Refilling behaviour of Atlantic salmon (*Salmo salar*) with different air-dome heights

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1 Abstract

The increased salmon lice (*Lepeophtheirus salmonis)*, issue causes welfare concerns in salmon aquaculture industry. The resistance of lice to different medicinal treatments has led research to increasingly focus on preventive measures rather than lice removal techniques. One preventive measure is to submerge sea cages and force the salmon to stay deeper in the water column, with the goal of mismatching the distribution of farmed salmon from the surface-searching infective salmon lice copepodids. Submergence, however, faces some challenges for the salmon, who have a physostomous swim bladder that requires them to access the surface to take in air to refill their swim bladder. To compensate for this need, an underwater air-dome installed in the center of the cage can ensure air access for the salmon. Different sizes of the dome have been tested, and this study aim to find a preferred height of the dome where the salmon can refill swim bladder, execute normal behaviour and maintain good welfare.

In this study we tested three different heights of a surface based dome to test potential differences in surface behaviour and welfare indicators (using SWIM, Salmon Welfare Index Model) between the different heights. All domes were 1 m diameter and mounted in the center of a 3 m diameter cylindric indoor tank. The different experimental heights of the dome were 2 cm, 10 cm and 95 cm with three replicate tanks of each heights, totalling of nine tanks. 3 600 salmon were distributed between the nine tanks (400 in each tank). After an acclimation period with domes, salmon lice were introduced in all tanks as a stressor. Behavioural observations and SWIM assessments were conducted regularly during the whole experimental period. Results indicate that both welfare and behaviour were not negatively affected by dome height, suggesting that 2 cm dome height is sufficient for swim bladder refilling and conducting natural behaviour. Results, however, revealed increased snout damage in 66 % of tanks, a condition that has been observed in previous submergence trials.

2 Introduction

2.1 The blue plate

The ongoing population growth will lead to an increased demand for food (Lee 2011; Alexandratos and Bruinsma 2012; FAO 2017). Agriculture is an important contributor for edible meat worldwide. Expansion of this industry, however, faces challenges as it requires excessive land use which is a limited natural resource (Costello et al. 2020). A change in diet habits will be necessary to maintain realistic production volume. An alternative food source is meat from the sea, including fish, shellfish and other aquatic organisms from fisheries and aquaculture. This group represents 17 % of all edible meat today (Costello et al. 2020). Edible food harvested from the ocean has a physical potential for expansion as 70 % of the earth is covered by water and the major part of the ocean is yet to be mapped (Jahren and Sui 2016). An increase in fishing efforts aiming to cover the food demand in the future is, however, not possible without affecting the sustainability of the ecosystem; the abundances of wild fish are largely sensitive to overfishing, and with the current rate of fishing, a lack of intervention will reduce fish stocks (Lucas and Southgate 2012; Costello et al. 2020). Overfishing has been a research topic for decades and different definitions have been introduced, but results generally indicate that overfishing has a negative impact on ecosystem health (Beamish et al. 2006; Trippel et al. 2014). The scope of overfishing has increased as the fishery industry grew, but increased knowledge of consequences of fishing has led to fishery management that regulate the use of marine resources (Jackson et al. 2001; Bergh et al. 2002). To avoid further overfishing and exploitation of wild stocks, aquaculture has become an important and efficient way of using available resources in the sea that can provide nutrition to a growing human population (Costello et al. 2020).

2.2 Aquaculture

Aquaculture is farming of aquatic organisms that are held in enclosures or artificial infrastructures, analogous to terrestrial agriculture. It differs from fisheries as farmers have ownership of and responsibility for feeding and husbandry of these organisms, and will mostly maintain the organisms for the majority of its life cycle (Stickney 2001). Modern aquaculture increasingly utilizes selective breeding programs to ensure efficient production and maximal economical value for farmers, while also considering welfare of the farmed fish (Teletchea and Fontaine 2014). Production is usually area-efficient and ensures edible meat harvesting without affecting the number of wild fish, as there ideally is no interaction between wild and farmed stocks (Nash 2011). Finfish aquaculture is the most widespread worldwide, being carried out in great parts of the world.

2.2.1 Atlantic salmon (*Salmo salar*) aquaculture in Norway

In Norway, aquaculture of Atlantic salmon (*Salmo salar*, hereafter salmon) started in the 1960´s, and despite its short history, it is the most valuable farmed species worldwide today (F.A.O. 2018). Norwegian salmon aquaculture has experienced huge growth and rapid development since the 1980´s as a result of technological innovation and targeted research (Kumar and Engle 2016). Despite the success and profitability of salmon aquaculture, it represents less than 5 % of total finfish production worldwide (Costello et al. 2020). SSB states that production along the coast of Norway has more or less stagnated the last decade (Statistsik sentralbyrå, 2020) as a response to the increased prevalence of the parasitic salmon lice (*Lepeophtheirus salmonis*) that are a threat to the sustainability of the industry (Murray et al. 2016; Myksvoll et al. 2018).

2.3 Salmon lice (*Lepeophtheirus salmonis*) in salmon aquaculture

The value of aquaculture is a product of the number of organisms harvested and the quality of them. Farmers aim to maximize production without compromising the quality, which leads to the aquaculture sites having high densities of farmed organisms. The unnaturally high density of salmon in a limited area of an aquaculture site ensures high availability of hosts for the salmon lice and creates a high source of salmon lice infection pressure (Jansen et al. 2012). An open mesh netting is the only barrier separating the wild and farmed fish, and the lice larvae can easily spread from farmed to wild fish, and elevate infection on wild salmon as well as other farmed salmon in the area (Taranger et al. 2015). In Norway, the Ministry of Trade, Industry and Fisheries requires all farms to have less than an average of 0.5 adult female lice per fish (0.2 during migration periods for wild salmon, in spring) by law (Forskrift om lakselusbekjempelse, §8, 2013) to ensure good welfare and reduce environmental impact from the lice on both wild and farmed salmon (Heuch and Mo 2001).

The salmon louse is an ectoparasitic crustacean with high fecundity that feeds on blood, skin and mucus on wild and farmed salmonids (e.g. salmon, brown trout (*Salmo trutta*) and rainbow trout (*Onochoryncus mykiss*)) (Heuch et al. 1995; Bricknell et al. 2006; Woo and Buchmann 2012; Costello 2006). Infections can cause erosion injuries on skin of the salmon (Torrissen et al. 2013), reducing the host’s capability for osmoregulation (Grimnes and Jakobsen 1996; Wootten et al.1982) and can be fatal, although only for fish with heavy infections (Finstad et al. 2000; Torrissen et al. 2013). The salmon louse develops through eight stages, whereby the three initial larvae stages (nauplii 1 and 2 and copepodid) are free-swimming and drift with the water currents before the infective copepodid find a host to attach to and feed on, and develops into the sessile stage chalimus 1 (Johnson and Albright 1991; Hamre et al. 2013). Through the two chalimus stages, the lice are attached to its host by two frontal filaments and is immobile. Following this, the louse develops into pre-adult in where the louse can move unrestricted around on the skin of the host between moults. The louse is mobile also in the following pre-adult 2 and adult stages. The unrestricted mobility of lice at mobile stages cause the most severe physiological challenges connected to lice (Finstad et al. 2000). Adult female louse are fertilized by an adult male and produces a pair of egg strings containing from 150-450 eggs per sac (Heuch et al. 2000). The eggs are carried by the mother until they hatch as nauplii into the water and are distributed as they flow by currents, which results in spatially wide-ranging infection pressure. Lice reproduction occur throughout the year, but temperature regulates the speed of the process (Johnson and Albright 1991; Stien et al. 2005). In the free-swimming stages, salmon lice naturally live near the surface or by the halocline in fjord systems.

