conducted at the Solheim cage-laboratory site of the Institute of Marine Research in Matre (Fig. 2.2). The environmental conditions on the inside and outside of both an empty and a stocked seacage (8.7 kg m^{-3}) were investigated.

Fish were measured (fork length) and weighed (to the nearest g) prior to the investigation (Sept 20, 2007). During sampling, the net was pulled up and fish were crowded near the surface. A random sample of 73 fish were collected and placed in a bath for anaesthesia with Benzocain (Norsk Medisinaldepot, Bergen) diluted according to the instructions on the label. Fish weighed 2498 ± 981 g (μ ± S.D.) and measured 55 ± 7 cm.

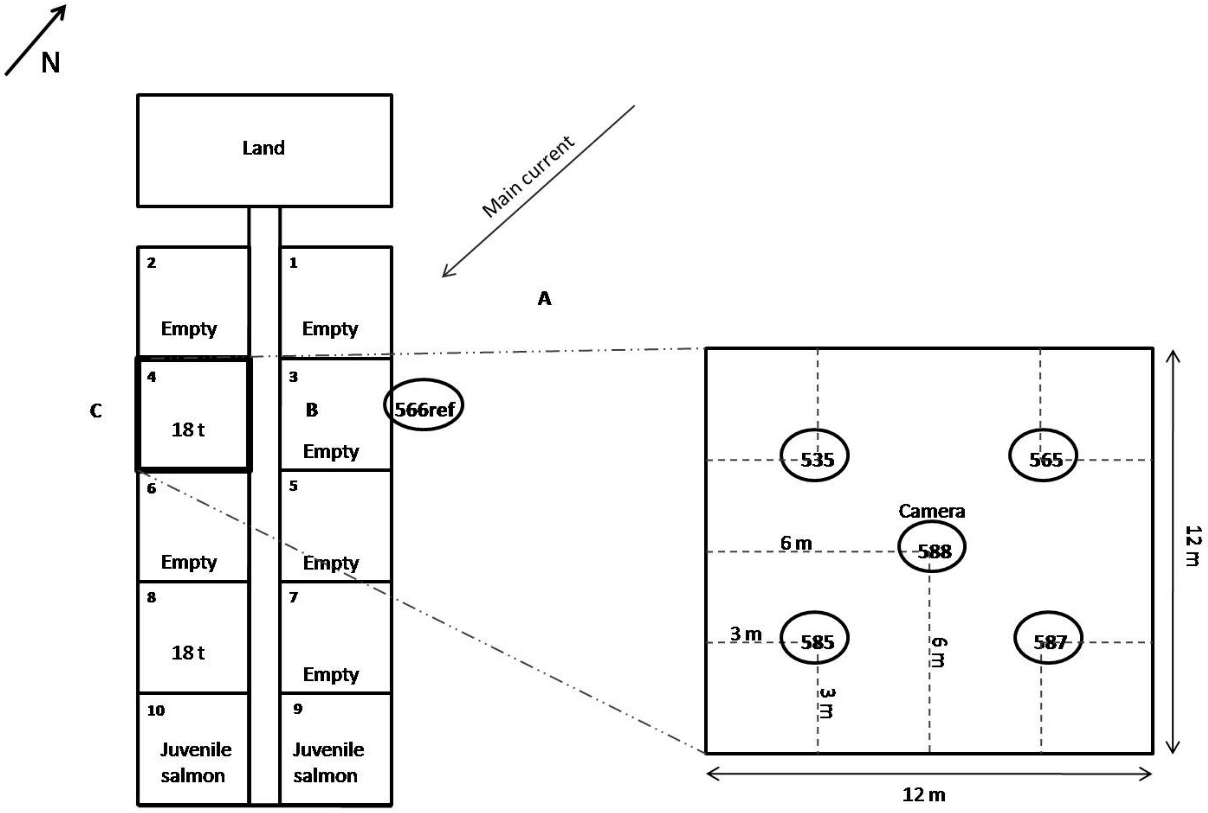

Figure 2.2: Layout of the Solheim cage-laboratory site of the Institute of Marine Research, Matre, Norway, with the position of the sea cage used in this study (sea cage 4, marked in bold), numbers 1-10 indicating the sea cage number, letters A, B, and C indicates the position of the Aquadopp profilers, and the location of the reference CTD marked with 566ref is shown. To the right is a detailed overview of the sea cage used in this study, and the location of the CTDs and Vectors (535, 565, 585, 587, and 588).

2.4.1. Control - Empty cage

The control with the empty cage was done September 10 - 12, 2007 in cage 4 (Fig. 2.2). Cage 4 was chosen because it was the “best suited” cage, with relatively deep waters below (> 40 m) and no fish in the nearest cages. The fish that used to be in cage 4 was moved into cage 2 the week before. Cage 4 would not be free of possible influences from other cages containing fish since cage 2 had fish in it, however it was regarded as the site which was least likely to be affected by other seacages with fish. The net was changed just prior to the study to minimalize fouling. The instruments were profiled from 1 - 10 m for a period of 50 hours covering several tidal cycles, 2 whole days, 2 whole nights, and at least 4 feedings; hence an adequate amount of data were obtained to describe the influence of these factors on the environment.

2.4.2. Empty cage with "skirt"

"Skirts" (supplied by ScanVacc) were put around the same seacage to create an environment similar to what the fish would experience when exposed to bath treatments. The "skirts" were ~6 m deep, and the depth of the sea cage was reduced to ~4 m by pulling the net. This created an environment with very little flushing of water and low inflow of oxygen. The instruments continuously profiled the water column from 1 to 4 m depth.

2.4.3. Cage with fish

After the control measurements, the procedure was repeated in a cage stocked with fish (Sept 25-27, 2007). The fish in cage 2 were moved into cage 4, and now the net cage would be in the best place considering the influence of other cages with fish since there were no cages with fish around (Fig. 2.2). Again, the water column was profiled from 1 - 10 m over a period of 50 hours. This time fish behaviour was observed as well. Once every hour, swimming speed was recorded for a total of 180 fish at 3 different depths; 1, 4, and 7 m (60 fish at each depth, in 4 different directions). Group structure and general swimming behaviour was also noted. All this was done, as far as it was possible to see, at night time as well, using infrared lights on two of the cameras.

2.4.4. Cage with fish and "skirt"

"Skirts" were placed around the same sea cage (now containing fish) and the depth of the cage was again reduced to ~4m. Two handheld oxygen measurement instruments (Oxyguard Handy Polaris, www.oxyguard.dk) were used during this trial to monitor oxygen levels online in case of actions needed due to unacceptable low oxygen levels. The same behavioural observations as described above was performed, however, instead of once every hour they were repeated every ten minutes, and now ventilation frequency was also measured.

2.4.5. Cage with fish, skirt and delousing treatment

After exposing fish to normal conditions for a few days (to make sure the fish had recovered from the last trial with the "skirts"), the "skirts" were put back onto sea cage 4. The fish were taken through a proper delousing process of ~45 min, including the actual treatment. 200 mL of Betamax Vet (ScanVacc, www.scanvacc.com) were added to the seacage, which gives a dosage of 0.35 mL m^{-3} (12 m x 12 m x 4 m = 576 m^3. 200 mL / 576 m^3 = 0.35 mL m^{-3}). The same behavioural observations were done every ten minutes.

2.5. Commercial marine farm site

Next phase included the commercial marine farm site. The survey was planned exactly the same way as the 50 hour observation period at Solheim, so it would be possible to see if the variations and the coherence observed at Solheim would be representative or not. However, a few problems did arise and will be discussed further. The set up of the instruments were done the same way as was done for Solheim (Fig. 2.3), with five sets of instruments inside one seacage, one reference CTD outside at a place supposedly not influenced by the facility, two Aquadopps located upstream and downstream from the main direction of the current and the last Aquadopp as a reference point (Fig. 3.3).

Two cameras were placed inside the sea cage, one that could be moved up and down the water column, and one remained stationary at ~15 m depth. The PC-based echo-sounder was placed under the seacage to record swimming depth and fish density during the observation period. Prior to the experiment it was assumed that the water current would not have a great effect on the movement of the seacage nets; however this was not the case. The nets moved sideways under periods with strong water currents making it impossible to allow constant profiling. Therefore, instead of 50 hours of recording data, from 1 - 10 m, only 22 hours were done, and sometimes the instruments were kept still at a certain depth for hours at the time waiting for a reduction in the current. 50 hours of data recording would be of preference, as for the other trials, however, a good picture the environmental changes in the water column could still be seen from the data obtained.

All ten seacages were stocked with salmon; hence the seacage would be influenced by the other cages, as was opposite to Solheim. In comparison to Solheim where the cage net was replaced prior to the survey, the cage net had not been changed; hence fouling of the net had to be quantified. Fouling was recorded by two skilled persons. It was measured visually based on the percentage of the net in an area covered by fouling organisms and given in % coverage.

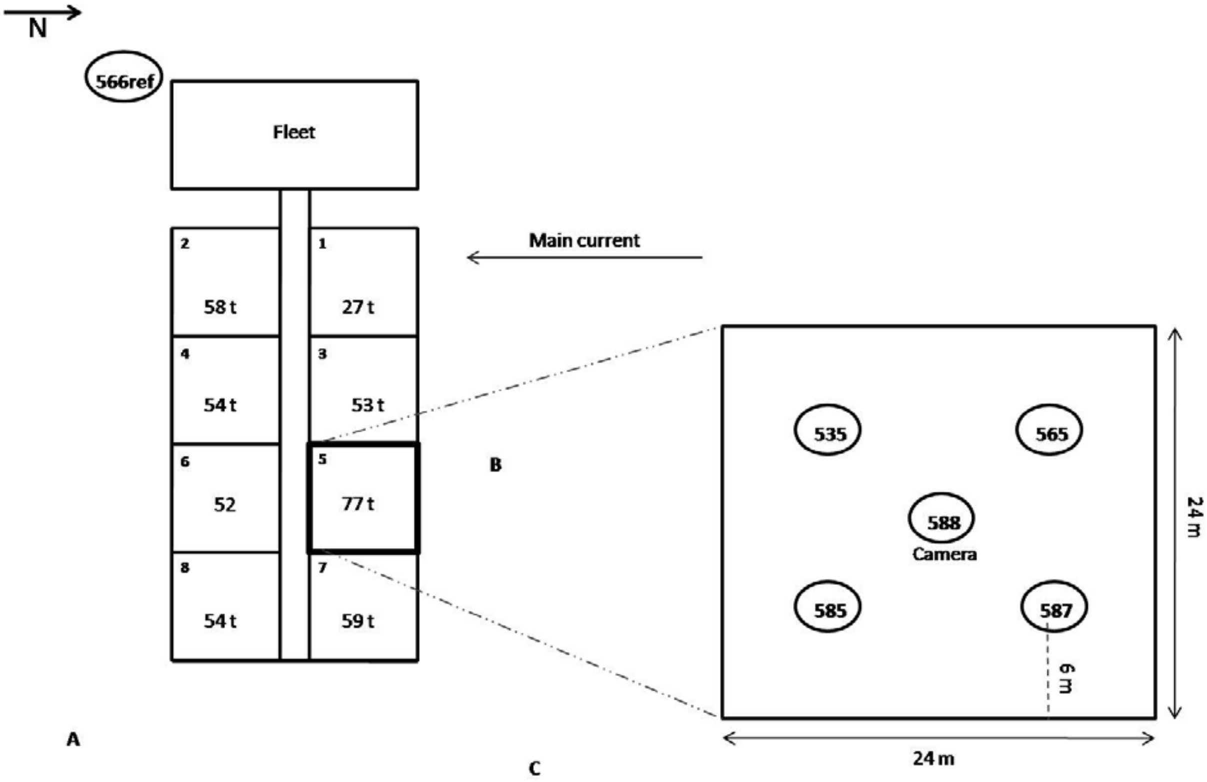

Figure 2.3: Layout of the commercial marine cage farm site with the position of the seacage used in this study marked with a bold line. Numbers 1-8 indicating the cage number, letters A, B, and C indicates the position of the Aquadopp profilers, and location of the reference CTD is marked 566ref. To the right is a detailed overview of the seacage used in this study (sea cage 5), and the location of the CTDs and Vectors (535, 565, 587, 588).

2.6. Data analyses

To get an overview over the variation in the environment and fish behaviour; temperature, salinity, OFD (OFD), water current velocity and DO were presented in figures made in Surfer8 (Golden Software) based on averages per hour for each depth. Average, standard deviation (S.D.), minimum and maximum values were calculated using the observed values at all depths for the whole observation period. Figures and tables were made using Excel and Statistica version 8 (StatSoft), and the statistical analyses was performed in Statistica.

To find out whether oxygen differed between the reference point and between the different positions within the seacage, delta DO was calculated and a one sample T-test was performed. If assumptions for normality were not met, a non parametric Wilcoxon test was used. Statistical analyses were only performed on the delta DO levels greater than 2, as the instruments had an accuracy level of ± 2 %. The data was corrected using a Bonferroni correction as the same data were compared several times, which increases the chances of getting a significant difference. Linear regression was used to check whether there was a correlation between DO and water current velocity. Correlation between DO and OFD was checked using correlation tests. Pearson correlation test was used if the sample were normally distributed, and if it deviated from the assumptions of normality, Spearman correlation test were used. The influence of time of day on swimming speed was investigated using a 2 – way ANOVA with day/night and depth as independent factors, and swimming speed as the dependent variable. A Tukey HSD post hoc test was performed to see which depths were significantly different, if any. Swimming speed at the commercial site was checked using a non-parametric Mann-Whitney test with depth as a factor. Day/night was excluded here as measurements only were taken during the day.

3. Results

3.1. Solheim control – Empty cage

3.1.1. Salinity and temperature

The temperature and salinity data showed a typical fjord locality with a fresher and colder surface layer down to about 3 m, a rapid change to warmer, more saline water in the middle of the water column and a colder marine layer at the bottom. Both temperature and salinity were relatively stable during the observation period. Salinity ranged from 6 ppt to 32 ppt, with an average of 26 ± 7 ppt (Table 3.1), with lower values near the surface and salinity increasing with depth (Fig.3.1.a). Temperature ranged from 10.6 °C to 14.9 °C with an average temperature of 13.4 ± 1.0 °C (Table 3.1). Warmest water was found in the middle of the seacage (Fig.3.1.b).

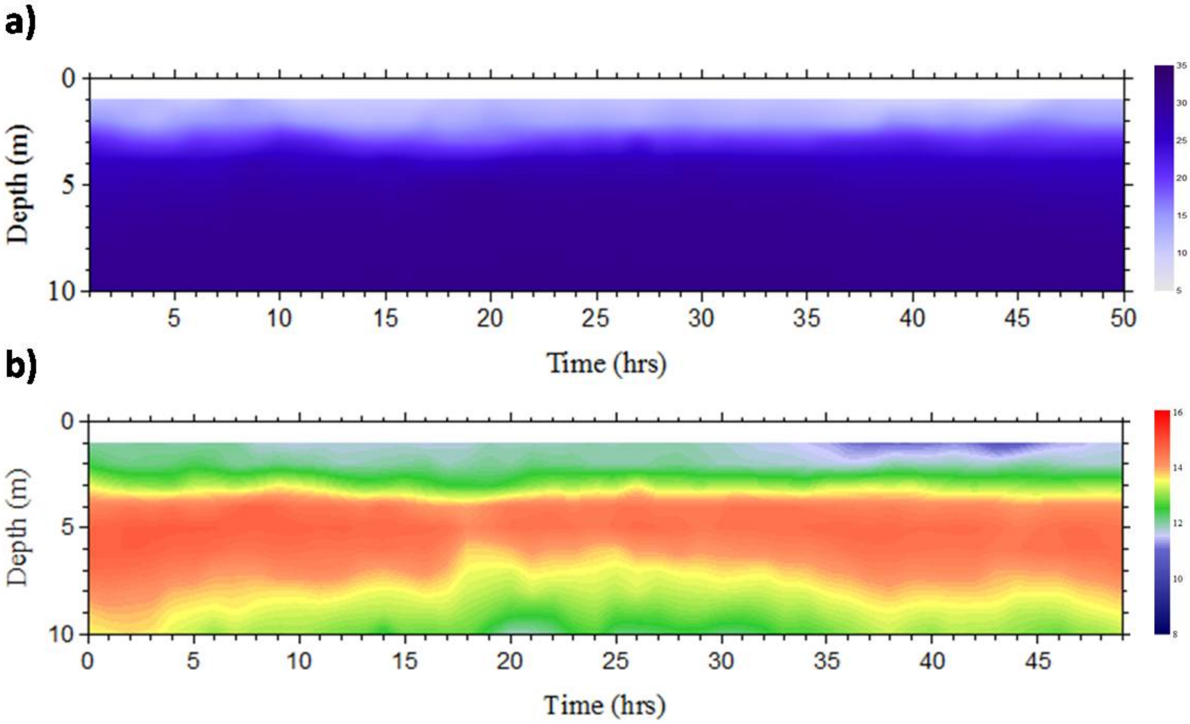

Figure 3.1: a) salinity (ppt) and **b)** temperature (°C) at the reference point for the 50 hour observation period at Solheim with the empty cage. Time 0 represent September 10, 14:45. Only the reference point is presented as all positions showed a similar picture (see Table 3.1).

3.1.2. Water current velocity

Relatively low water current velocities were observed during the whole period (Fig.3.2.a). Total average velocity was 0.03 m s^{-1}, with a maximum value of 0.23 m s^{-1} and a minimum level of 0.00 m s^{-1}. Highest current velocities were found in the surface layers with velocities up to 0.23 m s^{-1}.

3.1.3. Dissolved oxygen

DO levels showed a profile reflecting the same pattern as for salinity, with higher levels of oxygen near the surface and lower levels below the pycnocline for all the sites (Fig.3.2.b).

Average DO levels from the different positions within the seacage from the whole observation period ranged from 89 % to 90 % saturation, with minimum levels ranging from 72 % to 76 % saturation, and maximum levels ranging from 101 % to 112 % (Table 3.1). Values for the reference point was within this range, with 89 % saturation as the average DO level, and 108 % and 74 % saturation as the maximum and minimum levels respectively. DO levels of less than 90 % saturation were measured below the pycnocline throughout most of the observation period.

Table 3.1: DO (% saturation), temperature (^{o}C) and salinity (ppt) for the different sites inside the seacage, including the reference point, for the empty cage at Solheim during the 50 hour observation period.