Measures to control salmon lice levels have been initiated (Overton et al. 2019), but the lice have shown great capacity for resistance to different treatments (e.g. chemical and thermal) (Ljungfeldt et al. 2017; Igboeli et al. 2012) as the short reproduction time allows resistant survivors to generate offspring. Problems connected to the lice have increased in line with the growth of the industry (Torrissen et al. 2013; Vollset et al. 2018).

Salmon have several strategies to avoid salmon lice infection. Migrating salmon smolts often enter the fjord in stay within the brackish part of the water (Thorstad et al. 2012) to avoid fresh water sensitive infective salmon lice copepodids (Wright et al. 2016). However, if salmon get infected with salmon lice, Furevik et. al (1993) states that rolling activity of salmon increase as a response, but whether this is a strategy aiming to remove attached copepodid or to prevent lice infestation by reducing encounter time is unknown. Increased jumping and rolling at the surface, as well as increased swimming speed, often initiated by bursting, are suggested to be conducted as a response to the discomfort and itching an infection cause for the salmon (Bui et al. 2018b.). By increasing swimming speed, salmon can experience the benefit of reducing encountering time with infective copepodids (Bui et al. 2018a; Genna et al. 2005). The moderate swimming speed of farmed salmon could result in greater susceptibility to infection (Samsing et al. 2015; Oppedal et al. 2010), while migrating smolt may be intermittently lowering potential encounter rates with burst swimming or higher speeds during migration (Thorstad et al. 2012).

When salmon lice successfully infect a host, the most critical phase for the salmon is when the lice develop to the pre-adult I stage (Grimnes and Jakobsen 1996). The lice change morphology and shift from being attached at one specific place of the salmon during both chalimus stages (Bron et al. 1991), to be able to move around on the surface of the host as pre-adult. Pre-adult lice cause increased of osmoregulatory problems for the salmon (Wootten et al. 1982), as does the mechanical damage since settlement is no longer local (Grimnes and Jakobsen 1996), and salmon tend to respond with increased behavioural activity (Furevik et al. 1993).

2.4 Submergence as a preventive measures against salmon lice

Salmon lice copepodids depend on finding a host before energy reserves formed during embryogenesis is depleted (Tucker et al. 2000). Copepodids migrate with ocean currents and vertical dispersal occurs close to the surface, with an aggregation at or just beneath the halocline as they avoid salinities of <20 ppt (Heuch 1995; Crosbie et al. 2019; Heuch et al. 1995; Oppedal et al. 2010). Both salmon and salmon lice use daylight to orientate in the water column, but their response differ (Flamarique et al. 2000). Copepodids are positively phototactic and swim towards the surface or just below the halocline after dawn, actively searching for a host, and sink at night (Heuch et al. 1995). Wild and farmed salmonids seek against the surface searching for food, but will to a certain extent avoid high light intensities and prefer feeding when light is dim (e.g. Fernö et al. 1995; Oppedal et al. 2001; Oppedal, Dempster, and Stien 2010; Westerberg 1982; Holm et al. 1982; Eldøy et al. 2017). The opposite migration pattern increases the possibility of copepodids encountering a host at dusk and dawn, when their paths cross (Fernö et al. 1995; Flamarique et al. 2000; Johannessen 1977). The developing resistance of lice to medicinal treatments have resulted in increased focus on preventive measures rather than lice removal treatment methods (Barrett et al. 2020), and one category of prevention focuses on this principal of vertical lice dispersion. The concept of submerging sea cages and hindering contact between salmon in sea cages and the surface-oriented infective copepodids, by creating a spatial barrier between them, is such a measure (Heuch et al. 1995). A submerged sea cage is a modified cage that has a net roof, which prevents the salmon from accessing the surface. The salmon therefore cannot swim in the shallow depths, and submergence has thus far been conducted e.g 1, 4 and 10 m depth in salmon (Oppedal et al. 2020).

Submergence of sea cages creates a barrier between the habitat of salmon and salmon lice, reducing infection success of lice by removing host availability. Research on using submerged sea cages have had variable success considering lice infection (Samsing et al. 2016; Sievers et al. 2018), with a potential of up to 70 % reduction compared to standard cages (Sievers et al. 2018). For the purpose of preventing salmon lice infection, submergence can thus be successful. Aside from reducing lice infections, submerged fish can experience benefits of more stable conditions throughout all seasons (e.g. Bricknell et al. 2006; Oppedal et al. 2001), reduced levels of algae blooming (Dempster et al. 2009) and storms that can lead to cage damage and escapes (Jensen et al. 2009). Submergence of sea cages can make it possible to introduce aquaculture industry into more exposed areas, e.g. offshore.

2.4.1 Welfare of salmon in submerged sea cages

The varied lice reduction success achieved by submerging sea cages can be one benefit, however lice are only one of many indicators affecting the welfare of salmon. Using external physical indicators for evaluating welfare of fish in submerged cages (SWIM (Stien et al. 2013)), studies on short-term submergence show better results (Oppedal et al. 2020; Glaropoulos et al. 2019) than long-term periods applying submergence (Korsøen et al. 2009; Sievers et al. 2018). Fish exposed to long-term submergence tend to have higher snout damage compared to surface cages (Sievers et al. 2018; Korsøen et al. 2009). A lack of surface access can result in more physical damage on snout, skin and fins caused by i.e. interactions with the roof net when swimming upwards searching for the surface, and high stocking densities (Korsøen et al. 2009; Turnbull et al. 2005). Growth is, however, observed to be maintained at normal levels in submerged sea cages (Oppedal et al. 2020; Sievers et al. 2018). Growth rate is considered a long-term indicator for welfare (Huntingford et al. 2006) and should be within optimal ranges during the production cycle.