Position	DO μ ± S.D.	DO max	DO min	Temperature μ ± S.D.	Salinity μ ± S.D.
535	90 ± 5	101	76	13.4 ± 1.0	26 ± 7
565	89 ± 5	101	74	13.2 ± 1.0	26 ± 7
585	90 ± 5	112	74	13.4 ± 1.0	26 ± 7
587	89 ± 5	101	72	13.4 ± 1.0	26 ± 7
566ref	89 ± 5	108	74	13.4 ± 1.0	26 ± 7

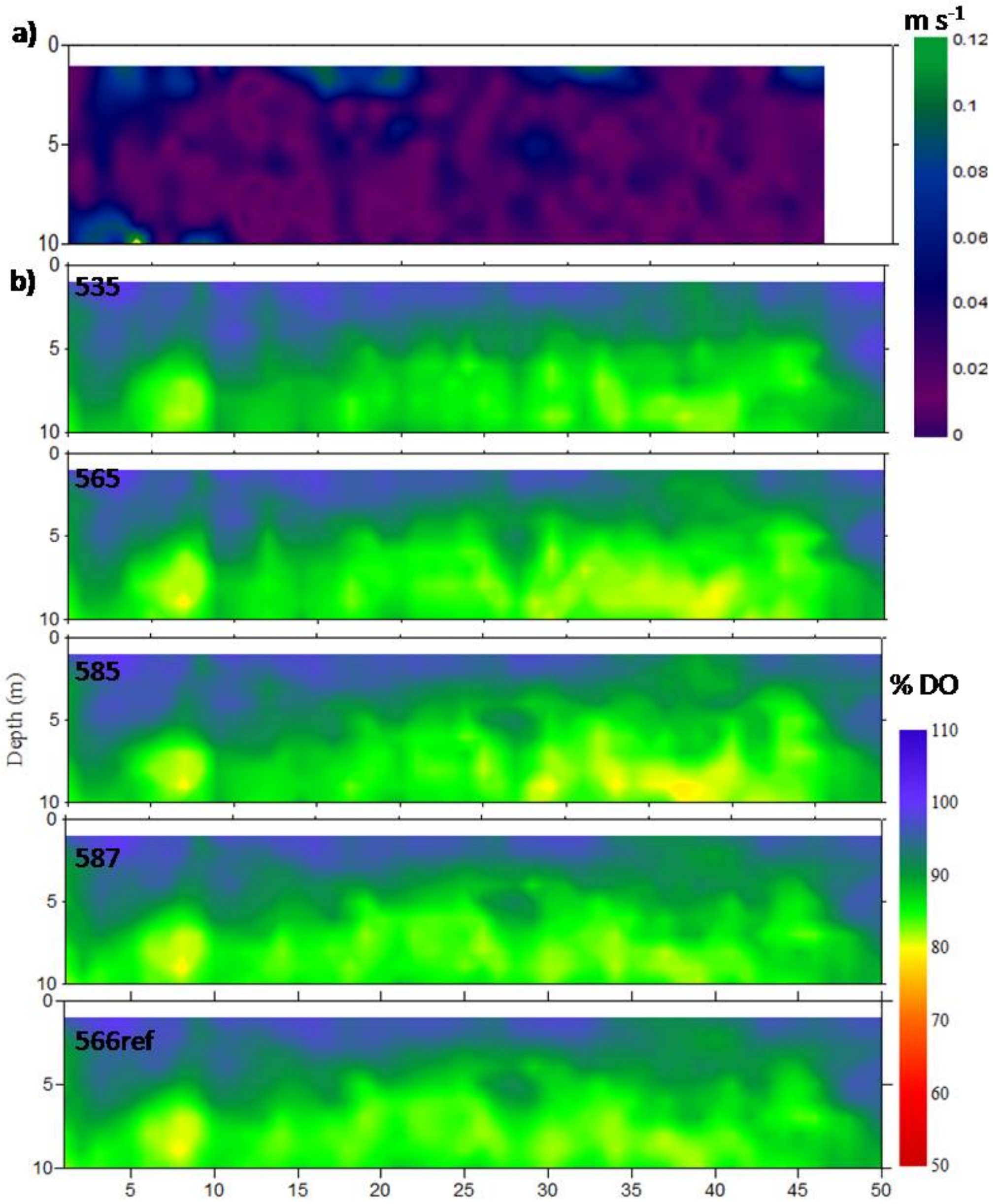

Figure 3.2: **a)** Water current velocity (m s^{-1}) from profiler B (Fig. 2.2). The white areas represent missing data, and **b)** DO (%) at the different positions within the seacage (535,565,585,587), including the reference point (566ref), for the empty cage at Solheim during the 50 hour observation period. Time 1 represent September 10, 14:45.

There was no differences between the reference point and the different positions within the seacage (Fig.3.3.a) or between the positions within the seacages (Fig.3.3.b). All the delta DO values were within the 2 % unit range, which is the accuracy level of the instruments.

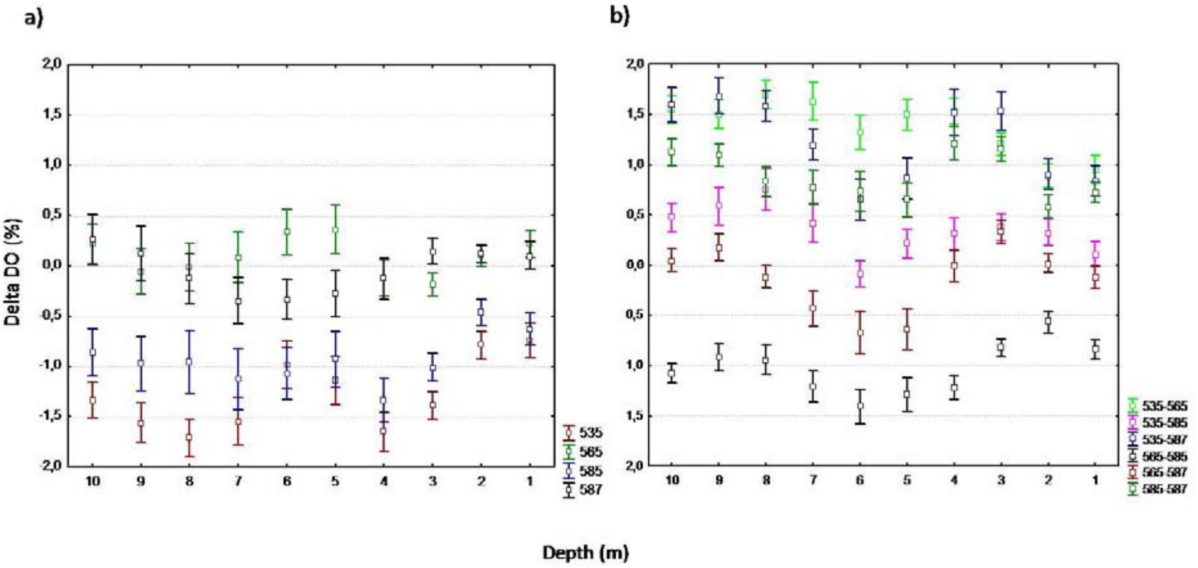

Figure 3.3: Delta DO (%) between the **a)** reference point and the different positions within the seacage and between the **b)** different positions within the seacage as a function of depth. Labels 535, 565, 585 and 587 in **a)** refers to the position subtracted from the reference point. Labels in **b)** represent the positions that have been compared (i.e. 535-565 is position 565 subtracted from position 535).

There was no obvious correlation between oxygen levels and current velocity (Linear regression, $p > 0.05$) as only up to 10.7 % of the observed variation in oxygen levels could be explained by water current velocity (Fig.3.4). Oxygen levels were relatively stable throughout the observation period, especially above the pycnocline. Below the pycnocline, oxygen levels varied slightly more with an overall lower level of oxygen. Lowest oxygen levels occurred when current velocities had a speed of approximately 0.02 m s^{-1}, while highest oxygen levels were found when current velocities were higher, at approximately 0.05 – 0.06 m s^{-1} (Fig.3.4).

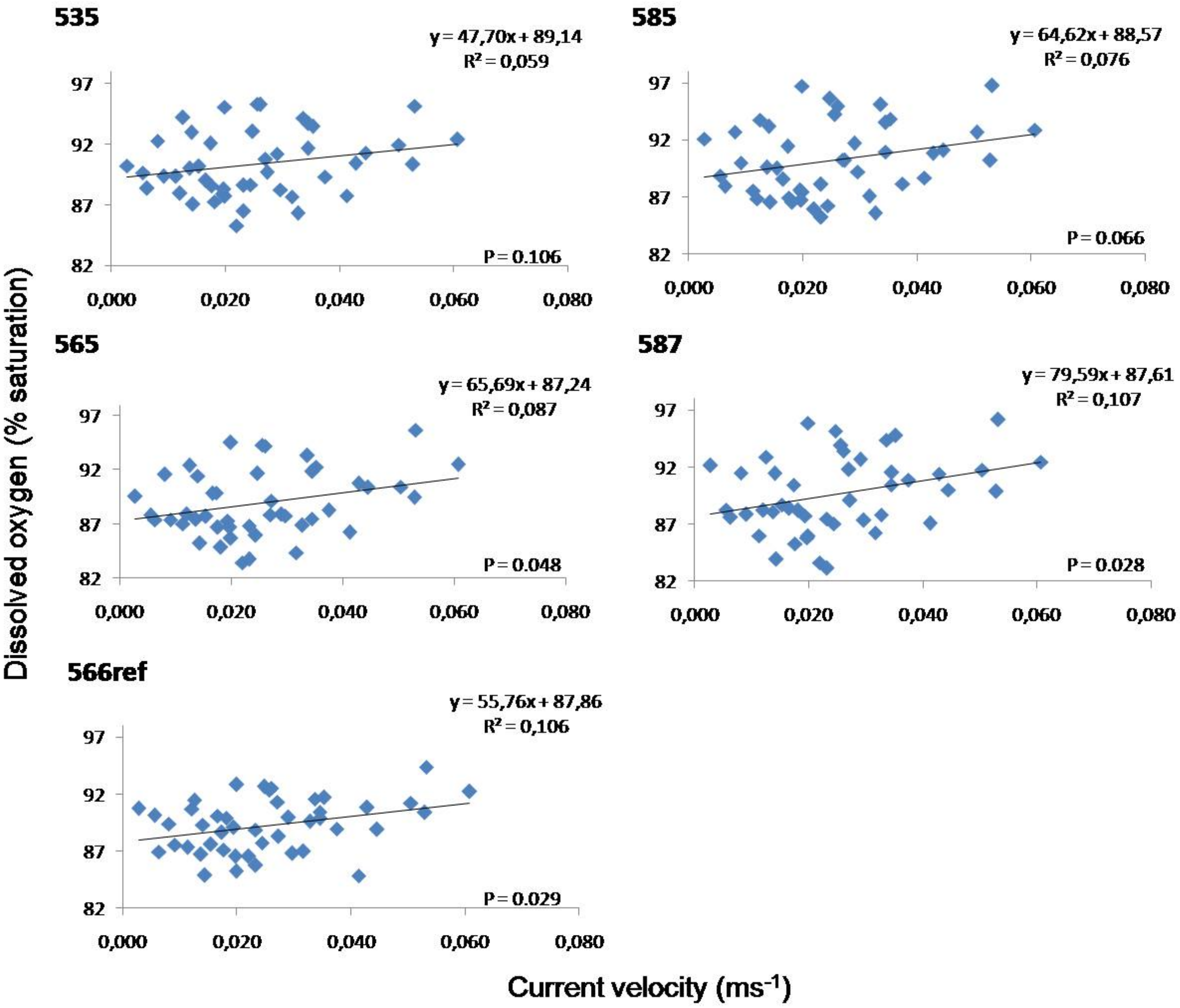

Figure 3.3: DO levels (% saturation) in relation to water current velocity (m s^{-1}) for the different positions within the seacage and the reference point (566ref) at 5 m depth throughout the observation period at Solheim.

3.2. Solheim (stocked cage)

The weather conditions were changing during the observation period. At the beginning it was raining and windy conditions, but it ceased as time went by, leading to calm sunny conditions towards the end.

3.2.1. Salinity and temperature

The presence of a pycnocline is evident also here, with fresher and colder water in the surface layers and more saline warmer water further down the water column (Fig.3.5). Temperature and salinity varied a bit more during this period with the weather shift towards the end of the observation period resulting in less freshwater input to the system and a rise in the pycnocline from around 5 m at the beginning of the observation period to around 2-3 m at the end (Fig.3.5). Salinity ranged from 4 ppt to 31 ppt, with an average of 24 ± 9 ppt (Table 3.2), with lower values near the surface and salinity increasing with depth (Fig.3.4.a). Temperature ranged from 8.4 °C to 12.9 °C with an average temperature of 11.8 ± 0.8 °C (Table 3.2). Coldest and least saline water was found in the surface layers of the seacage (Fig.3.5.b), and warmest and most saline waters were found further down.

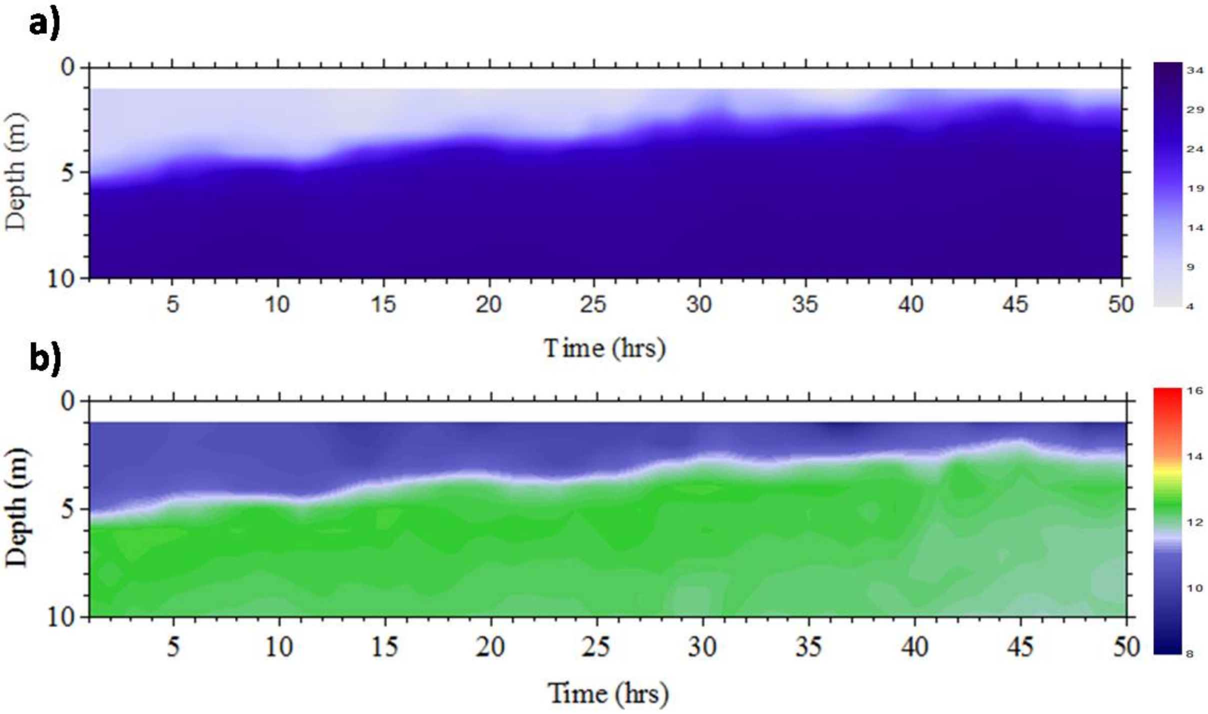

Figure 3.5: a) Salinity (ppt) and **b)** temperature (°C) at the reference point for Solheim stocked with salmon during the 50 hour observation period. Time 1 represent September 25, 12:00. Only the reference point is presented as all sites showed a similar picture (see Table 3.2).

3.2.2. *Fish density*

A general trend can be seen although about ten hours of data is missing. During the day fish were located deeper in the water column, with the majority of fish distributed between 5 – 12 m. Observed fish densities during the day was generally above 10 kg m^{-3} (Fig.3.6). At night, fish swam closer to the surface. Although the fish were more spread out in the water column using the whole available space, greater densities were observed in the upper layers, with < 10 kg m^{-3} compared to > 10 kg m^{-3} further down (Fig.3.6). Observed fish densities during the night were generally lower than during the day due to the fact that fish were more evenly spread out at night (Fig.3.6). OFD was predominantly around or below 10 kg m^{-3}. The first night (time 8 – 19 in Fig.3.6), the fish showed a bimodal distribution, with one part of the group located near the surface and another part located deeper down (Fig.3.6). During specific period and at certain depths, OFD reached a maximum of 25 kg m^{-3} which was almost three times the stocking density of 8.7 kg m^{-3}.

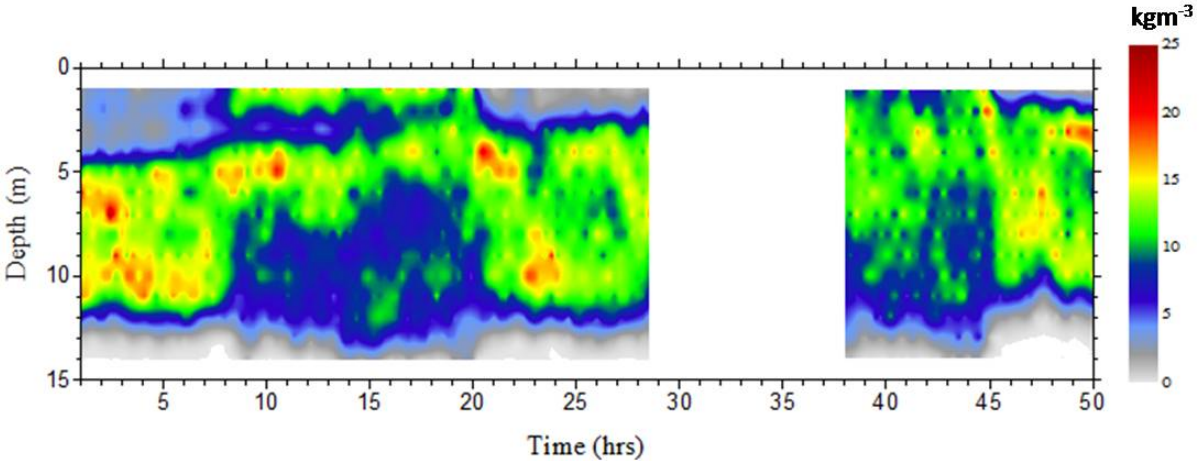

Figure 3.6: Observed fish density (OFD) in kg m^{-3} during the 50 hour observation period at Solheim. Time 1 represent September 25, 12:00. The white area at time 28.5 - 38 represent missing data.

3.2.3. *Water current velocity*

Water current velocity ranged from 0.00 m s^{-1} to 1.65 m s^{-1} (Fig.3.7.a). Periods of high velocities were observed throughout the observation period (Fig.3.7), with maximum levels reaching 1.65 m s^{-1} at 1 m. Minimum levels were 0 m s^{-1} and was found at 10 m. Strongest currents were observed in the surface layers and declined with depth during the periods of elevated current velocities (Fig.3.7.a).

3.2.4. Dissolved oxygen

DO levels for all the sites showed a profile reflecting that of salinity, with higher levels of oxygen near the surface and lower levels below the pycnocline (Fig.3.7.b). Average DO levels from the different sites within the seacage throughout the whole observation period ranged from 82 % to 85 % saturation, with minimum levels ranging from 71 % to 75 % saturation, and maximum levels ranging from 96 % to 118 % (Table 3.2). Lowest oxygen levels were found at position 587 throughout the whole observation period as reflected by an average oxygen level of 82 % saturation, which is about 2 % lower than the other positions (Table 3.2). The reference point had the lowest measured oxygen value with 70 % saturation, but the average value (85 %) and maximum value (101 %) was within the range of the positions within the seacage (Table 3.2).

Table 3.2: DO (% saturation), temperature (^{o}C) and salinity (ppt) for the different positions within the seacage (565, 585, 587, 588), including the reference point (566ref), for the survey done at Solheim stocked with salmon for the 50 hour observation period.

Position	DO μ ± S.D.	DO max.	DO min.	Temperature μ ± S.D.	Salinity μ ± S.D.
565	85 ± 6	96	75	11.6 ± 0.9	24 ± 9
585	85 ± 6	103	72	11.8 ± 0.9	24 ± 9
587	82 ± 6	98	71	11.8 ± 0.9	24 ± 9
588	85 ± 6	118	73	11.2 ± 0.9	25 ± 9
566ref	85 ± 6	101	70	11.8 ± 0.9	24 ± 9

As current velocity decreased oxygen levels dropped, and when current velocity increased oxygen levels rose (Fig.3.7). Low oxygen levels over a long period of time were observed below the pycnocline during the first night of the observation period, especially for position 587, which had prolonged periods of oxygen levels below 80 % saturation (Fig.3.7.b). The current data for this period showed that current velocity below the pycnocline was generally low throughout, resulting in less flushing of the water (Fig.3.7.a).