2.4.2 Buoyancy of salmon in submerged cages

Buoyancy of the fish is an important welfare consideration, but is not taken into account with SWIM, which only captures visual welfare indicators. Most fish, including salmon, regulate buoyancy by regulating the volume of their swim bladder (Fänge 1953). Salmon have an primitive, open physostomous swim bladder that constantly leak air through the mouth (Fänge 1953). The swim bladder volume is also regulated by changes in pressure caused by vertical movement in the water column and behaviours that deviates from swimming in normal speeds (e.g. feeding events (Bui et al. 2013) and stress) can cause the salmon to release air. Due to the constant change in volume, salmon need to refill their swim bladder to be able to maintain neutral buoyancy (Korsøen et al. 2009). Research suggests that when surface access is absent, salmon will show behaviour that indicates negative buoyancy in less than a week (Glaropoulos et al. 2019), and even after 24 hours (Dempster et al. 2011). Swim bladder will be emptied in 22 days (Dempster et al. 2009; Korsøen et al. 2009), which is a limiting factor and a time cap of submergence. To compensate for negative buoyancy, salmon and herring increase swimming speed and/or begin tilted swimming to create hydrodynamic lift, a behaviour that is described in different studies on depth-based aquaculture (Ablett et al. 1989; Korsøen et al. 2009; Huse and Ona 1996).

2.5 Principles of depth-based prevention in sea cages

Salmon have developed through centuries and adapted to a life style where they wander vertically in the water column, at all times searching for food and avoiding predators (Westerberg 1982). Migration patterns are affected by external factors like salinity, temperature, light and food (Westerberg 1982; Javaid and Anderson 1967; Sutterlin and Stevens 1992), suggesting that salmon seek the best conditions. Natural behaviour of both wild and farmed salmon include jumping and rolling at the surface daily to gulp air and express stress or unfavorable conditions; for example, salmon lice infestation leads to increased surface activity (Furevik et al. 1993). The upper meters of the water column are frequently a habitat for salmon, hence submergence will impact their behaviour. This have led further research on different strategies of depth-based sea cages to ensure surface access for salmon.

2.5.1 Snorkel cages as a solution

Current commercially-tested solutions using the depth-based principle are the tarpaulin skirt (e.g. Grøntvedt et al. 2018; Stien et al. 2018) and snorkel cages (e.g. Geitung et al. 2019; Oppedal et al. 2017), where both solutions include a physical barrier that separates the inside of the cage from the surroundings. The snorkel is a hollow tube, impermeable to parasites, that extends from the surface to beneath the habitat of the lice and leads down to a connected net cage that is lowered in the water column. The construction aims for the salmon to stay in the lowered net cage and minimize time spent in the snorkel, which should be used only for feeding and refilling at the surface. Research shows 20-84 % reduced salmon lice levels on salmon in snorkel cages compared to commercial surface based cages (Oppedal et al. 2017; Geitung et al. 2019; Stien et al. 2016; Oppedal et al. 2019), Oppedal et al. (2017) suggesting that reduction success increases with increased depth. This solution aim to reduce the number of delousing treatments during full seawater phases (Oppedal et al. 2017). Oppedal et al. (2017) found that surface activity was adequate to maintain normal behaviour in snorkel cages at all depths, although activity declined with depth. This assumption is supported by salmon conducting normal swimming speeds in snorkel cages (Oppedal et al. 2017; Oppedal et al. 2019; Stien et al. 2016), resulting in no observed negative buoyancy (Oppedal et al. 2017; Stien et al. 2016). Normal growth rate was maintained in the snorkel cage studies (Oppedal et al. 2017; Oppedal et al. 2019; Stien et al. 2016) and welfare (SWIM) did not differ significantly from surface based sea cages (Oppedal et al. 2019; Oppedal et al. 2017), except worse snout score in fish held in the modified cage (Stien et al. 2016). However, Wright et al. (2017) reported more positive scores for mouth damage in fish in snorkel cages compared to normal cage, which can indicate that variation in welfare indicators is normal in aquaculture and snorkel cages don´t necessarily impact welfare of the fish negatively. One concern about the snorkel cage is the potential for low oxygen levels in the snorkel (Wright et al. 2017). Being impermeable to parasites, the snorkel can implicitly reduce water flow and decrease water replacement, which can lead to welfare concerns. One approach to this problem is installation of water pump to circulate flow inside the snorkel and ensure oxygen exchange, which has been successful (Oppedal et al. 2017, 2019).

2.5.2 Full submergence of sea cages with air available from an air-dome

Another preventative solution against salmon lice is the use of submerged cages supplemented with air-domes, yet only commercially full-scale tested by one company (Olafsen and Tjølsen 2020). Unlike snorkel cages, this is a complete submergence where surface access is denied, but air is available from an air-dome sewn into the net roof (e.g. Oppedal et al. 2020; Korsøen et al. 2012). The dome can be filled with air by an air hose from a compressor on land, as done by Korsøen et al. (2012). Other than the sea cage itself, there is no further physical barrier between the farmed fish and the surrounding environment, ensuring approximately normal water flow and replacement. Full submergence aims to reduce or eliminate encountering rate with salmon lice as a spatial mis-match between them occurs (F. Oppedal et al. 2020). Results from recent studies show elevated swimming speed in submerged sea cages with an air-dome compared to surface-based cages (Oppedal et al. 2020; Korsøen et al. 2012), although velocities from both studies are within the normal range for speed in farmed salmon (0.2-1.9 BL s^{-1} (e.g. Oppedal et al. 2010; Korsøen et al. 2009). Oppedal et al. (2020) observed normal swimming behaviour with no tilted swimming during submergence for 5-7 weeks with an air-dome.

2.6.3 Learning capacity in salmon

Normal swimming speed and behaviour in salmon farmed in a submerged sea cage is an indicator that salmon can manage to refill in air-dome. Efficient refilling under these conditions demonstrates that salmon have the capacity to adapt to new methods of accessing air for buoyancy maintenance. Living in a predictable environment causes farmed salmon to have lower behavioural learning capacity than wild (Salvanes et al. 2013), although it is present in both (e.g. Wechsler and Lea 2007; Bratland et al. 2010). Studies show normal surface behaviour in air-domes after being submerged 5-7 weeks (Oppedal et al. 2020; Korsøen et al. 2012), and Korsøen et al. (2012) found that salmon in small-scale farming (5m x 5m (7 m deep) cages) can adapt to refill through an air-dome in a submerged sea cage, and resulted in surface activity comparable to surface-based sea cages (Furevik et al. 1993). In the study by Korsøen et al. (2012), salmon were introduced to air-dome in two rounds, where both refill frequency and the amount of fish using the dome increased from round 1 to round 2 of air-dome access. When surface access was restored at trial end, no increased leaping or rolling activity was observed (Korsøen et al. 2012), in contrast to behaviour that is typically observed in submerged sea cages after surface access is restored, when jumps and rolls are conducted in high frequency (e.g. Korsøen et al. 2009; Dempster et al. 2009). Adaptation success to an air-dome for farmed salmon is also found by Macaulay et al. (2020), which introduced one fish group to domes (Ø = 0.6 m, H = 0.225 m) in fresh water tanks (Ø = 3 m), while another group were introduced to domes once transferred to sea. When adapting to refilling in a dome as juveniles, refill frequency was three times higher when experienced fish were transferred to sea cages with air-domes than for fish naïve to domes, which indicates that it is expedient to start adaptation early (i.e. acclimation is a positive learning experience; Macaulay et al. 2020). Both studies were, however, conducted in small- scale cages (volume 175 m^3) (Macaulay et al. 2020; Korsøen et al. 2012), and is not representative for industrial cage sizes. In comparison, Bakketeig et al. (2013) conducted a trial where fish in cages of ~2 000 m^3 were introduced to air-domes in sea, and results showed that domes (area: 1 x 1 m, H: 0.3 m, covering 0.7 % of cage area) were not frequently used for refilling. This was supported by observations of increased swimming speed already one day after submergence, and by increased surface activity for 6-8 hours when surface access was restored after 49 days (Bakketeig et al. 2013). Bakketeig et al. (2013) suggested that the area of the dome relative to the total surface area of the cage is relevant for refilling success in air-domes. Domes used by Macaulay et al. (2020) covered 3.96 % of cage area in indoor tanks, and 0.7 % in sea cage area which may have had a positive adaptation success as juveniles. Stocking density and cage size are other factors highlighted as relevant for refilling success in air-domes by

Bakketeig et al. (2013). Different strategies can, however, be used to manipulate fish into learning, for instance feeding (Nilsson et al. Unpubl.) or lights (Wright et al. 2015) could be used near the dome to attract fish to the dome area.

2.5.4 How is welfare affected by submergence with access to air through a dome?

Oppedal et al. (2020) found that welfare scores (SWIM) were better in submerged cages with access to an air-dome compared to submerged cages with no dome after a submergence period of 5-7 weeks. Results in submerged cages with air-dome, showed little difference in SWIM scores from trial start to end. One cage had a decrease in skin condition scores, although results from both before and after submergence were within the upper 25th quartile for skin condition, meaning that the damage was visible as a scar tissue or scale loss (Oppedal et al. 2020). The other air-dome cages, on the other hand, experienced an increase in fin scores from start to end, which indicate that there are natural variations between individuals that are not necessarily affected by the use of a dome (Oppedal et al. 2020). Growth rates indicated that welfare was positive, with a specific growth rate (SGR, % growth per day) at 0.69, 0.94 and 1.23 in that trial (Oppedal et al. 2020). The welfare of salmon is also affected by lice infection through reduced immune responses and osmoregularity (Grimnes and Jakobsen 1996; Wootten et al. 1982; Dawson et al. 1999; Wagner et al. 2008), and indirectly through delousing treatments. If submergence manages to reduce salmon lice infection intensities and lower treatment frequency, the overall welfare can be improved in relation to disease control.

The successful prevention of infection by salmon lice in submerged cages is theoretically independent of the presence of an air-dome. Using lice reduction success from earlier submerged sea cages or snorkel cages (e.g. Samsing et al. 2016; Sievers et al. 2018) as basis, one can assume that salmon farmed in submerged sea cages will experience lower salmon lice levels than in surface-based aquaculture. Results from commercial submerged domes have, however, experienced average score of adult female lice exceeding 0.5 lice fish^{-1} at two occasions during 15 weeks of submergence (Olafsen and Tjølsen 2020), resulting in one delousing treatment. It is relevant to point out that salmon in this commercial trial were introduced to submerged sea cage at size 3 kg, and were transferred from standard surface based sea cage via thermal delousing (Optilicer) before they were submerged to 10 meters depth. Thermal delousing treatments do not have 100 % lice reduction success (Ljungfeldt et al. 2017), and there is a chance that submerged salmon in this case introduced salmon lice to the depth of the cage. Further research on lice levels on fish in submerged sea cages is therefore needed.

2.6 Engineering and logistics of an air-dome

If surface activity and behaviour increasingly normalizes with bigger domes as suggested by Bakketeig et al. (2013), the dome should ideally be as big as possible to meet welfare demands for the farmed salmon. Constructing an air-dome that can be kept stable submerged in the water column, however, requires complex calculations and can be technically challenging. Based on Archimedes´ principle, buoyancy can be described as the weight of displaced volume. Considering an air-filled dome with volume 120 l submerged in sea water, buoyancy of the dome (B ~1200 N) is significantly higher than the weight of the dome (W ~1.4 N), and the dome will thus rise in the water.

Buoyancy: $V \times \rho_{sea\ water} \times\ G$

Weight: $V \times \rho_{air} \times\ G$

Buoyancy is calculated by multiplying dome volume (V), density of sea water ($\rho_{sea\ water}$) and acceleration of gravity (G). Dome weight is a counterweight to buoyancy and is relevant for calculating total buoyancy of dome. Weight is calculated by multiplying volume (V), density of air (ρ_{air}) and acceleration of gravity (G). To stabilize the air-dome at a certain depth, a counterweight equal to the dome´s force of buoyancy is required. Dome trials have been conducted with different dome diameters. Previous studies have tested various surface areas for the domes used (Appendix Table 7.1), and the buoyancy of these would change dramatically with varying heights of the dome; Fig. 2.1 demonstrates the weight generated by buoyance if these domes were the heights tested in this study (2 cm, 10 cm and 95 cm).