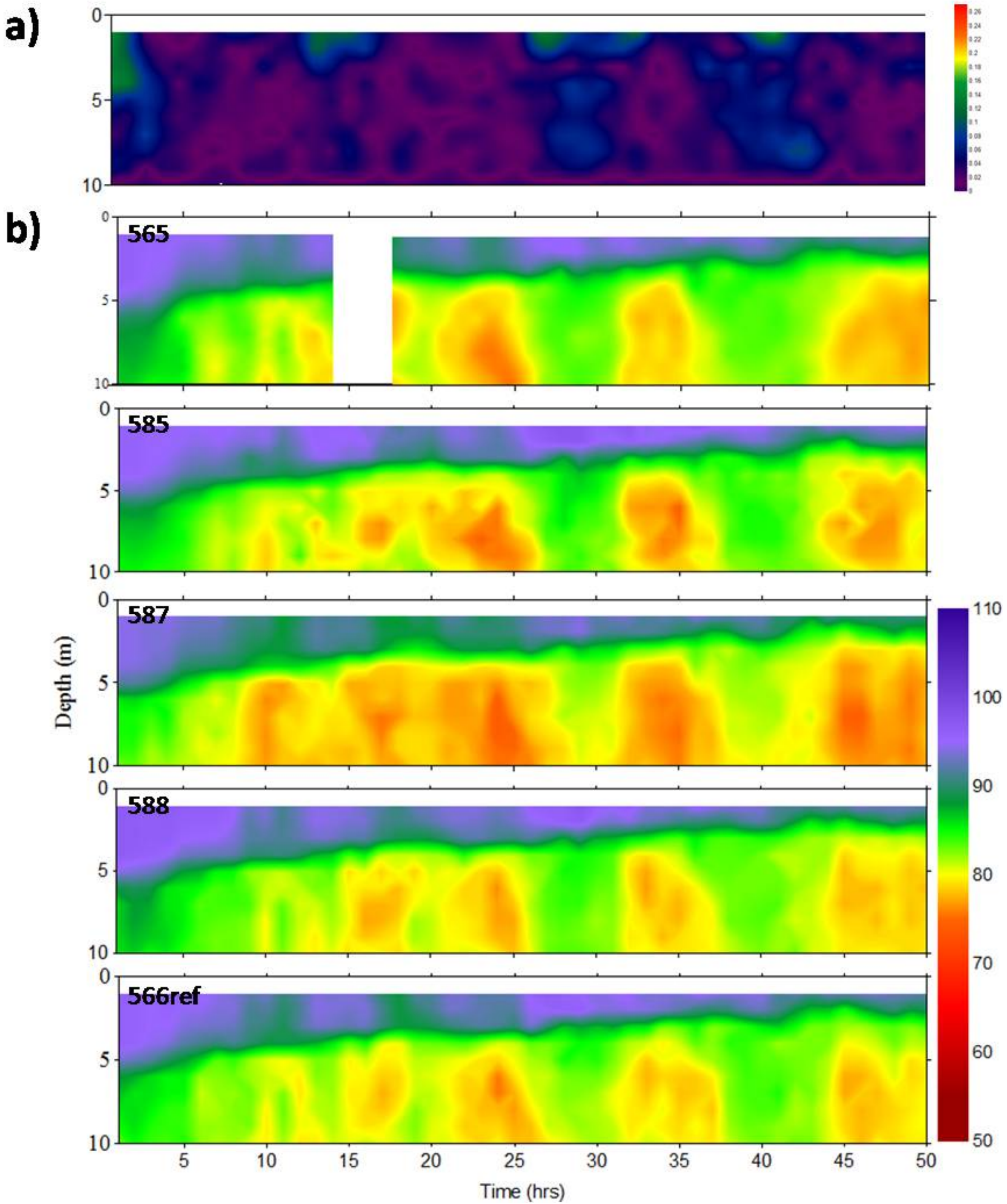

Figure 3.7: a) Water current velocity (m s^{-1}) from profiler B (Fig. 2.2) during the 50 hour observation period and **b)** DO (% saturation) at the different positions within the seacage (565, 585, 587, 588), and the reference point (566ref), for the survey done at Solheim stocked with salmon at ~9 kg m^{-3}. Time 1 represent September 25, 12:00. The white area at time 15-18 for position 565 represent missing data due to a technical failure.

Only one position (587) within the seacage differed significantly from the reference point (Wilcoxon test, $p < 0.001$), the rest were within the 2 % unit accuracy range (Fig.3.8.a). When comparing the different positions within the seacage, 587 was significantly lower than 585 and 588 at all depths (T-test, $p < 0.001$) (Fig.3.8.b). Position 587 was also lower than position 565 (Fig.3.8.b), however, it was lower than 2 % units difference hence within the accuracy range of the instruments. The differences in delta DO was a bit higher when fish was present, however, the degree of difference was still relatively low.

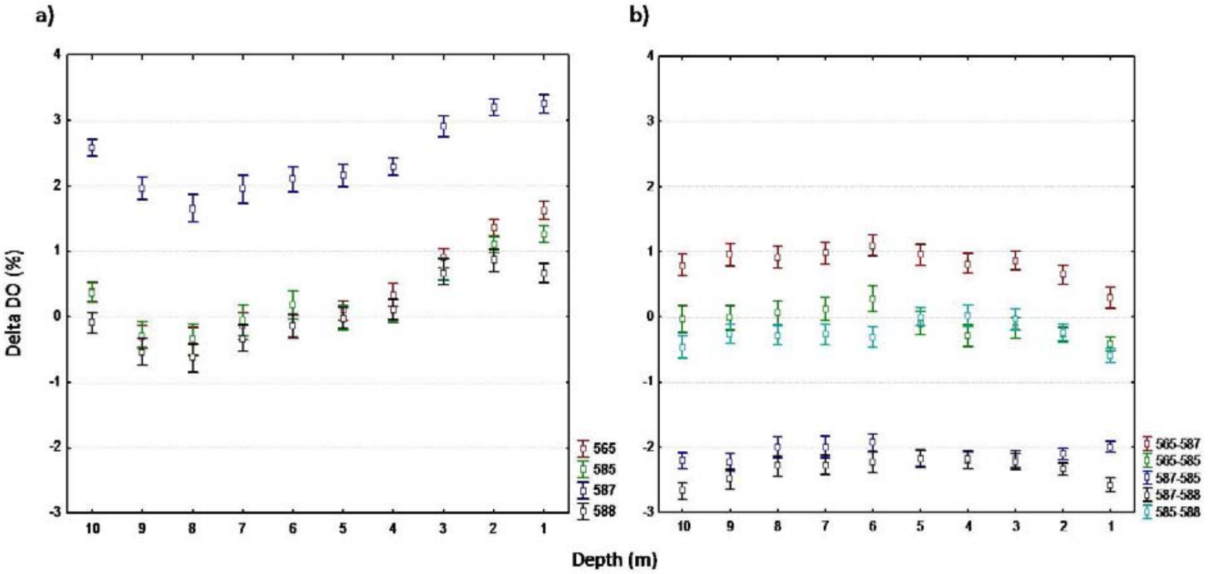

Figure 3.8: Delta DO (%) between **a)** the reference point and the different positions within the seacage and **b)** between the different positions within the seacage as a function of depth. Labels 565, 585, 587 and 588 in **a)** refers to the position subtracted from the reference point. Labels in **b)** represent positions that have been compared (i.e. 565-587 is position 587 subtracted from position 565).

There was a positive correlation between oxygen levels and water current velocity (Linear regression, $p < 0.001$). At least 43.1 % of the observed variation in DO could be explained by change in current velocity, for all the positions within the seacage including the reference point at 5 m depth. This depth was chosen as it showed relatively high OFD throughout the period (Fig.3.6).

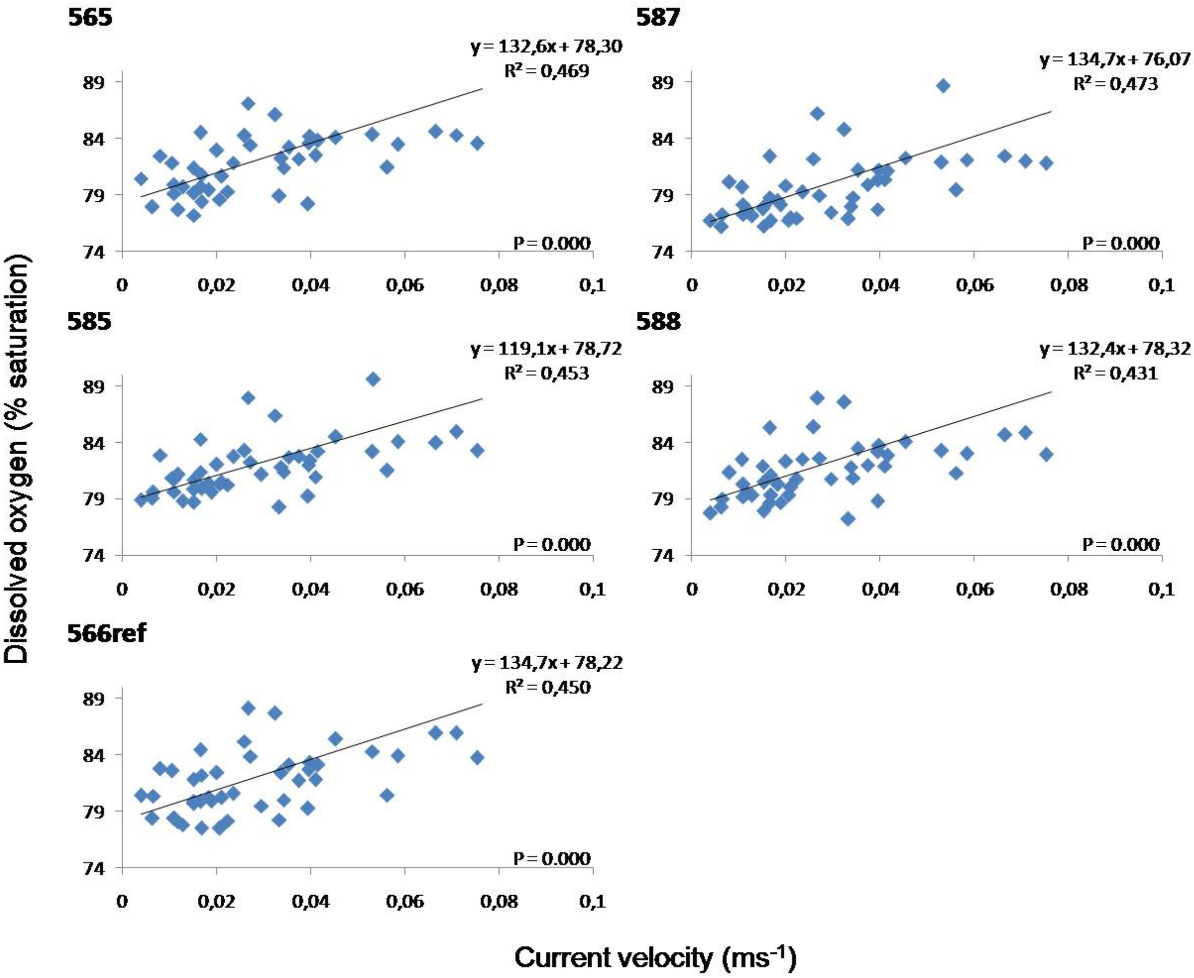

Figure 3.9: DO levels (% saturation) in relation to the water current velocity (m s^{-1}) for the different positions within the seacage and the reference point (566ref) at 5 m depth throughout the observation period at Solheim stocked with salmon at ~9 kg m^{-3}.

Measurements done at 2 m depth above the pycnocline revealed a negative correlation between DO levels and OFD during the day at both low (Pearson correlation test, see appendix for p-values) and high (Spearman correlation test, see appendix table 17 for p-values) current velocities (Fig.3.10.a and b). In contrast, no correlation was found during the night (Pearson correlation test, see appendix table 18 and 19 for p-values), but had instead relatively stable oxygen levels and OFD throughout (Fig.3.10.c and d).

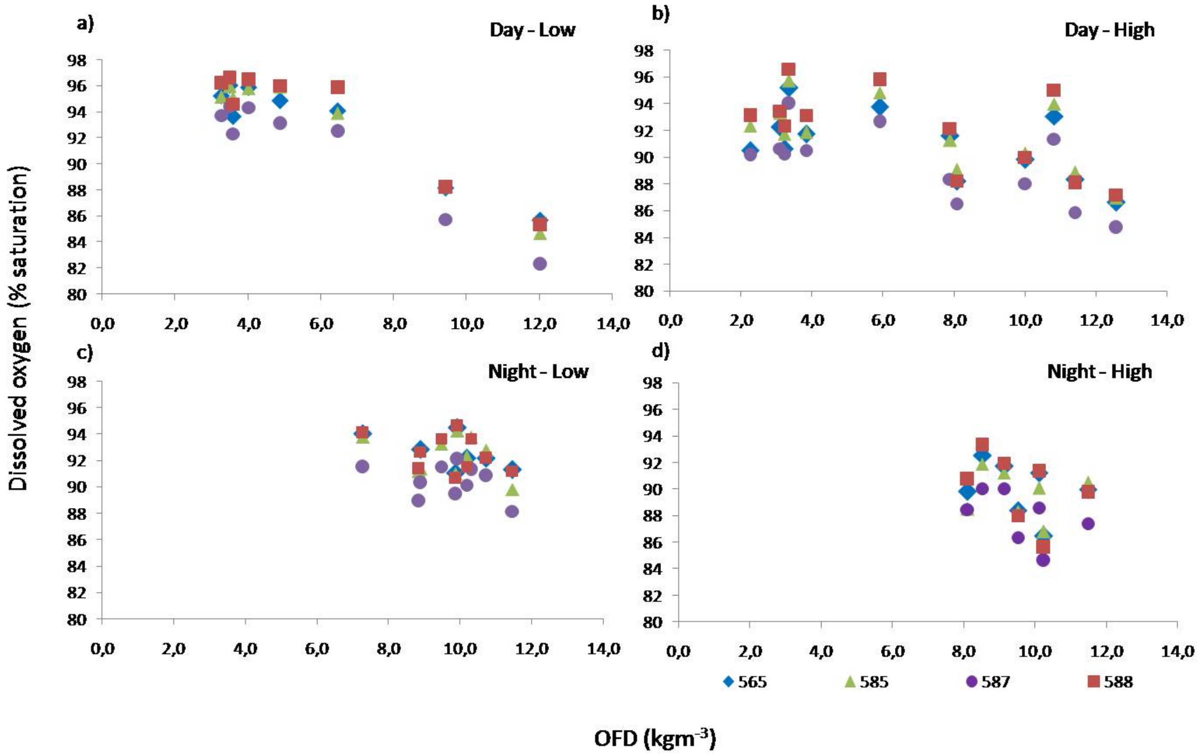

Figure 3.10: DO levels (% saturation) in relation to OFD (OFD) (kg m^{-3}) at **a)** day time, low velocity (< 0.03 m s^{-1}), **b)** day time, high velocity (> 0.03 m s^{-1}), **c)** night, low velocity (< 0.03 m s^{-1}), **d)** night, high velocity (> 0.03 m s^{-1}), for the different positions within the seacage at 2 m depth throughout the observation period at Solheim stocked with salmon at ~9 kg m^{-3}.

No correlation was found (Pearson correlation test, see appendix table 20 - 23 for p-values) between oxygen levels and OFD below the pycnocline (depth 8 m) during day or night, nor during periods of high or low current velocities (Fig.3.11).

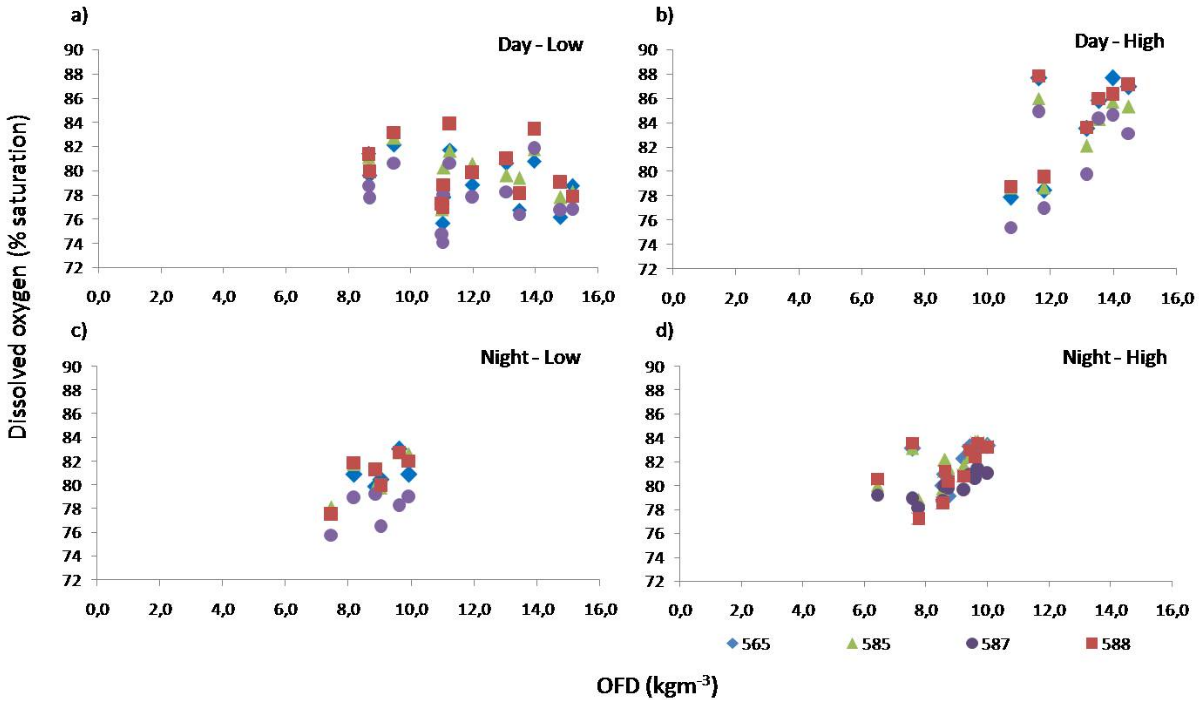

Figure 3.11: DO levels (% saturation) in relation to observed fish density (OFD) (kg m^{-3}) at **a)** day time, low velocity (< 0.03 m s^{-1}), **b)** day time, high velocity (> 0.03 m s^{-1}), **c)** night, low velocity (< 0.03 m s^{1}), **d)** night, high velocity (> 0.03 m s^{-1}), for the different positions within the seacage at 8 m depth throughout the observation period at Solheim stocked with salmon at ~9 kg m^{-3}.

3.2.5. Swimming speed

Swimming speed varied significantly on a daily basis (2-way ANOVA, $p < 0.000$), with higher swimming speeds during the day (generally between 0.4 - 0.8 BL s^{-1}) and lower swimming speed at night (generally between 0.2 - 0.4 BL s^{-1}) (Fig.3.12). Swimming speed generally increased right after dawn during feeding (time 22 and 44 from Fig.3.12), and was lowest in the hours just before dawn (time 17-18 and 41-42 from Fig.3.12). During the day, fish at 4 m depth had a significantly lower swimming speed compared to fish at 1m (Tukey HSD, $p < 0.004$). The fish at 1 m depth may not be fully representable because of the lower N, however it was included in order to provide a picture of the fish's behavioural pattern at that depth. There was no significant difference between 1 m and 7 m (Tukey HSD, $p > 0.1$) or between 4 m and 7 m depth (Tukey HSD, $p > 0.1$). No differences were found between depths at night (one-way ANOVA, $p < 0.1$).

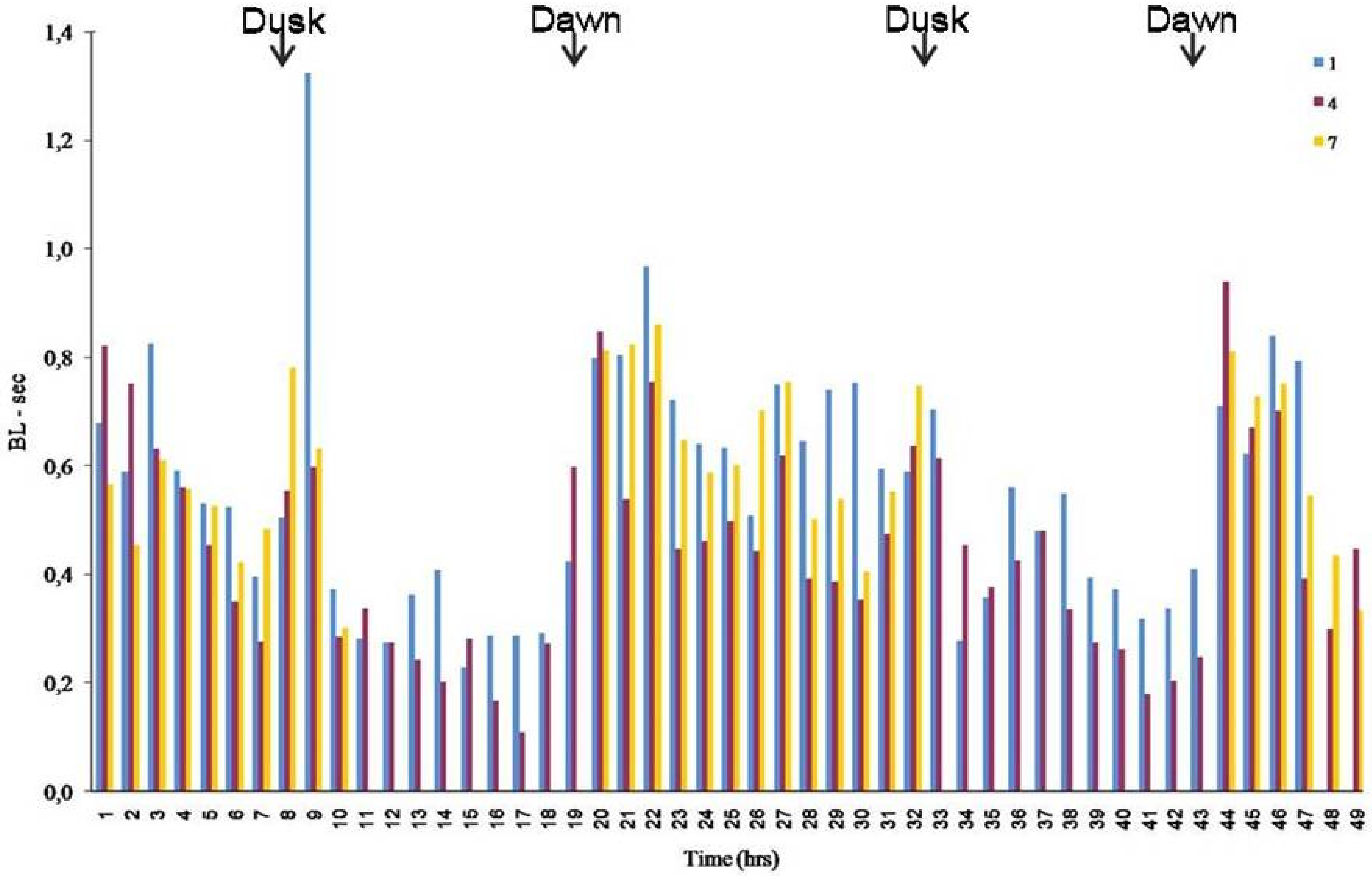

Figure 3.12: Swimming speed (body length (BL) sec^{-1}) of the fish during the 50 hour observation period at Matre research station, Solheim. 1, 4, and 7 represent different depths in meters.

3.3. Commercial marine farm site

3.3.1. Salinity and temperature

The temperature and salinity data showed a typical coastal site with homogenous water conditions (Fig.3.13). Both temperature and salinity was stable throughout the whole time period as well as with depth. Salinity ranged from 31 ppt to 33 ppt with an average of 32 ± 0.2 ppt (Table 3.3). Temperature ranged from 11.3 ^{o}C to 12.6 ^{o}C with an average of 12.2 ± 0.3 ^{o}C (Table 3.3).

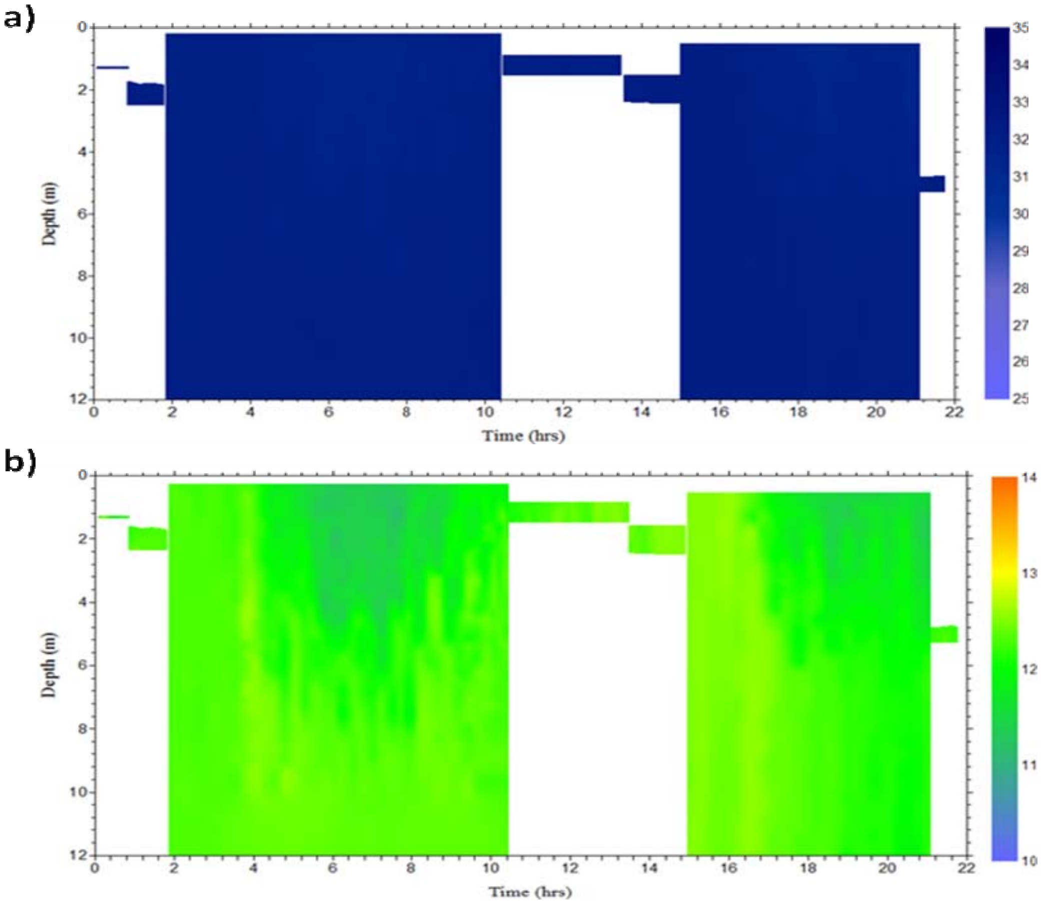

Figure 3.13: a) Salinity (ppt) and **b)** temperature (^{o}C) for the commercial farm stocked with salmon during the observation period. Time 1 represent October 9, 20:30. Only one of the instruments is represented as they showed similar values. The white areas represent missing data due to a stronger water current which made it impossible to profile the instruments without getting caught in the cage net.

3.3.2. Fish density

The fish were spread throughout the water column from 1 to 12 m during the night and in the early morning (hours 1 – 11) for the first period, with the highest OFD (~15kg m^{-3}) consistently at 5 m depth (Fig.3.14), which was twice the stocking density in the seacage. OFD decreased significantly below 12 m depth. The white area from hour 12 to 16 is missing data due to a strong current which forced the net up to about 10 m depth and pushing the fish outside the area covered by the echo sounder. This time period would not be representative for the actual vertical distribution as the fish was forced up towards the surface and was therefore excluded. During the day and afternoon (hours 16 and on), fish distributed itself in a bimodal manner, with one part of the fish biomass located near the surface from 1 to 5 m, and the other part further down the water column from around 15 m and deeper (Fig.3.14). Immediately after the period with missing data (hours 11 to 16, Fig.3.14) highest OFD was closest to the surface, coinciding with feeding, however, when feeding stopped at time 21 (16.30), the fish started to go deeper.

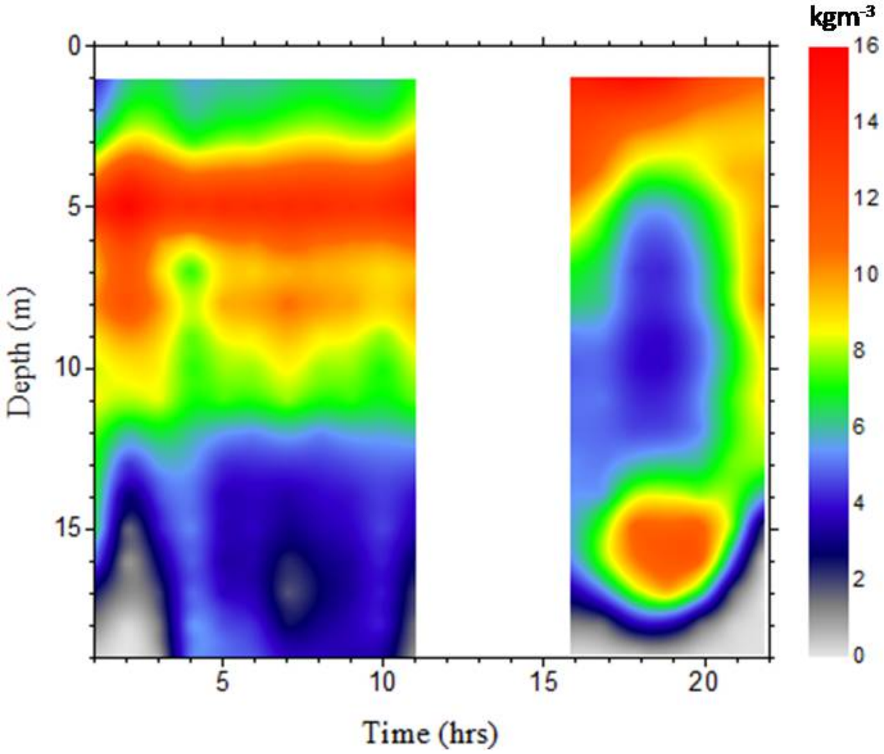

Figure 3.14: Observed fish density (OFD) in kg m^{-3} at the commercial farm site stocked with salmon. Time 1 represent October 9, 20:30. The white area from time 11-16 represent missing data due to a strong current which forced the cage net up to about 10 m depth disturbing the echo signals, making the data unrepresentative.

3.3.3. Water current velocity

Water current velocities varied greatly throughout the observation period with a strong surface current and periods with fluctuating velocities further down (Fig.3.15.a).

3.3.4. Dissolved oxygen

It is evident from the measurements conducted at the reference point that fluctuations in DO levels occur naturally, both over time and with depth (Fig.3.15.b), however, the magnitude of fluctuations were much lower than inside the seacages (Fig. 3.15.b) with a doubled S.D for positions within the cage compared to the reference point (Table 3.3). Average DO levels from the positions within the seacage during the whole observation period ranged from 76 % to 79 % saturation, with minimum and maximum levels ranging from 29 % to 57 %, and 90 % to 112 % saturation respectively (Table 3.3). The reference point had markedly higher oxygen values throughout the observation period (Fig.3.15.b) with an average of 87 % saturation, which is about 10 % higher than the oxygen values within the seacage.

Table 3.3: DO (DO) in %, temperature (^{o}C) and salinity (ppt) for the different positions within the seacage (535, 565, 587, 588), including the reference point (566ref), at a commercial farm stocked with salmon.

Position	DO μ ± S.D.	DO max.	DO min.	Temperature μ ± S.D.	Salinity μ ± S.D.
535	79 ± 7	92	57	12.2 ± 0.3	32 ± 0
565	79 ± 9	112	29	12.1 ± 0.3	32 ± 1
587	76 ± 8	90	51	12.3 ± 0.3	32 ± 0
588	77 ± 9	93	29	11.7 ± 0.3	33 ± 0
566ref	87 ± 4	99	69	12.3 ± 0.3	32 ± 1

Alarmingly low oxygen levels were observed, with a minimum of 28 % saturation at the time period 8-10 which represent 04.30 – 06.30, and the low levels extended throughout the water column (Fig.3.15.b). This was especially evident for positions 587 and 588 which had longer periods of low oxygen levels and this was more pronounced throughout the water column

(Fig.3.15.b). The low oxygen levels occurred right after the water currents had changed; either right after a stronger current or just before the currents increased (Fig.3.15.a). This was especially evident for the first period of measurements, (hour 2 – 10, Fig.3.15).

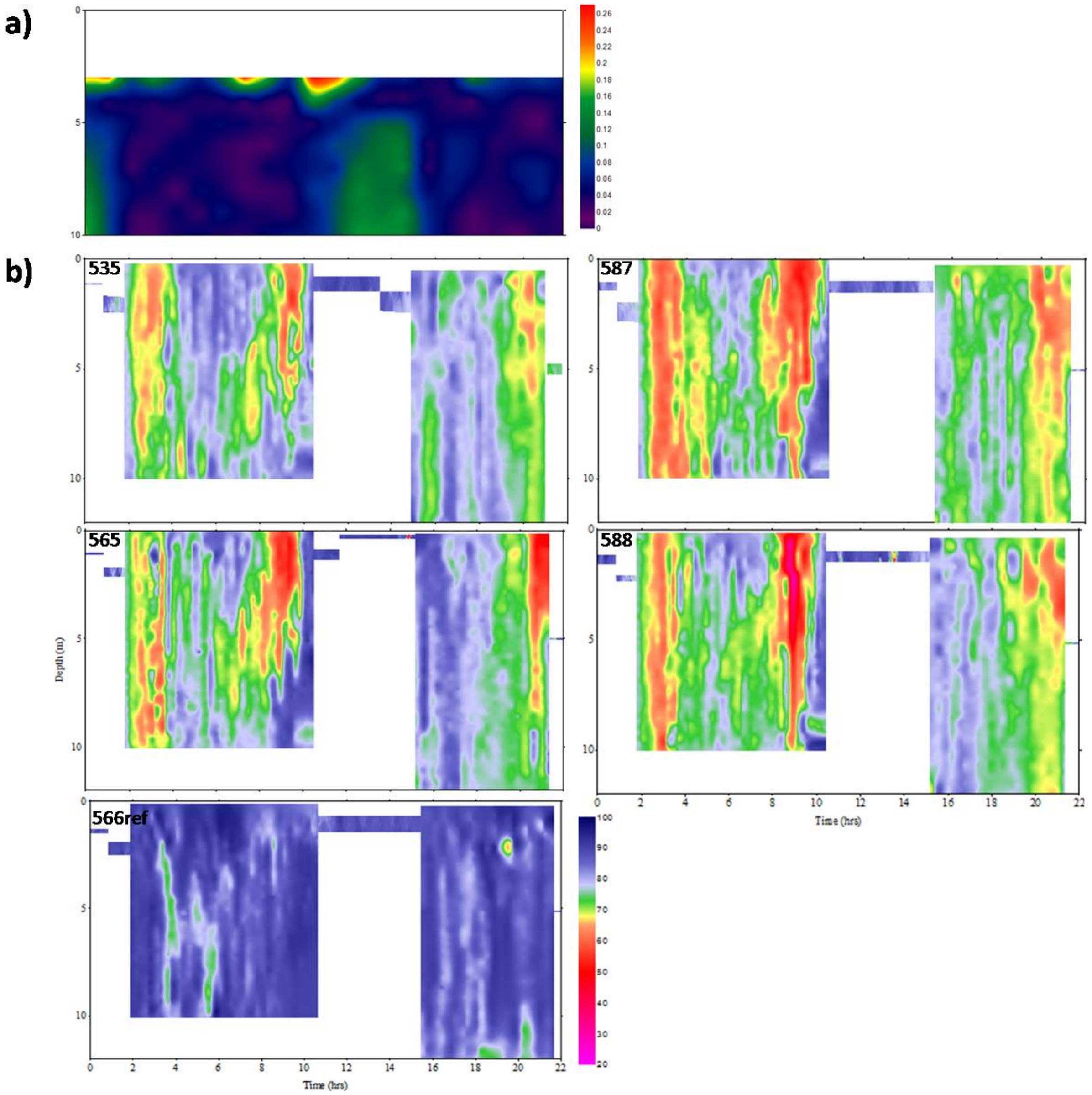

Figure 3.15: a) Water current velocity (m s^{-1}) for the observation period and **b)** DO (%) at the different positions within the seacage (535, 565, 587, 588), including the reference point (566ref), at the commercial farm stocked with salmon. Time 1 represent October 9, 20:30. No measurements were obtained before 3 m depth in **a)** due to the setup of the instrument. The white areas in **b)** are missing data due to a strong current which made it impossible to profile the instruments without getting stuck in the cage net.

Significant differences were found between the reference point and the positions within the seacage (Wilcoxon test and T-test, $p < 0.001$) and also between the positions within the seacage (T-test, $p < 0.001$). Delta DO decreased with depth, showing a clear trend that the differences in DO between the positions inside the sea cage and the reference point were greater in the top layers than further down the water column (Fig.3.16.a). When comparing the different positions within the seacage, greatest differences in DO levels were found in the top layers closest to the surface (Fig.3.16.b).

Position 587 and 588 had overall highest delta DO levels, both when compared to the reference point and between positions (Fig.3.16), and there was only a slight difference between the two positions, most pronounced closest to the surface (Fig.3.16.b). Positions 535 and 565 were not different, except at 1 m depth were a ~10 % difference in oxygen levels were found (Fig.3.16.a). The magnitude of differences between the outside and inside of the seacages, and between positions within the cage, was more pronounced at the commercial farm than at Solheim, with delta DO values constantly above 8 % when compared to the reference point, and differences up to around 10 % when comparing the positions within the seacage (Fig.3.16).

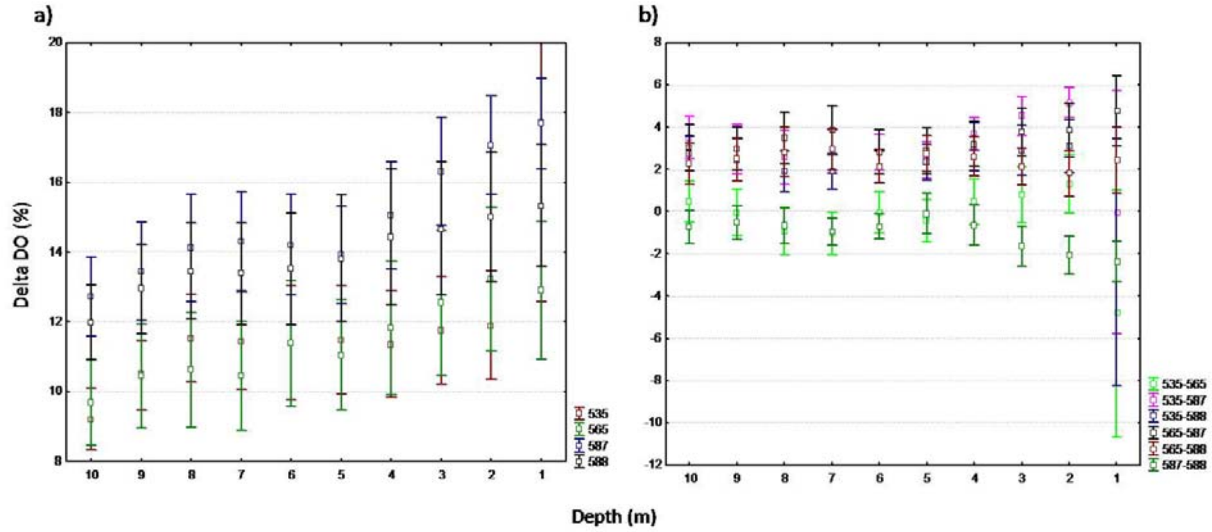

Figure 3.16: Delta DO (%) between **a)** the reference point and the different positions within the seacage, and **b)** between the different positions within the seacage as a function of depth. Labels 535, 565, 587 and 588 in **a)** refers to the position subtracted from the reference point. Labels in **b)** represent the positions that have been compared (i.e. 535-565 is position 565 subtracted from position 535).

DO levels were found to be positively correlated to water current velocity for 3 out of 4 positions ($R^2 > 0.292$) within the seacage (Linear regression, see Fig.3.14 for p-values), whereas no correlation was found for the reference point (Linear regression, $p > 0.1$) (Fig.3.17). These measurements were done at 1 m depth where OFD was relatively high throughout the observation period (Fig.3.14).