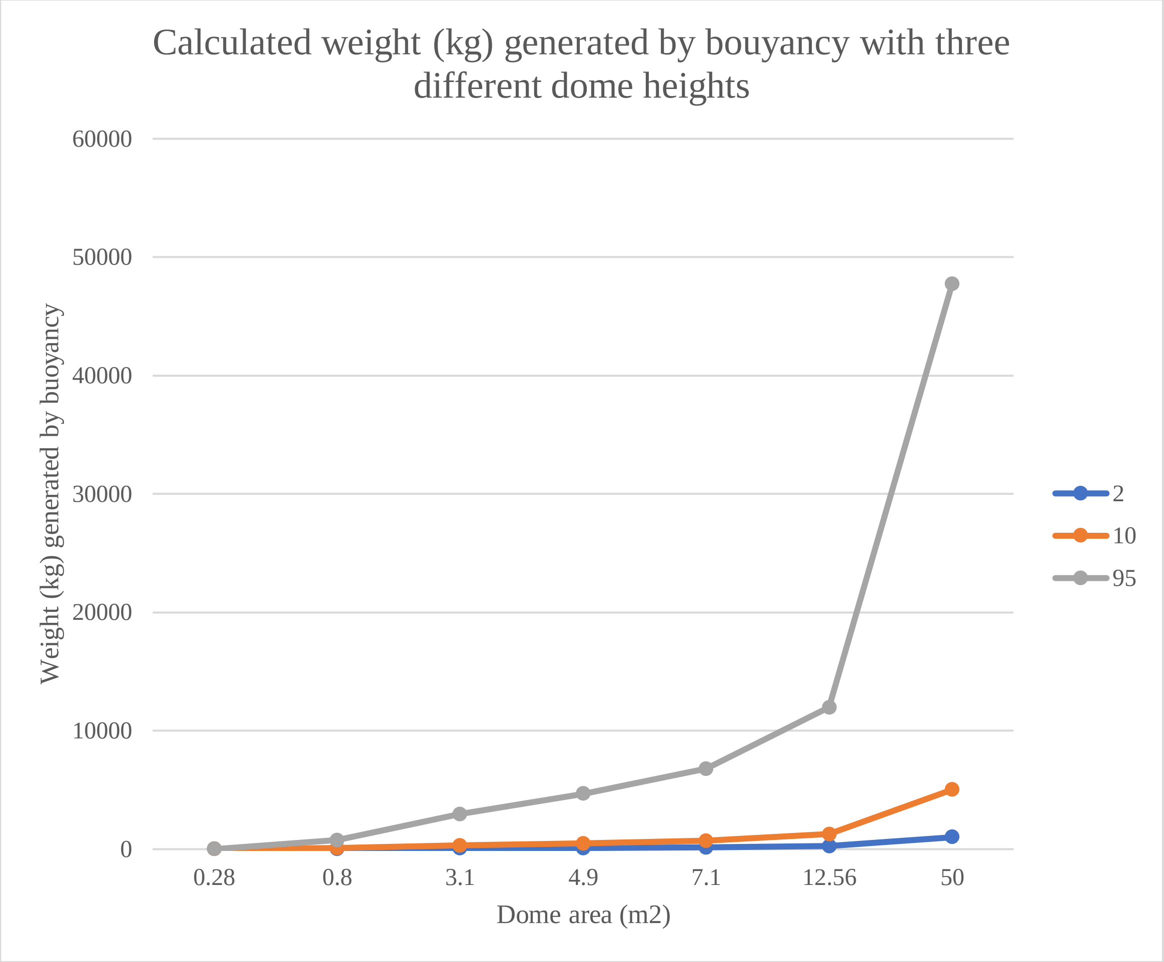


Fig. 2.1: Buoyancy generated by the three different dome heights used in this trial. Values on x-axis represent surface area from domes tested in other trials or commercially (Appendix Table 7.1). Difference in buoyancy between domes with different volume is prominent.

Technically, it is desirable to minimize dome weight to make it more practical, and furthermore, greater forces also generate greater risk. It is thus desirable to find the smallest possible dome size that still ensures adequate swim bladder refilling.

2.7 Aims and hypothesis

A variety of dome shapes (e.g. square (Korsøen et al. 2012; Bakketeig et al. 2013), cylindric (e.g. Macaulay et al. 2020), and octagonal (Oppedal et al. 2020)) and sizes (e.g. Ø = 0.6, 2, 4 m, H = 0.1, 0.3, 1 m) have been tested in submerged sea cages, and results suggest that with learning capacity or acclimation, the requirement for available dome size lowers (Nilsson et al. Unpubl). This study aimed to investigate submerged sea cages with air-domes aim to find the minimal dome height where salmon can execute normal behaviour. Salmon lice were introduced in tanks as an additional stressor to provoke natural behavioural responses in salmon.

By holding salmon submerged with three different dome heights, the aim was to determine whether dome height affected surface behaviour and welfare of the salmon. Observations during infection would reveal potential behavioural changes deviating from normal behaviour, and suggest whether the different dome heights are sufficient for salmon to express natural behaviour.

Secondarily, observations will reveal the capacity for salmon to adapt to the different dome heights and control surface behaviour accordingly.

The hypothesis was that reduced dome height would reduce a salmon´s capacity for refilling in the air-dome, and therefore welfare would be lower in tanks with lower dome height as fish either cannot refill air adequately, or they would acquire injuries from colliding into dome walls, lid or the net roof.

3 Materials and methods

Surface-based air-domes with three different heights (2, 10 and 95 cm) were installed in indoor tanks (Ø = 3 m), with three replicates per treatment. Focus during the experimental period was how the difference of dome height affected behaviour and welfare. In a subsequent period, salmon lice were introduced in tanks for observation on how these factors were affected by an additional stressor.

3.1 Location and experimental set- up

The experiment was conducted at the indoor facilities at Institute of Marine Research's station at Matre in Western Norway, from June to October 2020. The experiment was conducted according to the Norwegian legislation for animal use in experimentation, and approved by the Norwegian Food Safety Authority (application ID 22575).

The fish were held in cylindric tanks of 8.8 m^3 (Ø = 3 m, H = 1.25 m) with water level of 1.10 m (volume = 7.8 m^3). Mesh netting (5 x 5 m, mesh size = 15 mm) was placed over tank edge. Four lists of 3 mm PE- plates (solid plastic) with height 25 cm were fastened with vices vertically to the tank wall over the net, to pin the net roof against tank wall beneath the water line. Along the tank wall, the lowest point of the roof netting was 100 cm above tank bottom (10 cm beneath water level) (Fig. 3.1). At the surface, in the centre of the tank, the netting led up to the attachment point at the inside of a hollow, cylindric surface- based dome (Ø = 1 m, A = 0.8 m^2, 5.7 % of surface area in tank), with the bottom 105 cm above tank bottom (5 cm beneath water level) to ensure limited surface access. The dome was made out of two black PE- plates connected together into a cylindric construction by pop-nails. Depending on the treatment group, the height of the domes were either 2, 10, or 95 cm. Inside the domes with height 95 cm, soft pads were fastened from 10- 95 cm height to hinder the fish from getting damaged from the pop-nails. With this setup where the dome sat above the water surface, air was provided through surface access within the dome.

3.1.1 Construction

The dome was connected to a fixed structure installed across the tops of the tanks: two planks of timber were mounted to the tank above the water (L = 110 cm, W = 2.5 cm, H = 10 cm), and intersected two parallel traverses that ran perpendicular on the tank (L = 330 cm, W = 4.8 cm, H = 19.8 cm), creating a frame atop the tank that encased the dome in the centre (Fig. 3.1). The dome was attached to the traverse to guarantee its height (respective to water level) was stable throughout the experimental period. The walkway also provided physical access to the dome, to ensure husbandry and observation through the dome. To avoid stressing the fish when walking the bridge, one 2’’2’’ plank (height 150 cm) was nailed to the traverse at the end of the bridge and one close to the dome, and a garden cloth (150 x 130 cm) was nailed to both planks and the traverse. A parapet like this was mounted on each side of the bridge.

After fish were transferred to experimental tanks, net roof was placed onto tanks. Net roof was, however, secured above water level so fish could access the surface across the whole tank. Dome installation at the start of the experimental period therefore occurred by lowering and fastening the net roof to restrict surface access to only within the dome.