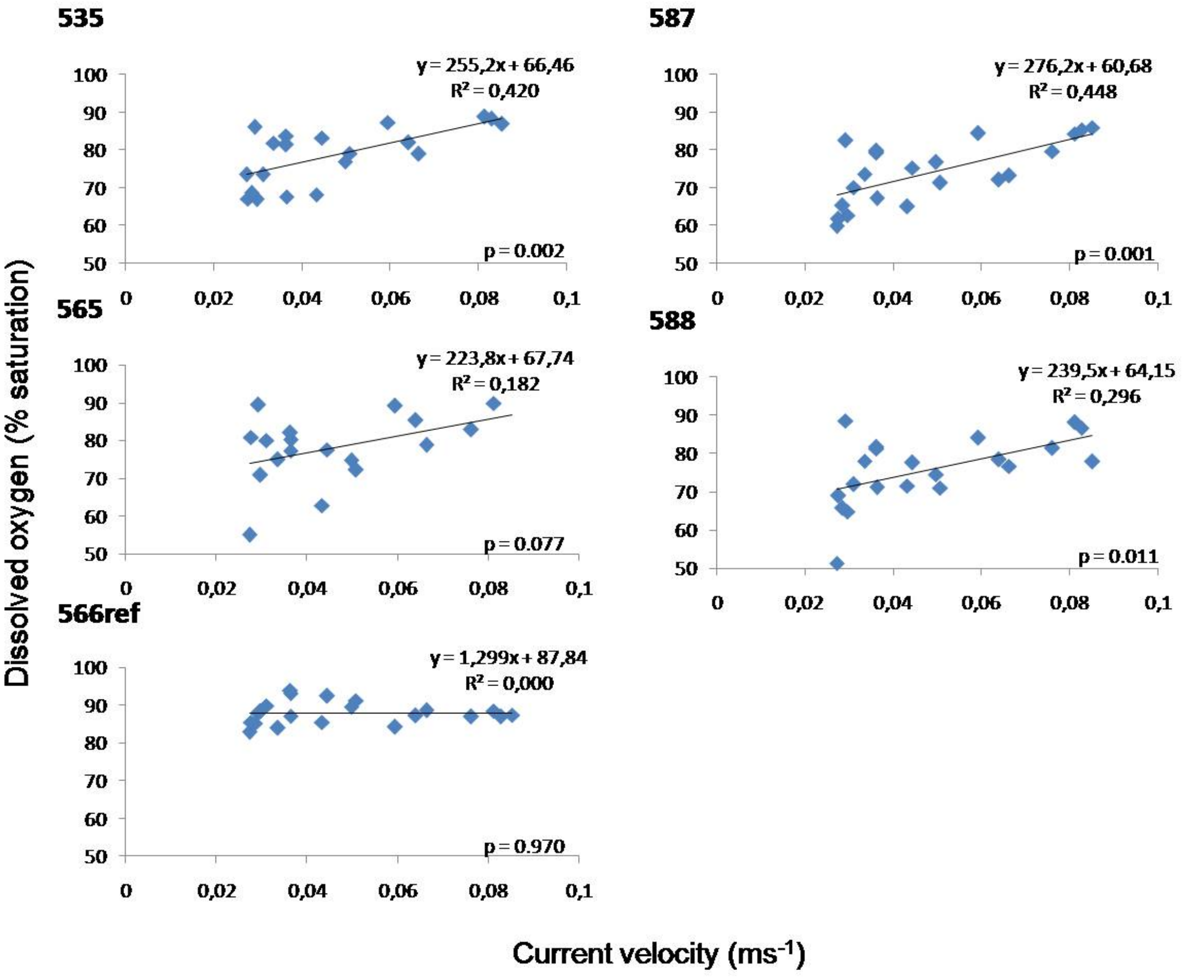

Figure 3.17: DO levels (% saturation) in relation to the current velocity (ms^{-1}) for the different positions within the seacage and the reference point (566ref) at 1 m depth throughout the observation period at the commercial farm site.

There was no correlation between DO levels and OFD at 5 m depth, neither during day or night, nor at high or low current velocities (Pearson correlation test, see appendix for p –

values). Higher OFD was observed at 5 m during the night compared to the day, but DO levels were in the same range, between ~55 and ~90 % saturation (Fig.3.18).

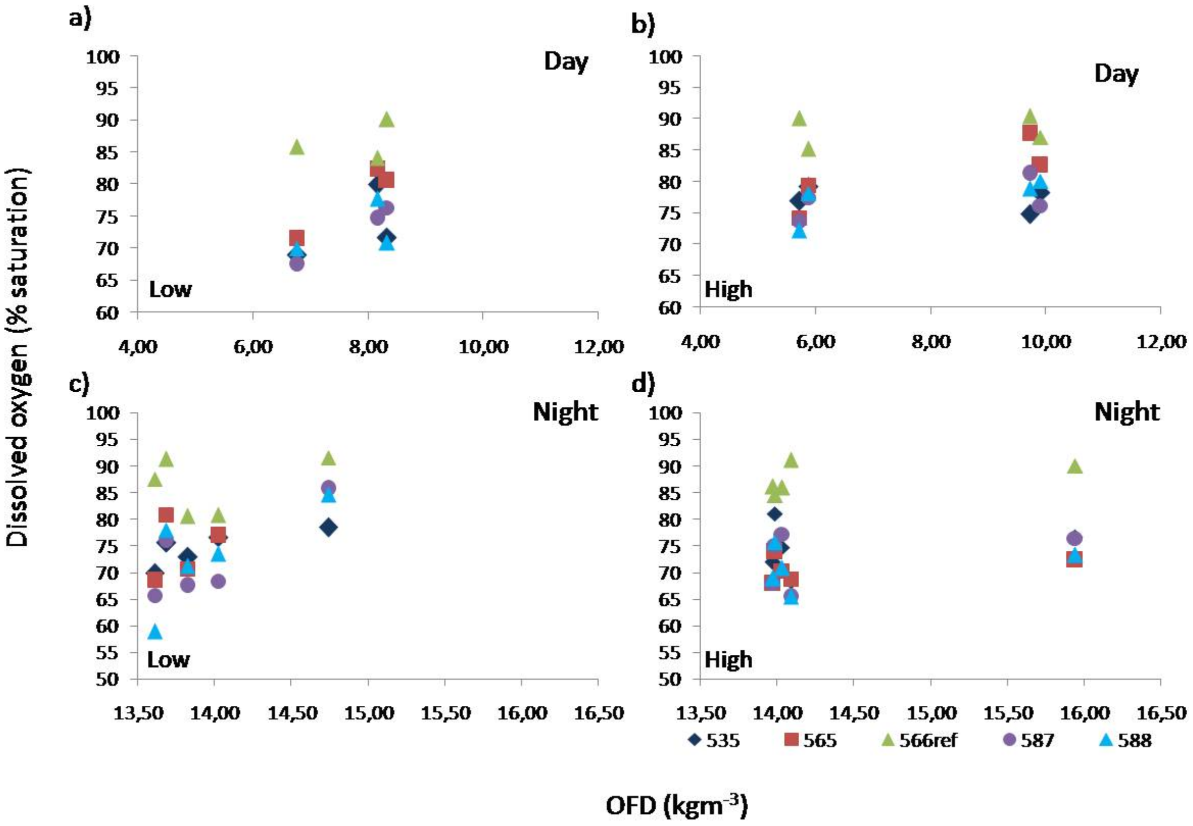

Figure 3.18: DO levels (% saturation) in relation to the observed fish density (OFD) (kgm^{-3}) at high or low water current velocities during day and night for the different positions within the seacage and the reference point (566ref) at 5 m depth throughout the observation period at the commercial site.

3.3.5. Swimming speed

Overall, swimming speed was higher at the commercial farm site than at Solheim (Fig.3.12 and Fig.3.19). There was a significant difference between swimming speed at different depths (one-way ANOVA, $p = 0.011$). Fish swam slowest at around 4 m depth and faster deeper down in the water column, as was similar to the seacage at Solheim. The swimming speed observed at 4 m was around 1 BL s^{-1}, compared to around 1.2-1.4 BL s^{-1} deeper down the water column (Fig.3.19). Significant differences in swimming speed at 4 m and 14 m were found (Tukeys HSD test, $p < 0.05$), but there was no significant difference between 4 m and 8 m at 0.05 significance level (Tukeys HSD test, $p > 0.05$). There was no difference between 8 m and 14 m (Tukeys HSD test, $p > 0.1$).

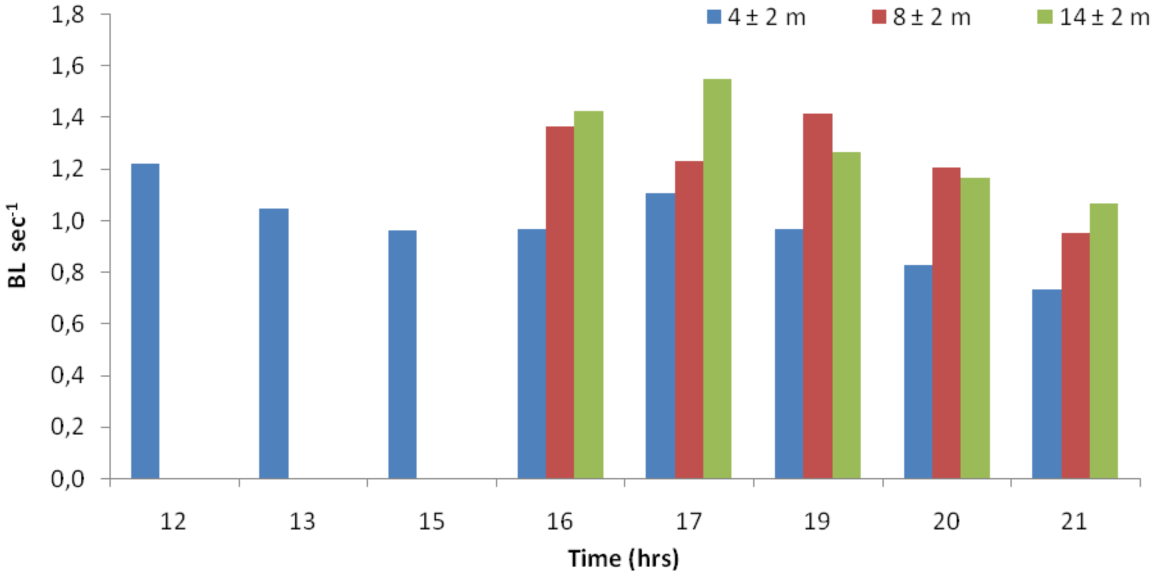

Figure 3.19: Swimming speed (BL s^{-1}) of the fish during the observation period at the commercial farm in Hordaland. 4,8, and 14 represent depths in meters. For time 12, 13 and 15 only observations from 4m were made due to a strong current making it impossible to haul the instruments up and down the water column without getting stuck in the cage net.

Underwater cameras were used as a tool to observe group structure and general fish behaviour as well as to estimate the amount of fouling on the nets. Fish were observed to show a more defined schooling structure deeper down, and less structured near the surface. The proportion of fouling organisms on the net was estimated to be approximately 30 % coverage in the upper part of the water column and decreasing to about 10 % coverage further down.

3.4 Skirt and delousing treatment

3.4.1. Fish density

During the trials with skirts, fish were confined in a volume of 12 m x 12 m x 4 m instead of 12 m x 12 m x 14 m as was the normal size of the seacage, resulting in a new stocking denisity of ~25 kg m^{-3}. There was a clear change in behavioural patterns when delousing treatment was added (Fig.3.20). During the trial done with only skirts, fish were spread out in the water column, using most of the available space. In contrast, when delousing treatment was added, fish showed a different type of behaviour, with the majority of fish located at or close to the surface or close to the cage net bottom (Fig.3.20.b).

For the trial done with only skirts, least amount of fish were found in the upper layer, around 1 m, with a fish density range of ~4 to ~26 kg m^{-3}. Highest OFD were found at 3 m depth, with 21 kg m^{-3} as the minimum observed density and 47 kg m^{-3} as the maximum. When delousing treatment was added, highest OFD were found closest to the surface, with a density of 107 kg m^{-3}. At 2 m and 3 m depth the density was approximately the same, ranging from 7 kg m^{-3} to 31 kg m^{-3}. An overall high density was found at the bottom of the seacage at depth 4, with 23 kg m^{-3} being the minimum observed density and 44 kg m^{-3} as the maximum.

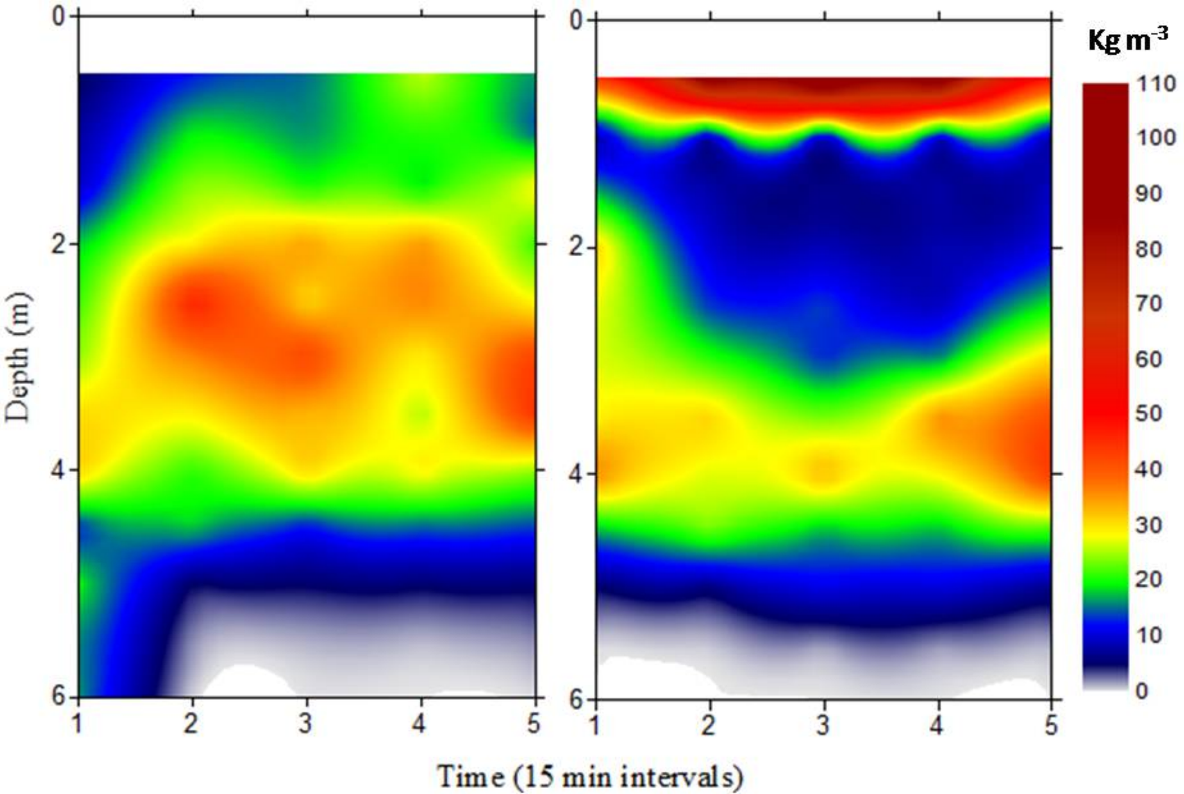

Figure 3.20: Observed fish density (OFD) in kg m^{-3} for the trials done with **a)** skirt, and **b)** skirt and delousing treatment. Time 1 represent the start of the observation period, when skirts have been put on. Delousing treatment was added at time 1.

3.4.2. Dissolved oxygen

The oxygen consumption by the fish within a seacage is shown in Fig.3.21. For the control run without fish, oxygen levels were relatively constant throughout the observation period, with oxygen levels around 90 % saturation and above. With fish present, the oxygen levles dropped rapidly after the skirts were put on, from around 90 % saturation at the start of the experiment to around 75 % saturation 15 minutes later, and had dropped to around 50 % saturation after 45 minutes (Fig.3.21). Oxygen levels were initially a bit lower than for the control. The addition of delousing treatment resulted in a more rapid decrease in DO levels, suggesting that the fish became more stressed. This is supported by the increased swimming speed and ventilation frequency (Fig.3.22 and Fig.3.23 respectively).

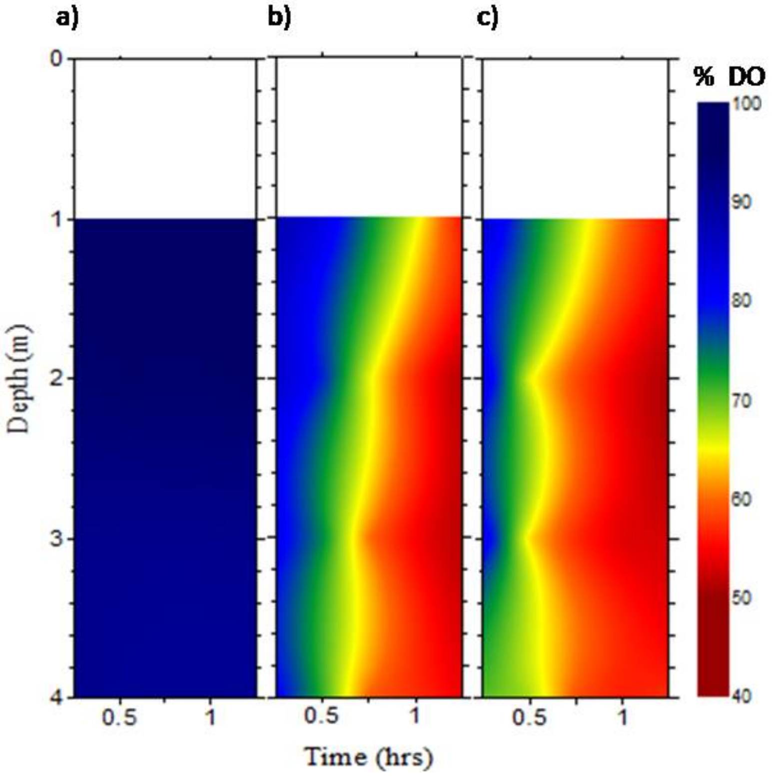

Figure 3.21: DO (% saturation) within a seacage with **a)** control (skirt but no fish), **b)** skirt and fish, and **c)** skirt, fish and delousing treatment. Skirts were put on after 0.25 hours, and delousing treatment was added after 0.30 hours for **c)**. Oxygen values are averages from all the five positions within the seacage. Averages were used because when the skirts were on it was assumed there was no current inside the seacage and hence the conditions would be the same.

3.4.3. *Swimming speed*

There was a significant difference in swimming speed between the experiment with skirts only and the experiment with skirts and delousing treatment (Mann-Whitney test, $p < 0.001$). Swimming speed was higher and more varied during the experiment with skirt and delousing treatment than when only the skirt was put on (Fig.3.22.a). Swimming speeds were generally around 0.4 BLs^{-1} for the experiment with skirts only compared to 0.4 to 0.8 BL s^{-1} when delousing treatment was added. Swimming speed reached a maximum after about 95 minutes with an average speed of ~1.0 BL s^{-1} and then decreased to ~0.5 BL s^{-1} for the experiment with skirts and delousing treatment (Fig.3.22.b).