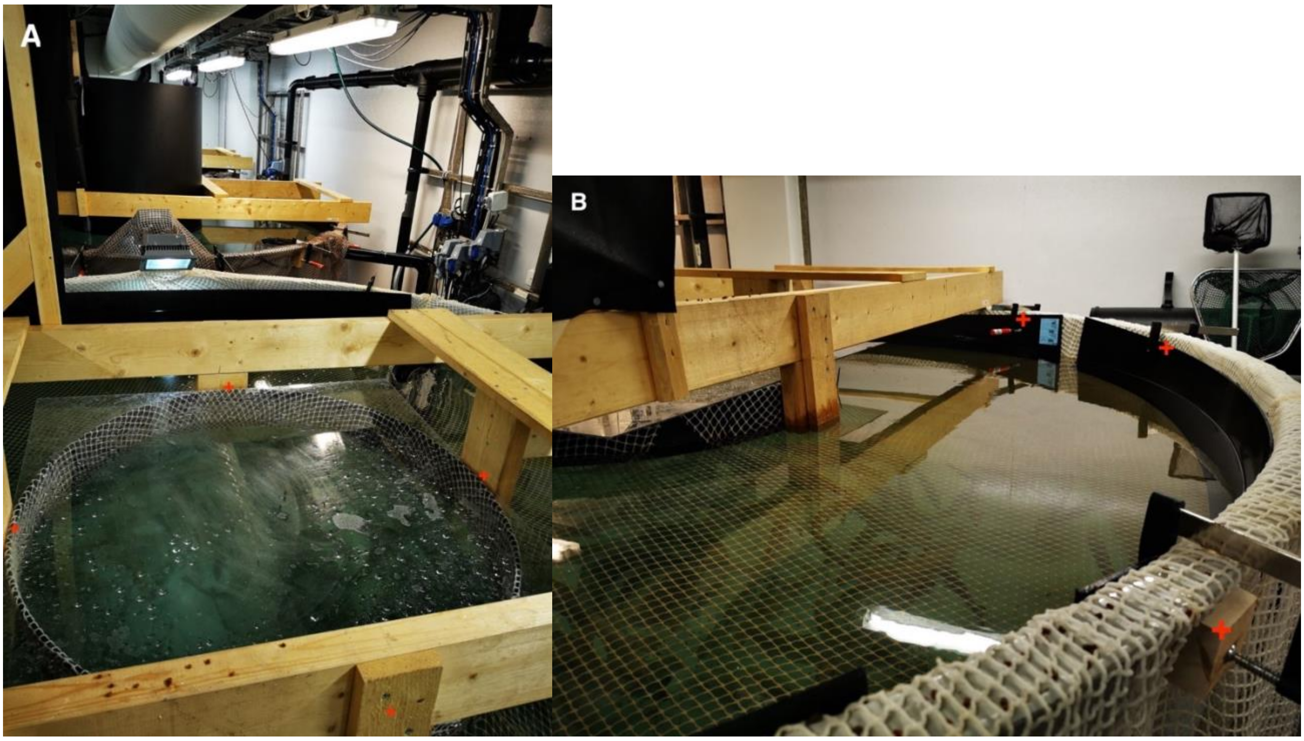


Fig. 3.1: *Photo of a 10 cm dome installed in tank with a transparent lid on top. A) Four attachment points (marked by “+”) connected the dome to the bridge. B) PE- list were fastened by vices to tighten the roof net (marked with “+”).*

Nine tanks were used for the experiment; three tanks were equipped with a dome of 2 cm height above water surface, three tanks of 10 cm and three tanks 95 cm. The 2 cm and 10 cm domes had a fitted lid made of transparent 5 mm plexiglass fixed to the top. Lid was installed to prevent fish from escaping through the top of the dome. The 95 cm groups were considered as control groups, since a dome of height 95 cm has practically no vertical limitation.

As a blocking factor to keep a robust experimental design, the tanks were divided into three groups: group 1 (G1), group 2 (G2) and group 3 (G3), where all three dome heights were represented in each group, and the three tanks experienced same treatment and timeline during trial period. Group 1 included tank 1 (height 2 cm), 2 (height 95 cm), 3 (height 10 cm); group 2 included tank 7 (height 2 cm), 8 (height 95 cm), 9 (height 10 cm); group 3 included tank 10 (height 2 cm), 11 (height 95 cm), 12 (height 10 cm).

3.2 Experimental Atlantic salmon

A total of 3 600 Atlantic salmon (*Salmo salar*) (weight at start: mean ± SE, 279.34 ± 8.28 g, fork length: 28.69 ± 0.22 cm) were evenly distributed and randomly netted into the nine tanks, 400 fish in each tank.

Fish in all nine tanks were raised at the same research facilities according to standard production procedures. In experimental tanks, fish were provided 15°C seawater that was pumped in from the adjacent fjord, filtered, and heated before entering the tank. The temperature and oxygen remained stable throughout the trial through control and monitoring by automated systems. Fish were also kept in a natural lightning regime with 24 hours light since trial was conducted during summer.

Fish were fed pellets (Spirit Supreme 3 mm and Nutra supreme 4 mm, Skretting®). Following a feeding regime standard to husbandry requirements at the facility, the quantity resulted in over-feeding and buildup of waste and biofouling on the roof net. Thus, feed provision was switched to hand-feeding from day 6 to the end of the trial. From day 61, all tanks were hand-fed medicinal feed (Floraqpharma vet 2g/ kg, 3 mm, Skretting®) to treat for bacterial infection, for 14 days (until day 75).

3.3 Experimental salmon lice

Adult female salmon lice (*Lepeophtheirus salmonis*) were collected from IMR sea cage research stations at Matre and Austevoll. The lice were reattached to salmon in 0.41 m^3 tanks (H = 0.5 m, W = 0.9 m, B = 0.9 m) at the facilities in Matre, to allow the lice to mature and reproduce, providing the larvae for this experiment.

To produce the copepodids used in this study, egg strings were harvested from the adult female lice and incubated in a 0.0023 m^3 (L = 17.5 cm, W = 15.5 cm, H = 8.5 cm) flow-through incubator until the larvae had moulted through the nauplii stages into the infective copepodid stage. At 15 °C, this took approximately 4 days since hatching (Hamre et al. 2019). The incubators were provided seawater from the same header tank that supplied the experimental tanks. The flow-through system ensured constant water exchange for the larvae, with seawater filtered through a fine-mesh sieve before entering the incubators through a 5 mm hose, illustrated in Fig. 3.2. The incubators were made of two boxes of same size, stacked into each other. The inner box had a fine-mesh bottom to ensure flow, and the water left the outer box from an outlet at height 8.5 cm.

Fig. 3.2: *Photo of flow-through incubator system. A 20 mm hose from the water in the level- tank was put into a sieve placed on top of the yellow bucket to filter the water. 5 mm hoses from the bucket supply filtered sea water into incubators. The inner box consisted of a bottom of mesh netting ensuring water replacement. Outlet on each incubator (black pipe on the outer box) ensure constant water replacement and determined water level in incubator.*

3.4 Salmon lice infestation

Salmon lice copepodids were collected from incubators at research station in Matre (see Section 3.3). Approximately 8 000 copepodids were introduced in all tanks. Infestation pressure was calculated by estimating an infection success of 50 %, and an infection level of 10 lice per fish. The number of lice was estimated by pouring the copepodids into a measuring jug, adding enough sea water for the total volume to be 2 000 ml. The mixture was mixed well before 20 ml of the mixture were pipetted into a counting tray. The number of lice in the tray was counted through a stereo microscope (counting only live copepodids and excluded dead larvae or nauplii) and the counted number was then multiplied by 100 to get an estimate of the number of lice in the jug. Estimation was achieved through six aliquots, and the average of these was the calculated total number of lice. How much of the mixture necessary to pour into the tank was calculated based on the total estimated number of lice in the incubator.

Infection challenges occurred a period of time after the domes had been installed (Table 3.1). For infestation in the experimental tanks, water level remained the same to maintain surface access only in the dome, while water flow was reduced to 10 liters min^{-1}. The lice were poured from a bottle into the water outlet in the tank for best possible distribution. Water flow remained reduced for 30 minutes after infestation. During these 30 minutes, both physical observations and camera observations was conducted. The three tanks in each group was infected on the same day, although infection day varied between groups.

3.5 Sampling procedure

Fish were transferred to the experimental tanks 11 days prior to domes being installed. During this trial, two different kinds of samplings were conducted. Physical observation of surface behaviour was conducted most frequently, and welfare evaluation using SWIM was conducted a total of four times per group (three times for G1). The three tank groups (G1, G2, G3) had different trial lengths as there was a shortage on salmon lice, and all groups could not be infected at the same time. Trial lasted 56, 78 and 92 days for G1, G2 and G3, respectively. Timeline for each group is illustrated in Table 3.1.

Table 3.1: Timeline showing all activities of the three treatment groups (G1,G2,G3). F: fish into tank, D: dome installed, green color: surface observation; grey color: SWIM (= including lice counting); orange color: lice infestation.*

Week	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**
G1	🟩 F	🟩	▨ D 🟩	🟩	🟩	▨ 🟩	🟩	🟧 🟩	🟩	🟩	▨ *						
G2	🟩 F	🟩	▨ D 🟩	🟩	🟩	▨ 🟩			🟩	🟩	🟧 ▨ 🟩	🟩	🟩	▨ *			
G3	🟩 F	🟩	▨ D 🟩	🟩	🟩	▨ 🟩							🟩	🟧 ▨ 🟩	🟩	🟩	▨ *

3.5.1 Behavioural sampling

Surface behaviour was recorded a minimum 49 separate occasions for each tank. All observations were conducted by the same person to standardize assessments, and were exclusively collected through visual observations. During acclimatization period in tanks immediately after transfer, behavioural observations were conducted for 10 minutes twice a day (before and after feeding) for two days, and were considered as control-behaviour. Observations separated between jumping and rolling at the surface, also referred to as surface searching and refilling, respectively. 11 days after being transferred, domes were installed, and the trial period started (Day 0). Acclimation period with domes lasted 25 days, and during this period, observations were conducted relative to feeding (15 minutes before and after feeding). There was, however, no clear pattern in activity before and after feeding (e.g. Fig. 4.5), and was therefore not taken into account in analyses. Duration of acclimation period was determined on basis of research suggesting that swim bladder should be emptied within 22 days if access to air is absent (Korsøen et al. 2009; Dempster et al. 2009). All observations were conducted through the dome in the middle of the tank a few minutes after the observer stepped on the walkaway, as a small acclimation period.

After the dome-only period, salmon lice were introduced in tanks in G1, and 31 observations per tank were conducted with same and increased frequency as in the dome-acclimation period. Four observations were conducted before salmon lice were introduced in tanks, one observation during the infection challenge, and 26 in the following period. For G2 and G3, observations were conducted twice a week until one week before tanks were infected with lice. Observations conducted between acclimation period with domes and lice infection (week 32, 33 and week 32- 37 for G2 and G3, respectively), are not included in results because observations were conducted to ensure normal behaviour and that fish were healthy, and were not relevant for the aims of this trial.

When being infected with salmon lice, behaviour was recorded ten minutes prior to and 30 minutes during lice infection, with a camera (GoPro™, San Mateo, CA, USA). In addition, physical observation was conducted for the 30 minutes after lice were introduced. The first two days after infestation, behavioural observations were frequently conducted (15 minutes four times a day). Frequent observations were also conducted when > 90 % of the lice had developed to pre-adult 1 stage (10 and 11 days post-infestation). Salmon lice infection is suggested to cause immediate increased frequencies of twitching and bursting (Bui et al. 2018a), while when moulting to pre-adult, lice are suggested to cause increased activity of infected salmon (Furevik et al. 1993).

In the period related to lice infections, frequency of bursting, twitching and side swimming deeper were also recorded in addition to jumping and rolling, because these behaviours were observed to appear at high frequency and are known to be correlated to infection (Bui et al. 2018). Jumping and rolling behaviour occasionally resulted in fish coming into contact with the lid, and therefore were qualitatively distinguished between ‘into lid’ and no lid, for domes that had lids present or absent. However, analyses did not distinguish differences with lid presence or absence. Standardised descriptions of specific behaviours are clarified in Table 3.2.

Table 3.2: *Description of behavioural parameters recorded during behavioural observations during salmon lice infestation period.*

Behaviour	**Description**	**Measure**
Jumping	Upwards acceleration under water before breaking the surface in high speed, head first. In the top position, the whole body is above surface (Furevik et al. 1993; Bui et al. 2018a).	Frequency per minute
Rolling	Upwards acceleration with slower and more controlled movement towards the surface than when jumping. Breaking the surface in a smooth movement/ like whale surfs and only dorsal part of the fish is above surface (Furevik et al. 1993; Bui et al. 2018a).	Frequency per minute
Burst	A sudden increased swimming speed, at or close to maximum capacity. The movement is set in motion by caudal fin. Most bursts start with a twitch (Bui et al. 2018a).	Frequency per minute
Twitching	A twitching of the body in an “S”- form from side to side while swimming, like shaking off an irritation. Powerful movement, not to be confused with a normal change of direction. Ending and starting in the same position (Bui et al. 2018a).	Frequency per minute
Side- swimming	A mild twitching when the fish is swimming either horizontally on the side or turning upside down. The twitching that occurs while side- swimming is not as powerful as the twitching when it occurs alone.	Frequency per minute

3.5.2 Welfare evaluation (SWIM)

Welfare evaluation, using the salmon welfare index model (SWIM; (Stien et al. 2013)), was conducted prior to installation of domes (pre-installation sampling), 25 days after installation (post-installation sampling), prior to salmon lice infestation (pre-infection sampling), and after salmon lice had reached adult stage 21 days after infestation (end sampling). For G1, only three samplings were conducted as sampling post-installation and pre-infection were combined because lice infestation occurred done only 10 days after sampling post-installation. Results from sampling post-installation (G1) are presented as pre-infection. Basis for SWIM score and growth calculations are the individual score of each welfare indicator, separated between tanks. SWIM was assessed in 5 %, 5.2 %, 5.6 % and 11.7 % of the total amount of fish for sampling pre- and post- installation, pre- infection and end, respectively.