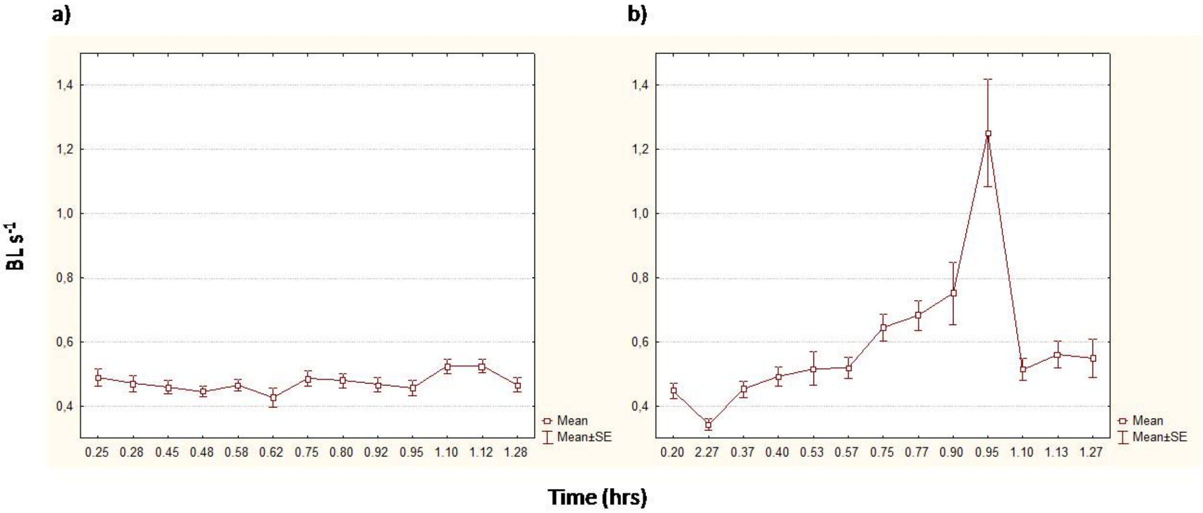

Figure 3.22: Change in swimming speed (body length (BL) s^{-1}) over time for the fish during the experiment when **a)** skirts were put on and when **b)** delousing treatment was added. Skirts were put on after 0.25 hours for both, and delousing treatment was added after 0.30 hours for **b)**. The observations were done at approximately 2 m depth.

3.4.4. *Ventilation frequency*

Ventilation frequency was significantly different between the two experiments (Mann-Whitney test, $p < 0.001$), being higher (~2 to ~3 gill movements s^{-1}) during the experiment where delousing treatment was added than when only skirts were put on (~1.5 to ~2.0 gill movementss^{-1}) and had also a higher degree of variation (Fig.3.23). Ventilation frequency increased slightly after the skirt were put on, with an initial VF of around 1 gill movements s^{-1}, reaching a maximum of around 2 gill movements s-1 after 1.17 hours (Fig.3.23.a).

Fig.3.23.b showed a marked increase in ventilation frequency after the addition of delousing treatment. As for the swimming speed, ventilation frequency reached a maximum after 95 minutes with ~2.7 gill movements s^{-1} when delousing treatment was added and declined to just over 2 gill movements s^{-1} after (Fig.3.23).

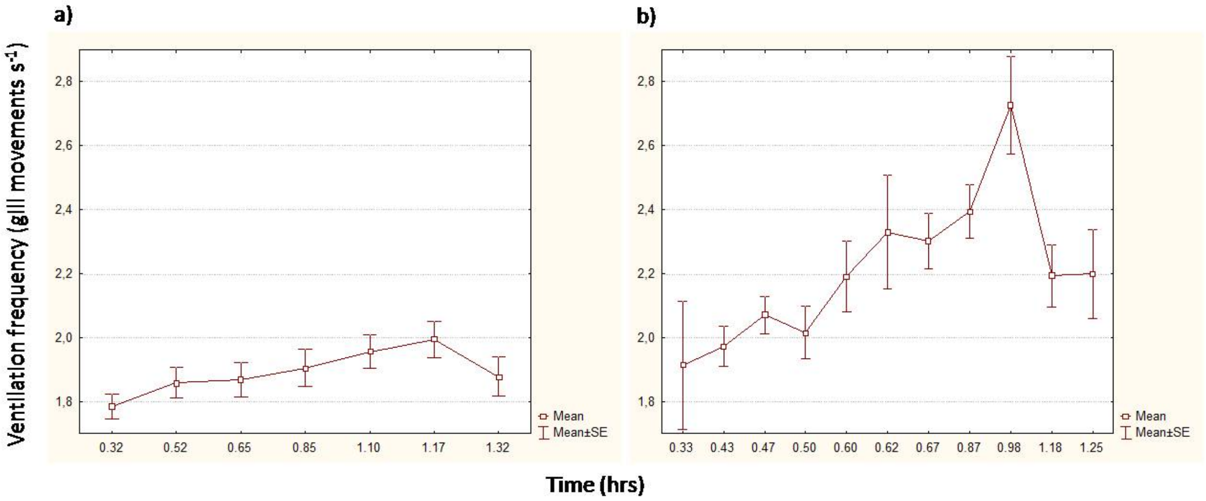

Figure 3.23: Change in ventilation frequency (gill movements s^{-1}) over time for the fish during the experiment when **a)** skirts were put on and when **b)** delousing treatment was added. Skirts were put on after 0.25 hours for both and delousing treatment was added after 0.30 hours. The observations were done at approximately 2 m depth.

4. Discussion

4.1. Discussion of methods

September and October was chosen as the time for this study as this was the time of the year with high specific growth rate (SGR) of fish in the seacages, and thus high metabolic rates and oxygen demands (Grøttum and Sigholt, 1998). The poorest oxygen conditions are generally experienced in late summer and early fall due to high water temperatures which result in less DO than colder water. In addition, the combination of shorter day length and a lower sun position, with less light penetrating the water, leads to reduced photosynthesis with less oxygen produced by the algae and therefore less oxygen available for fish. Conditions experienced during the night, with fish and algae competing for the available oxygen, become more common, and the risk of prolonged periods of sub-optimal oxygen levels increases.

A 50-hour observation period was chosen to cover several tidal cycles, two days and two nights (dusk and dawn), and several feeding periods. It is important to obtain adequate information about the naturally occurring fluctuations to determine how much oxygen variation was due to natural processes and how much was caused by the fish. Only 22 hours of data were collected for the commercial farm site. I experienced unexpected challenges with strong currents that caused large movements in the net, making it impossible to profile without the instrumentation getting caught. In an ideal situation, the commercial farm site should have mimicked the situation at Solheim. Weaker currents, seacages with better weighted nets or a lack of fouling on the nets would have improved sampling conditions; however, none of these factors are easy to control at commercial fish farms.

The different trials were done on different dates. It would have been optimal to do all the trials at the same time to enable direct comparison between the different scenarios, but this was not possible. Simultaneous sampling of all locations would have required more equipment and more people. Despite this, we got a good picture of what took place during the different trials, and even if they cannot be directly compared, the magnitude of the variations in the different trials could be observed.

The reference points were selected based on information provided by the fish farmer with regard to the main current direction. The intention was to place the reference point in a place that was not affected by the fish farm so it would be easy to distinguish the effect of the fish on the oxygen levels within the sea cage. After analyzing the data from the two farm sites it became clear that a better reference point could have been chosen for the cage-laboratory site at Solheim. Oxygen levels were expected to be significantly higher outside the seacage (as was clearly seen for the commercial farm site) than inside when fish are present, but this was not the case. The oxygen levels for the reference point fluctuated in the same way as the sites within the seacage. A better approach for selecting the best reference point would have been to measure the current velocity and direction before the start of the surveys.

4.2. Discussion of results

The data obtained in these surveys demonstrates considerable variations in oxygen levels within a single seacage, both over time and with depth. Both the variation within the seacage and the variation between the reference point and within the cage increased with increasing cage size and the total biomass at the farm. As a seacage becomes larger and more fish are put into the cage it becomes more difficult to control the environment within the cage. As observed in this survey, larger seacages exhibited greater variation in oxygen levels, as would be expected as the volume of water is much greater. At times the oxygen levels were close to critical levels (< 50 %). It has been reported from earlier studies that Atlantic salmon stopped swimming at a speed of 0.55 m s^{-1} at DO levels below 44 % saturation (Kutty and Saunders, 1973). A DO concentration of minimum 80 % saturation has been recommended for salmonid species to avoid respiratory stress (Iwama et al., 1997). Normal oxygen consumption by fish in an aquaculture situation is around 200 – 400 mg kg^{-1} h^{-1} and may increase to double that amount if the fish are excited or become stressed (Wedemeyer, 1997). These findings emphasize the importance of understanding the complex dynamics in the environment within seacages in order to achieve optimal farming conditions and acceptable welfare standards (Ellis et al., 2002; Turnbull et al., 2005).

4.2.1. Water currents, fish biomass and oxygen

In the natural environment, gradients frequently occur due to several factors. Some of these factors are tidal cycles, the alternation between photosynthesis during the day and respiration during night, and changes in weather conditions (i.e. rainy periods vs. dry periods) (Kramer, 1987). This could clearly be seen from the data obtained in this study. The cycles of tidal flushing were evident for both surveys with fish in the cages, with both systems experiencing oxygen levels positively correlated with the current velocity. Stronger currents create greater flushing of the system whereby the oxygen depleted water is replaced with fresh, oxygen-rich water (Beer, 1997). However, no correlation was found at the reference point at the commercial farm, indicating that the fish, in conjunction with the water currents, were responsible for the fluctuating oxygen levels inside the seacages. When current velocities are low, the oxygen produced by photosynthetic pathways is not enough to support typical fish farm biomass. Physical transport of water seems to be the most important for the supply of oxygen levels in seacages, as suggested by Wildish et al. (1993). This demonstrates the importance of constant water exchange at a farm site. This is especially important at larger farm sites where both cages and fish biomass are higher. Similar to the reference point at the commercial fish farm, no correlation was found between DO levels and water current velocity during the survey without fish at Solheim, but a positive correlation was found for the survey with fish, with presumably higher oxygen consumption than what was supplied during periods of low current velocities. The reference point might not have been fully representative as it may have been affected by the seacages. It was placed outside the seacage based on knowledge of the main current direction, but if the current went in another direction it would be affected by the farm. It is also possible that there were no differences in the oxygen levels inside and outside the seacage, and that the natural fluctuations in tidal cycles and current velocities were responsible for the variation; however this is not likely when considering the trial done without fish at Solheim and the trial done at the commercial farm.

No correlation was found between DO levels and OFD, which is contradictory to the findings of Johansson et al. (2006) who found lower DO levels where OFD was high. Johansson et al. (2006) also found that depth had a great influence on OFD levels and that the highest densities were found in water bodies with highest temperature, consistent with the current study.

4.2.2. Degree of stratification and oxygen

For the cage-laboratory site at Solheim the presence of a pycnocline seemed to be the major contributor to the variation in oxygen, as also found by Johansson et al. (2006, 2007). A pycnocline is formed when the water surface is protected from wind, or when there is stagnation; i.e. from a reduction in water currents. A pycnocline resulting from a brackish layer with denser water below is generally strong, and this limits the mixing of the different layers (Kramer, 1987; Beer, 1997) resulting in different environments above and below the pycnocline. In the present study, the pycnocline consisted of cold brackish water on top of denser more saline water, each layer with different oxygen profiles. Above the pycnocline the water was, for the most part, saturated with oxygen, while below the pycnocline lower oxygen levels were found. When mixing of the different layers is reduced, the oxygen environment is determined by the rate of oxygen production from algal photosynthesis and the respiratory demand of organisms (Kramer, 1987). The DO data from the smaller seacage at Solheim stocked with fish showed the importance of this. As mentioned, the water above the pycnocline was normally saturated with oxygen, but during the night when no oxygen was produced by photosynthesis and fish moved closer to the surface, oxygen levels dropped, hence more oxygen was consumed by the fish and the primary producers (algae) than was produced.

A change in weather conditions from rainy days to more dry days created a shift in the pycnocline due to reduced freshwater inflow to the system which again caused an overall drop in the oxygen levels, particularly below the pycnocline.

At the commercial farm site, the water was more homogenous, with limited changes in salinity and temperature profiles with changing depth or time. Here, variations in oxygen levels extended throughout the water column. The reductions in oxygen levels were more pronounced within the seacages than on the outside, and there are several possible explanations for this. Firstly, salmon affect the environment in the cage by their oxygen consumption (Grøttum and Sigholt, 1998). This is supported by the fact that the cage at the commercial fish farm (~446 tonnes) showed the lowest levels of oxygen compared to the smaller seacage at Solheim (~37 tonnes). Furthermore, the reduction could have been the result of net fouling on the cages (Braithwaite and McEvoy, 2005). According to Lars Gansel (Sintef Fiskeri og Havbruk, pers. comm.) coverage by fouling organisms above 15 % results in a significant reduction in current velocity, which may explain the lower oxygen levels observed in the upper layers of the water column at various times during low current velocities at the commercial site. Fouling was not an issue at Solheim as the net were changed prior to the start of the surveys to minimize fouling.

The total biomass was much higher at the commercial farm site than at Solheim and it is highly likely that this had a great influence on the oxygen levels within the seacage. At the commercial farm site there were eight seacages, all of which were stocked with salmon. At Solheim, only four of ten seacages were stocked with fish, with two of them containing juveniles. It would therefore be expected that the stocked seacages at Solheim would have reduced effects on the oxygen levels in comparison to the commercial site, because they were not located next to the seacage used in this study, nor would the seacage be affected with regard to the main current. It is possible that the reference point fluctuated with the fluctuating DO levels inside the seacage due to its placement in the main water current pathway outside the seacage used in this study (see Fig.2.2).

4.2.3. Fish behaviour

4.2.3.1. Vertical distribution

The fish at Solheim showed a heterogeneous vertical distribution. During the day the fish were located at depths with the highest water temperatures, which coincide with findings by Oppedal et al. (2007), Johansson et al. (2006) and Dempster et al. (2008). During the night, fish were more dispersed throughout the water column, but the highest densities were found close to the surface, as also found by Oppedal et al. (2001). The vertical distribution of the fish at the commercial farm was strongly affected by movements of the net. Despite this, fish in the commercial cage remained near the surface at night, with the highest density at approximately 5m depth. The fish were spread throughout the water column, displaying a bimodal distribution with a second peak deep in the water column. A reason why the fish were close to the surface during the day might be feeding, as earlier observed by Juell et al. (1994). When feeding stopped, fish in the surface layers migrated down to the deeper waters as can clearly be seen in Fig.3.14.

4.2.3.2. Stress response

When fish experience stressful situations, such as environmental changes and predators, behavioural responses are their first line of defense (Iwama et al., 1997; Iwama et al., 2004; Huntingford et al., 2006). Reduced availability of DO results in several behavioural responses by fish, such as change in activity, increased air breathing, increased air surface respiration

(ASR), and habitat changes, both vertically and horizontally (Døvig and Reimers, 1992; Iwama et al., 1997; Kramer, 1987). The best documented activity change to reduced oxygen levels is an increase in ventilation frequency (Kramer, 1987). The level of activity and the amount of available oxygen are linked, due to coupling between energy budgets and oxygen. The Krebs cycle and the electron transport chain are the main pathways for the production of energy in most organisms. As oxygen is the final electron acceptor of these pathways, oxygen could be considered as important as the energy obtained from food when calculating the energy budget. Thus, when oxygen availability is reduced the fish needs more energy for breathing to keep the same oxygen supply to tissues not involved in oxygen uptake. If the energy used for breathing is kept at the same level as when oxygen levels are high, then the oxygen allocated for other processes has to be reduced (Kramer, 1987). Ventilation frequency increased during the periods with skirts, and was more pronounced when delousing treatment was added. Ventilation frequency increases with falling oxygen in water breathers (Holeton, 1980; cited in: Kramer, 1987). As for bimodal species (capable of water breathing and surface breathing), ventilation frequency rises to a peak at intermediate oxygen levels, and as oxygen levels drop further, ventilation frequency declines again (Gee, 1980). This fits with the observed ventilation frequency during the trials with skirts. Here the ventilation frequency increased as oxygen levels dropped, but when oxygen levels became too low for the fish to cope (~50 %), the ventilation frequency was reduced.

Based on the fact that salmon has been shown to exhibit symptoms of oxygen distress when levels fell below ~70 % saturation (Davis, 1975) it would be assumed that the low DO values found in this study would have affected the behaviour of the salmon. Kramer (1987) has classified the response of fish to lowered DO availability as a) change in activity, b) increased use of air breathing, c) increased use of ASR and d) vertical or horizontal habitat changes. This was not seen for the 50 hour observation period carried out at Solheim, thus it can be assumed that DO levels occurring throughout that survey was not strong enough to induce a behavioural response. At the commercial farm, elevated ventilation frequencies were observed, and as mentioned earlier, this can be a stress response.

The observed swimming speed at the smaller seacages at Solheim reflects a situation found under normal farming conditions, where observed average swimming speeds are approximately 0.5 BL s^{-1} during the day, and range from 0.3 to 0.9 BL s^{-1} (Dempster et al., 2008). The fish in the large commercial seacage showed a higher swimming speed than at the smaller seacage at Solheim, possibly due to the difference in cage size as fish can swim faster in larger spaces. Increased stress at the commercial farm site due to the alarmingly low DO levels may have also caused increased locomotor activity (van Raaij et al., 1996).

Low oxygen levels lead to stress (Iwama et al., 1997; Iwama et al., 2004), but fluctuating temperatures may also play a role. Bevelhimer and Bennett (2000) modeled stress accumulation during periods of fluctuating water temperatures. The two locations used in this study had approximately the same daily mean temperatures, but the magnitude of the fluctuations differed. The results indicated that the fish at the location experiencing largest temperature fluctuations would have a stress index 2 - 3 times higher than the fish located at the site with less temperature fluctuations (in magnitude). Hokanson et al. (1977) found more rapid growth when temperature fluctuated within the preferred temperature range than if temperatures were held constant with the same means. However, better growth was achieved under constant temperature conditions than when the mean of the fluctuating temperatures exceeded the optimal temperature range. This implies that some fluctuations in physical factors are beneficial and may lead to increased growth, however, when the magnitude of the fluctuations gets larger, fish will have more problems adjusting and this will eventually lead to decreased growth and other negative impacts. At the commercial farm, the magnitude of fluctuations was much higher than at Solheim, which suggests that the fish might have been more chronically stressed.

The behavioural response the fish showed with regards to ventilation frequency and swimming speed may be explained in adaptive terms. It has been shown that fish exposed to osmotic stress schooled less and had a shorter escape distance than unstressed fish when faced with predators after being exposed to a stressful medium. These changes in antipredator behaviour in response to osmoregulatory problems are considered to be adaptive (Handeland et al., 1995). In the present survey, fish were exposed to a stressful situation, that of drastically sinking oxygen levels. Initially, the fish compensated by increasing ventilation frequency and swimming speed. When oxygen levels dropped further, a higher ventilation frequency and swimming speed would be necessary if the fish were to get sufficient oxygen. Water is a dense medium and requires the use of a high amount of energy to overcome the frictional drag when swimming. As drag increases with increasing velocity, increasing swimming speed becomes very energy demanding (Wedemeyer, 1997). Thus, the fish may eventually adapt to the new environment by decreasing both ventilation frequency and swimming speed as was observed. When comparing the skirt trial and the skirt trial with the addition of delousing treatment, there was a clear trend that the fish got more stressed when the delousing treatment was added, which could be seen by the already explained increase in ventilation frequency and swimming speed. The OFD data showed the same trend. It seemed like the fish that were exposed to the delousing treatment tried to avoid the treatment by swimming up close to the surface or down toward the bottom of the seacage, while when only the skirts were on fish were located throughout the water column, but highest densities were found in the middle, at 2 – 3 m depth.

To summarize, fish are able to acclimatize to fluctuations in environmental conditions and recover in between periods of unfavorable conditions. However, when fish are exposed to environmental conditions of a higher magnitude than their tolerance range, such as the low DO levels found at the commercial farm site, the fish will no longer be able to fully recover in between periods of unfavorable conditions. Hence, the fish will eventually become chronically stressed, which can lead to reduced growth and higher mortality rates, such as those suffered by the commercial farm site (Anon, pers. comm.).

The swimming speed also differed with depth. At both locations higher swimming speeds were observed deeper down in the water column. An explanation for this might be that the fish located further down were less neutrally buoyant. Water pressure increases with depth (Beer, 1997) and this leads to a decrease in swim bladder volume (Evans and Claiborne, 2006). Faster swimming may then have been necessary to avoid sinking by generating sufficient hydrodynamic lifting. Another explanation for the higher swimming speed further down in the water column might be that the fish were observed to have a more pronounced schooling behaviour than higher up; and schooling behaviour is generally linked to high swimming speeds (Dempster et al., 2008). Predator avoidance might be the reason for the schooling behaviour (Juell, 1995), as great numbers of cod and saithe were observed under and close to the bottom of the seacage. Responses typical for encounters with predators are flight, immobilization and schooling (Sundström et al., 2005).

During the trials with skirts, and especially when delousing treatment was added, spontaneous locomotor activity (a sudden increase in swimming speed and a change in swimming direction) was observed. Reduced oxygen levels can initiate spontaneous locomotor activity (Kramer, 1987). This type of movement requires increased energy and it would have been expected that this kind of “unnecessary” activity should decline with the decreasing oxygen availability. However, it has been suggested that this activity is an attempt to avoid areas with unfavorable conditions (Kramer, 1987). As an example, female threespine sticklebacks in salt marsh pools showed reduced activity during periods of hypoxia (Whoriskey et al., 1985). Weber and Kramer (1983) found that surface access influenced the rate of activity of juvenile guppies, with increased activity with surface access and decreased activity with denied surface access.

Due to the complexity of the system, it is hardly likely that a single factor would be responsible for an alteration in the environmental conditions. Current velocity and oxygen levels were not correlated when the 50 hour observation period for the empty cage was done, but a correlation in current velocity and oxygen levels were found when fish were present. No correlation was found between oxygen levels and OFD. Therefore, a combination of low current velocity and OFD seem to influence the oxygen levels inside the seacage, with fish consuming more oxygen than is being supplied by the weak currents, leading to low oxygen levels, and at times with stronger currents, no such trend was found. Another example is the differences observed within the seacages. Fish are not evenly distributed as seen in many studies (Fernö et al., 1995; Juell and Fosseidengen, 2004; Johansson et al., 2006; Oppedal et al., 2007). Although the current study investigated vertical distributions, it can be assumed that the fish were not evenly distributed on the horizontal plane either. During the trial with the stocked cage at Solheim it was observed that one of the positions within the seacage had an overall lower level of oxygen. This might be due to the water current direction and the swimming behaviour of the fish combined. If the water current direction was as for the assumed main direction, the fish would experience most friction at that particular position when swimming round and round, and swimming speed might be reduced. This means that the fish spend more time passing that position compared to the rest of the seacage. And since frictional drag increases exponentially with water current velocity (Schreck et al., 1997), more energy is needed for swimming, hence more oxygen is consumed. This was not measured, and is thus only a theory, so to be able to make conclusions about this, a deeper analysis of the data has to be done.

6. Conclusion

This survey reveals considerable variations both within seacages and between the reference point and the seacage, both over time and space. The magnitude of variations became larger with increasing seacage size and higher biomass. Alarmingly low DO levels were found at the commercial farm site, with an elevated swimming speed compared to the fish at Solheim, suggesting the fish were more stressed or even chronically stressed. Water current velocities and oxygen levels correlated when fish were present, but not for the empty cage or at the reference point, suggesting that both water current velocity and OFD were responsible for the fluctuating DO levels, with lower levels of oxygen during periods of low current velocities. These findings stress the importance of locating fish farms in places where environmental conditions are good and with a constant flushing of the system to avoid low oxygen levels. However, this is a complex system and a deeper understanding of the complex dynamics in the environment both inside and in the near vicinity is necessary.

5. References

Ashley, P.J. (2007) Fish welfare: current issues in aquaculture. *Applied Animal Behaviour Science*. **104:** 199 – 235.

Beer, T. (1997) *Environmental Oceanography*. CRC Press.

Bergheim, A., Gausen, M., Næss, A., Hølland, P. M., Krogedal, P. and Crampton, V. (2005) A newly developed oxygen injection system for cage farms. *Aquaculture Engineering.* **34:** 40-46.

Bevelhimer, M. and Bennett, W. (2000) Assessing cumulative thermal stress in fish during chronic intermittent exposure to high temperatures. *Environmental Science & Policy*. **3:** 211-216.

Beveridge, M. C. M. (2004) Cage Aquaculture. *3rd ed*. Blackwells, Oxford.

Bjordal, A., Juell, J.-E., Limdem, T. and Fernö, A. (1993) *Hydroacoustic monitoring and feeding control in cage rearing of Atlantic salmon (Salmo salar* L*)*. In: Reinertsen, H., Dahle, L. A., Jørgensen, L. and Tvinnereim, K. (Eds.) *Fish Farming Technology.* Trondheim, Norway, pp. 203 – 208.

Braastad, B. O., Damsgård, B. and Juell, J.-E. (2006) *Welfare in Farmed Fish.* Norwegian Institute of Fisheries and Aquaculture Research, Report 5.

Brett, J. R. (1952) Temperature tolerance in young Pacific salmon, genus *Oncorhyncus*. *Journal of the Fisheries Research Board of Canada.* **9:** 265 – 323.

Braithwaite, R. A. and McEvoy, L. A. (2004) Marine biofouling on fish farms and its remediation. *Advances in Marine Biology*. **47:** 215-252.

Dahl, E., Hansen, P. K., Haug, T. and Karlsen, Ø. (2007) *Kyst og Havbruk 2007.* Institute of Marine Research.

Davis, J.C. (1975) Minimal DO requirements of aquactic life with emphasis on Canadian species: a review. *Journal of the Fisheries Research Board of Canada*. **32:** 2295-2332.

Dempster, T., Juell, J.-E, Fosseidengen, J.E., Fredheim, A. and Lader, P. (2008) Behaviour and growth of Atlantic salmon (*Salmo salar* L.) subjected to short-term submergence in commercial scale sea-cages. *Aquaculture*. **276:** 103-111.

Døvig, K. and Reimers, E. (1992) *Fiskens Fysiologi*. John Grieg Forlag.

Elliott, J. M. (1991) Tolerance and resistance to thermal stress in juvenile Atlantic salmon, *Salmo salar*. *Freshwater Biology*. **25:** 61 – 70.

Ellis, T., North, B., Scott, A. P., Bromage, N. R., Porter, M. and Gadd, D. (2002) Review paper: The relationships between stocking density and welfare in farmed rainbow trout. *Journal of Fish Biology*. **61:** 493-531.

Evans, D. and Claiborne, J. B. (2006) *The Physiology of Fishes Third Edition*. Taylor and Francis Group LLC, pg. 601.

Fernö, A., Huse, I., Juell, J.-E. and 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:** 285-296.

Gee, J. H. (1980) Respiratory patterns and antipredator responses in the central mudminnow, *Umbra limi*, a continuous, facultative, air-breathing fish. *Canadian Journal of Zoology*. **58:** 819 – 827.

Grøttum, J. A. and Sigholt, T. (1998) A model for oxygen consumption of Atlantic salmon (*Salmo salar*) based on measurements of individual fish in a tunnel respirometer. *Aquaculture Engineering*. **17:** 241-251.

Guinea, J. and Fernandez, F. (1997) Effect of feeding frequency, feeding level and temperature on energy metabolism in *Sparus aurata*. *Aquaculture.* **148:** 125-142.

Handeland, S. O., Järvi, T., Fernö, A. and Stefansson, S. O. (1996) Osmotic stress, antipredator behaviour, and mortality of Atlantic salmon (*Salmo salar*) smolts. *Canadian Journal of Fisheries and Aquatic Sciences*. **53:** 2673-2680

Hokanson, K. E. F., Kleiner, C. F. and Thorslund, T. W. (1977) Effects of constant temperatures and diel temperature fluctuations on specific growth and mortality rates and yield of juvenile rainbow trout, *Salmo gairdneri*. *Journal of the Fisheries Research Board of Canada*. **34:** 639-648.

Huntingford, F. A., Adams, C., Braithwaite, V. A., Kadri, S., Pottinger, T. G., Sandøe, P. and Turnbull, J. F. (2006) Review paper: current issues in fish welfare. *Journal of Fish Biology*. **68:** 332-372.

Huse, I. and Holm, J. C. (1993) Vertical distribution of Atlantic salmon (*Salmo salar*) as a function of illumination. *Journal of Fish Biology*. **43** (Supplement A): 147 – 156.

Iwama, G. K., Pickering, A. D., Sumpter, J. P. and Schreck, C. B. (1997) *Fish stress and health in aquaculture*. Cambridge University Press. Cambridge, U.K.

Iwama, G. K., Afonso, L. O. B. and Vijayan, M. M. (2004) *Stress in Fish*. AquaNet Workshop on Fish Welfare, Campbell River, B.C., Canada.

Jobling, M. (1994) *Fish Bioenergetics*. Chapman & Hall, London, UK, pp. 166-168.

Johansson, D., Juell., J.-E., Oppedal,. F., Stiansen, J.-E. and Fosseidengen, J. E. (2004) *Lokalisering av oppdrettsanlegg: Merd-miljø og fiskevelferd i lakseproduksjon på kyst- og fjordlokaliteter på Vestlandet*. Havforskningsinstituttet, Institute of Marine Research.

Johansson, D., Ruohonen, K., Kiessling, A., Oppedal, F., Stiansen, J.-E., Kelly, M. and 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:** 594-605.

Johansson, D., Juell, J.-E., Oppedal, F., Stiansen, J.-E. and Ruohonen, K. (2007) The influence of the pycnocline and cage resistance on current flow, oxygen flux and swimming behaviour of Atlantic salmon (*Salmo salar* L.) in production cages. *Aquaculture.* **265:** 271-287.

Johnson, S. C., Treasurer, J. W., Bravo, S., Nagasawa, K., and Kabata, Z. (2004) A review of the impact of parasitic copepods on marine aquaculture. *Zoological Studies.* **43:** 229-243

Juell, J.-E. (1995) The behaviour of Atlantic salmon in relation to efficient cage-rearing. *Reviews in Fish Biology and Fisheries.* **5:** 320 – 335.

Juell, J-E. and Fosseidengen, J.E. (2004) Use of artificial light to control swimming depth and fish density of Atlantic salmon (*Salmo salar*) in production cages. *Aquaculture.* **233:** 269-282.

Juell, J-E., Fernö, A., Furevik, D. and Huse, I. (1994) Influence of hunger level and food availability on the spatial distribution of Atlantic salmon, *Salmo salar* L., in sea cages. *Aquaculture and Fisheries Management.* **25:** 439-451.

Juell, J-E., Oppedal, F., Boxaspen, K. and Taranger, G.L. (2003) Submerged light increases swimming depth and reduces fish density of Atlantic salmon (*Salmo salar*) in production cages. *Aquaculture Research.* **34:** 469-477.

Kramer, D. L. (1987) Dissolved oxygen and fish behaviour. *Environmental Biology of Fishes* **18:** 81-92.

Kristiansen, T. S., Johansson, D., Oppedal, F. and Juell, J. E. (2007) *Hvordan har oppdrettsfisken det i merdene?* In: Dahl, E., Hansen, P. K., Haug, T. and Karlsen, Ø. (Eds.) *Kyst og Havbruk 2007*. Havforskningsinstituttet, Institute of Marine Research.

Kutty, M. N. and Saunders, R. L. (1973) Swimming performance of young Atlantic salmon (*Salmo salar*) as affected by reduced ambient oxygen concentration. *Journal of the Fisheries Research Board of Canada*. **30:** 223 – 227.

Kvamme, B. O., Oppedal, F., Torgersen, T., Fridell, F., Sundt, H. and Sundell, K.S. (2008) *Fiskevelferd : Oksygennivået viktig for oppdrettsfisken sin helse og velferd*. In: Boxaspen, K. K., Dahl, E., Gjøsæter, J. and Sunneset, B. H. (Eds.) *Kyst og Havbruk 2008*. Havforskningsinstituttet, Institute of Marine Research.

Lymbery, P. (1992) *The welfare of farmed fish*. Petersfield: Hampshire. Compassion in World Farming.

Lymbery, P. (2002) *In too deep – the welfare of intensively farmed fish*. Petersfield, Hampshire: A Compassion in World Farming report.

Oppedal, F., Juell, J.-E., Taranger, G. L. and Hansen, T. (2001) Artificial light and season affects vertical distribution and swimming behaviour of post-smolt Atlantic salmon in sea cages. *Journal of Fish Biology*. **58:** 1570-1584.

Oppedal, F., Juell, J.-E. and Johansson, D. (2007) Thermo- and photoregulatory swimming behaviour of caged Atlantic salmon: implications for photoperiod management and fish welfare. *Aquaculture*. **265:** 70-81.

Rimmer, D. M. and Paim, U. (1990) Effects of temperature, photoperiod, and season on the photobehaviour of juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Zoology*. **68:** 1098 – 1103.

Schreck, C. B., Olla, B. L. and Davis, M. W. (1997) *Behavioural responses to stress*. In: Iwama, G. K., Pickering, A. D., Sumpter, J. P. and Schreck, C. B. (Eds.) *Fish Stress and Health in Aquaculture*. Cambridge University Press. Cambridge, U.K.

Sigholt, T. and Finstad, B. (1990) Effect of low temperature on seawater tolerance in Atlantic salmon (*Salmo salar*) smolts. *Aquaculture*. **84:** 167 – 172.

Staurnes, M., Nordtvedt, R. and Rosseland, B. O. (1998) *Vannkvalitet*. In: Hansen, T. (1998) *Oppdrett av Laksesmolt*. A/S Landbruksforlaget.

Stevenson, P. (2007) *Closed Waters: The Welfare of Farmed Atlantic Salmon, Rainbow Trout, Atlantic Cod & Atlantic Halibut*. Compassion in World Farming and World Society for the Protection of Animals.

Sundström, L. F., Petersson, E., Johnsson, J. I., Dannewitz, J., Höjesjö J. and Järvi, T. (2005) Heart rate responses to predation risk in *Salmo trutta* are affected by the rearing environment. *Journal of Fish Biology*.**67:** 1280-1286

Treasurer, J. W., Hannah, F. and Cox, D. (2003) Impact of a phytoplankton bloom on mortalities and feeding response of farmed Atlantic salmon, *Salmo salar*, in west Scotland. *Aquaculture*. **218:** 103-113.

Turnbull, J., Bell, A., Adams, C., Bron, J. and Huntingford, F. (2005) Stocking density and welfare of cage farmed Atlantic salmon: application of a multivariate analysis. *Aquaculture*. **243:** 121-132.

van Raaij, M. T. M., Pit, D. S. S., Balm, P. H. M., Steffens, A. B. and van den Thillart, G. E. E. J. M. (1996) Behavioural strategy and the physiological stress response in rainbow trout exposed to severe hypoxia. *Hormones and Behaviour*. **30:** 85-92.

Weber, J.-M. and Kramer, D.L. (1983) Effects of hypoxia and surface access on growth, mortality, and behavior of juvenile guppies *Poecilia reticulata*. *Canadian Journal of Fisheries and Aquatic sciences*. **40:** 1583-1588.

Wedemeyer, G. A. (1997) *Effects of rearing conditions on the health and physiological quality of fish in intensive culture*. In: Iwama, G. K., Pickering, A. D., Sumpter, J. P. and Schreck, C. B. (Eds.) *Fish stress and health in aquaculture*. Cambridge University Press. Cambridge, U.K.

Whoriskey, F.G., Gaudreault, A., Martel, S., Campeau, S. and FitzGerald, G.J. (1985) The activity budget and behavior patterns of female threespine sticklebacks, *Gasterosteus aculeatus* (L.). *Nat. Can. (Rev. Ecol. Syst.)* **112:** 113-118.

Wildish, D.J., Keizer, P.D., Wilson, A.J. and Martin, J.L. (1993) Seasonal changes of dissolved oxygen and plant nutrients in seawater near salmonid net pens in the macrotidal Bay of Fundy. *Canadian Journal of Fisheries and Aquatic sciences*. **50:** 303-311.

Appendix

Appendix Table 1: results of a one-sample T-test for the difference between position 587 and 566ref at Solheim stocked with salmon.

Depth (m)	Mean	Std.Dv.	N	Std.Err.	Reference Constant	t-value	df	p
all	2.409350	1.283327	500	0.057392	0.00	41.98050	499	0.00
10	2.584157	0.886883	50	0.125424	0.00	20.60334	49	0.000000
9	1.965618	1.188632	50	0.168098	0.00	11.69330	49	0.000000
8	1.661274	1.458034	50	0.206197	0.00	8.056723	49	0.000000
7	1.949643	1.504335	50	0.212745	0.00	9.164221	49	0.000000
6	2.102741	1.365624	50	0.193128	0.00	10.88779	49	0.000000
5	2.158824	1.236062	50	0.174806	0.00	12.34985	49	0.000000
4	2.300399	0.940125	50	0.132954	0.00	17.30225	49	0.000000
3	2.906527	1.107229	50	0.156586	0.00	18.56188	49	0.000000
2	3.205670	0.915331	50	0.129447	0.00	24.76428	49	0.000000
1	3.258651	1.008411	50	0.142611	0.00	22.84994	49	0.000000

Appendix Table 2: results of a one-sample T-test for the difference between position 585 and 587 at Solheim stocked with salmon.

Depth (m)	Mean	Std.Dv.	N	Std.Err.	Reference Constant	t-value	df	p
all	2.106649	0.905257	500	0.040484	0.00	52.03615	499	0.00
10	2.214757	0.878696	50	0.124266	0.00	17.82266	49	0.000000
9	2.242692	0.937028	50	0.132516	0.00	16.92396	49	0.000000
8	2.011890	1.137427	50	0.160856	0.00	12.50737	49	0.000000
7	2.005226	1.156727	50	0.163586	0.00	12.25794	49	0.000000
6	1.927146	0.954158	50	0.134938	0.00	14.28168	49	0.000000
5	2.178991	0.850717	50	0.120310	0.00	18.11154	49	0.000000
4	2.204494	0.894687	50	0.126528	0.00	17.42299	49	0.000000
3	2.183688	0.913758	50	0.129225	0.00	16.89836	49	0.000000
2	2.102592	0.604063	50	0.085427	0.00	24.61261	49	0.000000
1	1.995015	0.558431	50	0.078974	0.00	25.26163	49	0.000000

Appendix Table 3: results of a one-sample T-test for the difference between position 587 and 588 at Solheim stocked with salmon.

Depth (m)	Mean	Std.Dv.	N	Std.Err.	Reference Constant	t-value	df	p
all	-2.35074	0.964878	500	0.043151	0.00	-54.4775	499	0.00
10	-2.67616	0.894641	50	0.126521	0.00	-21.1518	49	0.000000
9	-2.49947	1.072714	50	0.151705	0.00	-16.4759	49	0.000000
8	-2.29204	1.087792	50	0.153837	0.00	-14.8991	49	0.000000
7	-2.27698	1.033740	50	0.146193	0.00	-15.5752	49	0.000000
6	-2.23433	1.134084	50	0.160384	0.00	-13.9311	49	0.000000
5	-2.17829	0.987730	50	0.139686	0.00	-15.5942	49	0.000000
4	-2.18972	0.987491	50	0.139652	0.00	-15.6798	49	0.000000
3	-2.22848	0.846265	50	0.119680	0.00	-18.6203	49	0.000000
2	-2.34301	0.675208	50	0.095489	0.00	-24.5370	49	0.000000
1	-2.58893	0.765107	50	0.108202	0.00	-23.9268	49	0.000000

Appendix Table 4: results of a one-sample T-test for the difference between position 535 and 566ref for the commercial farm.

Depth (m)	Mean	Std.Dv.	N	Std.Err.	Reference Constant	t-value	df	p
alle	11.82931	8.144803	150	0.665020	0.00	17.78789	149	0.00
10	9.219244	3.365201	15	0.868891	0.00	10.61035	14	0.000000
9	10.47786	3.850058	15	0.994081	0.00	10.54025	14	0.000000
8	11.53664	4.850868	15	1.252489	0.00	9.210975	14	0.000000
7	11.45823	5.396395	15	1.393343	0.00	8.223550	14	0.000001
6	11.39526	6.335022	15	1.635696	0.00	6.966616	14	0.000007
5	11.47811	6.040229	15	1.559580	0.00	7.359742	14	0.000004
4	11.35245	5.925071	15	1.529847	0.00	7.420643	14	0.000003
3	11.75979	5.962859	15	1.539604	0.00	7.638193	14	0.000002
2	11.89823	6.007313	15	1.551082	0.00	7.670922	14	0.000002
1	17.71730	19.91556	15	5.142177	0.00	3.445486	14	0.003940

Appendix Table 5: results of a Wilcoxon test for the difference between position 565 and 566ref for the commercial farm.

Depth (m)	Valid N	T	Z	p-level
10	15	0.00	3.407771	0.000655
9	15	0.00	3.407771	0.000655
8	15	0.00	3.407771	0.000655
7	15	1.000000	3.350975	0.000805
6	15	1.000000	3.350975	0.000805
5	15	0.00	3.407771	0.000655
4	15	0.00	3.407771	0.000655
3	15	0.00	3.407771	0.000655
2	15	0.00	3.407771	0.000655
1	14	0.00	3.295765	0.000982

Appendix Table 6: results of a Wilcoxon test for the difference between position 575 and 566ref for the commercial farm.

Depth (m)	Valid N	T	Z	p-level
10	15	0.00	3.407771	0.000655
9	15	0.00	3.407771	0.000655
8	15	0.00	3.407771	0.000655
7	15	0.00	3.407771	0.000655
6	15	0.00	3.407771	0.000655
5	15	0.00	3.407771	0.000655
4	15	0.00	3.407771	0.000655
3	15	0.00	3.407771	0.000655
2	15	0.00	3.407771	0.000655
1	15	0.00	3.407771	0.000655

Appendix Table 7: results of a one-sample T-test for the difference between position 588 and 566ref for the commercial farm.

Depth (m)	Mean	Std.Dv.	N	Std.Err.	Reference Constant	t-value	df	p
alle	13.85192	6.188032	150	0.505251	0.00	27.41594	149	0.00
10	11.97611	4.168406	15	1.076278	0.00	11.12734	14	0.000000
9	12.93479	4.912900	15	1.268505	0.00	10.19687	14	0.000000
8	13.45382	5.357459	15	1.383290	0.00	9.725961	14	0.000000
7	13.38071	5.632178	15	1.454222	0.00	9.201285	14	0.000000
6	13.51504	6.170511	15	1.593219	0.00	8.482854	14	0.000001
5	13.82114	7.013709	15	1.810932	0.00	7.632058	14	0.000002
4	14.42204	7.519420	15	1.941506	0.00	7.428276	14	0.000003
3	14.66931	7.369547	15	1.902809	0.00	7.709290	14	0.000002
2	15.01401	7.210407	15	1.861719	0.00	8.064593	14	0.000001
1	15.33227	6.740014	15	1.740264	0.00	8.810313	14	0.000000

Appendix Table 8: results of a one-sample T-test for the difference between position 535 and 587 for the commercial farm.

Depth (m)	Mean	Std.Dv.	N	Std.Err.	Reference Constant	t-value	df	p
1	-0.041819	22.28104	15	5.752940	0.00	-0.007269	14	0.994303
2	5.174281	2.768947	15	0.714939	0.00	7.237373	14	0.000004
3	4.544963	3.562640	15	0.919870	0.00	4.940877	14	0.000217
4	3.692248	2.990670	15	0.772188	0.00	4.781542	14	0.000293
5	2.440449	3.387877	15	0.874746	0.00	2.789893	14	0.014465
6	2.815394	3.196689	15	0.825381	0.00	3.411022	14	0.004219
7	2.852185	4.052924	15	1.046461	0.00	2.725554	14	0.016414
8	2.580577	4.941571	15	1.275908	0.00	2.022541	14	0.062655
9	2.958323	4.557982	15	1.176866	0.00	2.513730	14	0.024800
10	3.505834	3.857165	15	0.995916	0.00	3.520212	14	0.003396

Appendix Table 9: results of a one-sample T-test for the difference between position 535 and 588 for the commercial farm.

Depth (m)	Mean	Std.Dv.	N	Std.Err.	Reference Constant	t-value	df	p
1	-2.38503	22.70421	15	5.862201	0.00	-0.406848	14	0.690271
2	3.115780	4.859942	15	1.254832	0.00	2.483026	14	0.026315
3	2.909517	4.567411	15	1.179300	0.00	2.467155	14	0.027133
4	3.069596	4.451015	15	1.149247	0.00	2.670962	14	0.018266
5	2.343029	3.306068	15	0.853623	0.00	2.744805	14	0.015805
6	2.119780	2.884077	15	0.744665	0.00	2.846621	14	0.012936
7	1.922485	3.277899	15	0.846350	0.00	2.271502	14	0.039421
8	1.917182	3.703635	15	0.956275	0.00	2.004845	14	0.064714
9	2.456933	3.913167	15	1.010375	0.00	2.431703	14	0.029048
10	2.756866	3.135921	15	0.809691	0.00	3.404835	14	0.004272

Appendix Table 10: results of a one-sample T-test for the difference between position 565 and 587 for the commercial farm.

Depth (m)	Mean	Std.Dv.	N	Std.Err.	Reference Constant	t-value	df	p
1	4.772695	6.401531	15	1.652868	0.00	2.887523	14	0.011933
2	3.859258	4.906028	15	1.266731	0.00	3.046628	14	0.008708
3	3.763184	4.375090	15	1.129643	0.00	3.331303	14	0.004945
4	3.222964	4.126344	15	1.065418	0.00	3.025072	14	0.009088
5	2.869629	4.192511	15	1.082502	0.00	2.650923	14	0.018995
6	2.839761	4.067606	15	1.050251	0.00	2.703886	14	0.017126
7	3.872147	4.430978	15	1.144074	0.00	3.384526	14	0.004448
8	3.497416	4.725014	15	1.219993	0.00	2.866750	14	0.012432
9	2.986879	3.915272	15	1.010919	0.00	2.954618	14	0.010450
10	3.033214	4.270371	15	1.102605	0.00	2.750952	14	0.015616

Appendix Table 11: results of a one-sample T-test for the difference between position 565 and 588 for the commercial farm.

Depth (m)	Mean	Std.Dv.	N	Std.Err.	Reference Constant	t-value	df	p
1	2.429487	6.104090	15	1.576069	0.00	1.541485	14	0.145494
2	1.800757	4.186175	15	1.080866	0.00	1.666032	14	0.117915
3	2.127739	3.405975	15	0.879419	0.00	2.419483	14	0.029737
4	2.600312	3.562081	15	0.919725	0.00	2.827270	14	0.013439
5	2.772209	3.341423	15	0.862752	0.00	3.213217	14	0.006254
6	2.144147	3.093698	15	0.798789	0.00	2.684246	14	0.017797
7	2.942447	3.791073	15	0.978851	0.00	3.006022	14	0.009438
8	2.834022	4.534205	15	1.170727	0.00	2.420737	14	0.029666
9	2.485489	3.907591	15	1.008936	0.00	2.463476	14	0.027326
10	2.284246	3.728861	15	0.962788	0.00	2.372533	14	0.032534

Appendix Table 12: results of a one-sample T-test for the difference between position 587 and 588 for the commercial farm.

Depth (m)	Mean	Std.Dv.	N	Std.Err.	Reference Constant	t-value	df	p
1	-2.34321	3.721442	15	0.960872	0.00	-2.43863	14	0.028664
2	-2.05850	3.479941	15	0.898517	0.00	-2.29100	14	0.037993
3	-1.63545	3.660597	15	0.945162	0.00	-1.73033	14	0.105542
4	-0.622652	3.742173	15	0.966225	0.00	-0.644418	14	0.529722
5	-0.097420	3.745512	15	0.967087	0.00	-0.100735	14	0.921189
6	-0.695614	2.214761	15	0.571849	0.00	-1.21643	14	0.243933
7	-0.929700	2.494984	15	0.644202	0.00	-1.44318	14	0.170971
8	-0.663394	3.241303	15	0.836901	0.00	-0.792680	14	0.441191
9	-0.501390	3.103298	15	0.801268	0.00	-0.625746	14	0.541549
10	-0.748968	3.025824	15	0.781264	0.00	-0.958661	14	0.353994

Appendix Table 13: results of a linear regression between DO and current velocity for position 535, 565, 585 and 587 for the empty cage at Solheim.

	SS	Degr. of Freedom	MS	F	p
535					
	0.000295	1	0.000295	1.641396	0.207000
	0.000490	1	0.000490	2.730118	0.105757
	0.007722	43	0.000180		
565					
	0.000444	1	0.000444	2.545457	0.117936
	0.000719	1	0.000719	4.125421	0.048455
	0.007493	43	0.000174		
566					
	0.000635	1	0.000635	3.721142	0.060345
	0.000876	1	0.000876	5.135503	0.028531
	0.007336	43	0.000171		
585					
	0.000365	1	0.000365	2.069443	0.157516
	0.000628	1	0.000628	3.562989	0.065842
	0.007584	43	0.000176		
587					
	0.000549	1	0.000549	3.222422	0.079667
	0.000881	1	0.000881	5.168675	0.028050
	0.007331	43	0.000170		

Appendix Table 14: results of a linear regression between DO and current velocity for position 565, 566, 585, 587 and 588 for the stocked cage at Solheim.

	SS	Degr. of Freedom	MS	F	p
565					
	0.006303	1	0.006303	27.50152	0.000004
	0.008109	1	0.008109	35.38389	0.000000
	0.010313	45	0.000229		
566					
	0.006605	1	0.006605	29.45428	0.000002
	0.008480	1	0.008480	37.81219	0.000000
	0.010764	48	0.000224		
585					
	0.006887	1	0.006887	30.92899	0.000001
	0.008556	1	0.008556	38.42560	0.000000
	0.010688	48	0.000223		
587					
	0.006960	1	0.006960	32.25841	0.000001
	0.008887	1	0.008887	41.18937	0.000000
	0.010357	48	0.000216		
588					
	0.006240	1	0.006240	26.82140	0.000004

0.008077	1	0.008077	34.71552	0.000000
0.011167	48	0.000233		

Appendix Table 15: results of a linear regression between DO and current velocity for position 535, 565, 566, 587 and 588 for the stocked cage at Solheim.

	SS	Degr. of Freedom	MS	F	p
535					
	0.001223	1	0.001223	5.22779	0.034563
	0.003057	1	0.003057	13.06864	0.001980
	0.004211	18	0.000234		
565					
	0.000071	1	0.000071	0.279006	0.604603
	0.000913	1	0.000913	3.574829	0.076912
	0.004088	16	0.000256		
566					
	0.000044	1	0.000044	0.103294	0.751421
	0.000001	1	0.000001	0.001440	0.970127
	0.008068	19	0.000425		
587					
	0.001272	1	0.001272	5.43170	0.030945
	0.003619	1	0.003619	15.45406	0.000897
	0.004450	19	0.000234		
588					
	0.000550	1	0.000550	1.840739	0.190767
	0.002393	1	0.002393	8.011803	0.010688
	0.005675	19	0.000299		

Appendix Table 16: Pearson correlation test between OFD and DO at 2 m depth during day and low current velocity at Solheim.

	Means	Std.Dev.	ofd	565	585	587	588
ofd	3.43619	1.860187		1.000000	-0.609722	-0.618072	-0.681650
565	6.87238	3.720375	1.000000		-0.609722	-0.618072	-0.681650
585	92.19320	2.094846	-0.609722	-0.609722		0.964393	0.956323
587	91.67482	2.592223	-0.618072	-0.618072	0.964393		0.983332
588	89.41992	2.782369	-0.681650	-0.681650	0.956323	0.983332	

Appendix Table 17: Spearman correlation test between OFD and DO at 2 m depth during day and high current velocity at Solheim.

	ofd	565	585	587	588
ofd		1.000000	-0.428571	-0.714286	-0.761905
565	1.000000		-0.428571	-0.714286	-0.761905
585	-0.428571	-0.428571		0.832168	0.650350
587	-0.714286	-0.714286	0.832168		0.923077
588	-0.761905	-0.761905	0.650350	0.923077	

Appendix Table 18: Pearson correlation test between OFD and DO at 2 m depth during night and low current velocity at Solheim.

	Means	Std.Dev.	ofd	565	585	587	588
ofd	9.59499	1.143892		-0.341439	-0.120650	-0.497801	-0.455490
565	90.01999	2.088457	-0.341439		0.947716	0.971931	0.986650
585	89.61608	1.803807	-0.120650	0.947716		0.882133	0.898473
587	87.93314	1.974502	-0.497801	0.971931	0.882133		0.983939
588	90.09446	2.590466	-0.455490	0.986650	0.898473	0.983939	

Appendix Table 19: Pearson correlation test between OFD and DO at 2 m depth during night and high current velocity at Solheim.

	Means	Std.Dev.	ofd	565	585	587	588
ofd	9.77405	1.348358		-0.604234	-0.503337	-0.562028	-0.569930
565	92.56268	1.308441	-0.604234		0.862740	0.889888	0.988534
585	92.18930	1.575533	-0.503337	0.862740		0.969389	0.835860
587	90.34919	1.309881	-0.562028	0.889888	0.969389		0.867299
588	92.40997	1.474285	-0.569930	0.988534	0.835860	0.867299	

Appendix Table 20: Pearson correlation test between OFD and DO at 8 m depth during day and low current velocity at Solheim.

	Means	Std.Dev.	ofd	565	585	587	588
ofd	11.82004	2.174099	1.000000	-0.357237	-0.389204	-0.096880	-0.206743
565	79.02235	2.209759	-0.357237	1.000000	0.829323	0.857039	0.889814
585	79.84198	1.771757	-0.389204	0.829323	1.000000	0.901505	0.876950
587	77.87385	2.256333	-0.096880	0.857039	0.901505	1.000000	0.955807
588	80.02615	2.353025	-0.206743	0.889814	0.876950	0.955807	1.000000

Appendix Table 21: Pearson correlation test between OFD and DO at 8 m depth during day and high current velocity at Solheim.

	Means	Std.Dev.	ofd	565	585	587	588
ofd	12.74686	1.386821	1.000000	0.693302	0.656605	0.644414	0.659262
565	83.99794	4.232750	0.693302	1.000000	0.996107	0.975120	0.990606
585	82.95832	3.200660	0.656605	0.996107	1.000000	0.974719	0.989420
587	81.28230	3.928274	0.644414	0.975120	0.974719	1.000000	0.970685
588	84.17013	3.678973	0.659262	0.990606	0.989420	0.970685	1.000000

Appendix Table 22: Pearson correlation test between OFD and DO at 8 m depth during night and low current velocity at Solheim.

	Means	Std.Dev.	ofd	565	585	587	588
ofd	9.12097	0.676837	1.000000	0.409089	0.459405	-0.033604	0.311631
565	81.00835	1.189761	0.409089	1.000000	0.755364	-0.044237	0.710037
585	81.30976	1.430064	0.459405	0.755364	1.000000	0.397382	0.884544
587	78.34930	1.102151	-0.033604	-0.044237	0.397382	1.000000	0.665488
588	81.55739	1.058391	0.311631	0.710037	0.884544	0.665488	1.000000

Appendix Table 23: Pearson correlation test between OFD and DO at 8 m depth during night and high current velocity at Solheim.

	Means	Std.Dev.	ofd	565	585	587	588
ofd	9.04759	0.756492	1.000000	0.400118	0.379993	0.852417	0.263939
565	82.02352	1.627199	0.400118	1.000000	0.779988	0.561341	0.868443
585	82.38278	1.284014	0.379993	0.779988	1.000000	0.676940	0.929182
587	80.10142	0.932892	0.852417	0.561341	0.676940	1.000000	0.617387
588	81.82091	1.718071	0.263939	0.868443	0.929182	0.617387	1.000000

Appendix Table 24: Pearson correlation test between OFD and DO at 7 m depth during day and high current velocity at the commercial farm.

	Means	Std.Dev.	ofd	535	565	566	587	588
ofd	6.00805	1.284081	1.000000	-0.592210	-0.289585	0.691581	-0.544209	-0.494227
535	75.93681	4.929768	-0.592210	1.000000	0.901780	-0.956856	0.966729	0.970723
565	75.22353	4.446938	-0.289585	0.901780	1.000000	-0.891487	0.804435	0.972957
566	86.80855	2.011162	0.691581	-0.956856	-0.891487	1.000000	-0.857309	-0.966987
587	73.05759	4.674661	-0.544209	0.966729	0.804435	-0.857309	1.000000	0.886615
588	74.11321	4.754240	-0.494227	0.970723	0.972957	-0.966987	0.886615	1.000000

Appendix Table 25: Pearson correlation test between OFD and DO at 7 m depth during night and low current velocity at the commercial farm.

	Means	Std.Dev.	ofd	535	565	566	587	588
ofd	9.27772	0.249110	1.000000	-0.406226	-0.399939	0.361596	0.633790	0.155175
535	74.08956	3.839173	-0.406226	1.000000	0.811261	-0.938768	0.382306	0.765832
565	73.20778	3.511134	-0.399939	0.811261	1.000000	-0.684791	0.063651	0.764538
566	85.59162	3.970780	0.361596	-0.938768	-0.684791	1.000000	-0.452245	-0.763098
587	71.20421	2.972596	0.633790	0.382306	0.063651	-0.452245	1.000000	0.660720
588	72.24135	3.160425	0.155175	0.765832	0.764538	-0.763098	0.660720	1.000000

Appendix Table 26: Pearson correlation test between OFD and DO at 7 m depth during night and high current velocity at the commercial farm.

	Means	Std.Dev.	ofd	535	565	566	587	588
ofd	9.33317	1.930901	1.000000	0.759814	0.290517	0.773596	0.448307	0.512697
535	76.97978	2.340466	0.759814	1.000000	0.837992	0.986002	0.788610	0.751244
565	79.06514	6.910405	0.290517	0.837992	1.000000	0.825627	0.716559	0.599178
566	88.43372	5.147465	0.773596	0.986002	0.825627	1.000000	0.676352	0.631137

587	73.61153	8.582422	0.448307	0.788610	0.716559	0.676352	1.000000	0.985546
588	72.86149	5.425532	0.512697	0.751244	0.599178	0.631137	0.985546	1.000000

Appendix Table 27: 2-way ANOVA output of swimming speed as a factor of time and depth at Solheim.

	SS	Degr. of Freedom	MS	F	p
Intercept	8.394300	1	8.394300	348.5671	0.000000
Time	0.846047	1	0.846047	35.1315	0.000000
Depth	0.692304	2	0.346152	14.3737	0.000004

Appendix Table 28: Tukey HSD post hoc test for the difference in swimming depths at Solheim.

	Time	Depth	1	4	7	1	4	7
			,1,3237	,53508	,60552	,37994	,33961	,55710
1	0	1		0.000156	0.000352	0.000122	0.000122	0.001632
2	0	4	0.000156		0.556394	0.011150	0.000536	0.999965
3	0	7	0.000352	0.556394		0.000155	0.000122	0.998219
4	1	1	0.000122	0.011150			0.956758	
5	1	4	0.000122	0.000536		0.956758		
6	1	7	0.001632	0.999965		0.637890	0.410180	

Appendix Table 29: One-way ANOVA output of swimming speed as a factor of depth at the commercial farm

	SS	Degr. of Freedom	MS	F	p
Intercept	23.42289	1	23.42289	784.8467	0.000000
dyp	0.37306	2	0.18653	6.2501	0.010609
Error	0.44766	15	0.02984		

Appendix Table 30: Tukey HSD post hoc test for the difference in swimming depths at the commercial farm

	Depth	4	8	14
		,97820	1,2336	1,2949
1	4		0.050526	0.015125
2	8	0.050526		0.842551
3	14	0.015125	0.842551	

Appendix Table 31: Mann Whitney test for the difference in swimming speed between trials with skirt and skirt + delousing treatment.

Rank Sum Group 1	Rank Sum Group 2	U	Z	p-level	Z adjusted	p-level	Valid N Group 1	Valid N Group 2	2*1sided exact p
21745.50	1690.500	1414.500	2.841280	0.004494	2.841982	0.004484	193	23	0.004035

Appendix Table 32: Mann Whitney test for the difference in ventilation frequency between trials with skirt and skirt + delousing treatment.

Rank Sum Group 1	Rank Sum Group 2	U	Z	p-level	Z adjusted	p-level	Valid N Group 1	Valid N Group 2	2*1sided exact p

20535.50	2900.500	1425.500	-2.28573	0.022271	-2.28584	0.022264	195	21	0.021528