For the SWIM samples, fish were collected from the tanks for physical assessment. Water level in tanks was lowered to a volume of 1000 liters, water flow was regulated to 10 liters min^{-1}, and 30 g Finquel (tricaine methanesulfonate) were added to lightly sedate the fish and ensure randomised netting. The roof net was loosened from one side of the bridge to be able to net the fish. When the salmon were calm in the tank, 20 fish were netted into a holding tank with 100 liters of seawater with same water quality as in the tanks, and 20 g Finquel for euthanizing was added. For all fish, weight (g) and length (cm) were measured. Specific growth rate (SGR) was calculated by the formula $((e^{G})-1)100$, where $G = (\ln(X_2)-\ln(X_1))/(t_2-t_1)$. X_2 and X_1 represents body weights at times t_2 and t_1.

Welfare indicators and score range in the SWIM model were adjusted after sample pre-installation because the scale was not specific enough. At sample pre-installation, indicators scored were vertebral deformity, fin status, scale loss, eye bleeding, cataract status, gill status, skin bleeding, snout wound, and emaciation. At subsequent sample points, the indicator “fin status” was divided into fin split, fin bleeding and fin erosion, and an indicator for presence of wounds was added to the skin status category (Table 3.3). Also, in subsequent samplings, scaling for all indicators were also changed to have the same range within the same category (Table 3.3). Scoring scales increase with severity, with the highest score indicating a condition so severe that the fish would be ethically considered at a humane endpoint for euthanasia (Stien et al. 2013; Folkedal et al. 2016; Noble et al. 2018).

Table 3.3: Welfare indicators with scoring range on sampling pre-installation (prior to dome installation) and samplings post-installation, pre-infection and end (after dome installation). Scoring scale was changed after sampling pre-installation after determining that changes would give a more detailed result. Scoring scales increase with severity.

Welfare indicator	**Score scaling (prior to dome installation)**	**Score scaling (after dome installation)**
Vertebral deformity	1-6	1-6
Cataract status	1-6	1-4
Gill status	1-4	1-6
Snout wound	1-4	1-6
Emaciation	1-4	Not assessed
Eye bleeding	1-6	1-4
Skin bleeding		1-6
Scale loss	1-8	1-6
Wounds		1-6
Fin status	1-5	
Fin bleeding		1-4
Fin split		1-4
Fin erosion		1-4
Skull damage		1-6

The same sample procedure was followed for end sampling, but 40 salmon were assessed instead of 20, and lice abundance recorded. During the trial period, an increased prevalence of skull wound was observed, which resulted in skull wound being included in SWIM for end sampling for G1 and pre-infection and end sampling for G2 and G3.

3.6 Data analysis and statistics

Analyses were conducted in R (R Core Team, 2020) using the packages '*glmmTMB*', '*MASS*', and '*lsmeans*'. Models were run in R by S. Bui, and results interpreted by Henrikke Brekken Oppedal.

3.6.1 Behaviour

Each behaviour was converted to behaviour min^{-1} to standardise the different observation durations. Observations were pooled between before or after feeding within a day. The behaviours were separated into the Periods before dome installation, after dome installation, immediately prior to infection, during infection, and the days after infection occurred. For the period after infection, days post-infection (DPI) was used as the time factor due to the slight difference in sample day between Groups.

Three models were tested using the ‘glmmTMB’ function (‘glmmTMB’ package in R): for behaviours pre- vs post-dome installation (before infection; jumping and rolling behaviour only), behaviours the days prior to infection vs during infection, and behaviours prior to infection vs days after infection. Each behaviour was individually tested using generalised linear mixed effect models which included Dome Height, Period or DPI, and Group as fixed factors, and Tank as a random effect. The full model was compared to the null model using a Chi-Squared test, and if significant, the full model run. Post hoc was not conducted for sample time as factor, as there was only two sample times in the Sample factor.

3.6.2 Welfare scores

As the scoring system was different between the pre-dome installation and the subsequent samplings, pre-dome welfare was analysed alone among Dome Heights and Groups. Post-dome installation, welfare scores were compared between the sample point prior to infection and the sample at the conclusion of the trial. Differences in scores due to treatment factors or sampling time were evaluated using a proportional odds logistic regression with a two-sided hypothesis test, using the ‘polr’ function (‘MASS’ package in R). The models with cumulative factor inclusion were compared with the null model based on AICc values, and the most suitable model selected. For models that had a significant Dome Height or Group factor, post-hoc pairwise comparisons were conducted to determine differences among the levels in the factor, using the ‘lsmeans’ function. Welfare indicators that had a high prevalence of single scores (e.g. almost all scores = 1) could not be analysed because of the limitations of the regression with this dataset, and therefore are only qualitatively presented.

3.6.3 Growth

Because of the different timelines between Groups and varying durations of dome acclimation (i.e. number of days before infection), and the single tank replicates for Dome Height within each Group, body size and growth parameters (length, weight, SGR) were not analysed.

4 Results

4.1 Growth

Average weight of experimental salmon increased from 279.34 ± 8.28 g (mean ± SE) to 321.51 ± 2.66 g, 366.85 ± 11.21 g, and 408.93 ± 11.28 g for G1, G2 and G3 respectively (Fig. 4.1) by trial end. Length increased from 28.69 ± 0.23 cm to 31.03 ± 0.08 cm, 32.94 ± 0.35 cm and 33.55 ± 0.18 cm in G1, G2 and G3 respectively (Fig. 4.2). G1 was in the experimental period for 56 days, G2 78 days, and G3 92 days. SGR, which accounts for study duration, varied between 0.19 in tank 7 to 0.65 in tank 1 (Table 4.1). Because of different study duration and bacterial infection leading to high mortality occurrence, SGR was not focused on.

Fig. 4.1: Average weight at all samples of each tank. All tanks were measured Day 0, the other samples occurred at different times. Graph shows a slight decreased weight from pre- to post-installation, but overall, weight increased from pre-installation to end sampling. Weight was not measured for G3 day 56. Weight for G1 was no measured after end sampling day 56, the same counts for G2 (end sampling day 78). Error bars represent standard deviation for the replicate tanks in each group. NB: y-axis starts at 150 g.

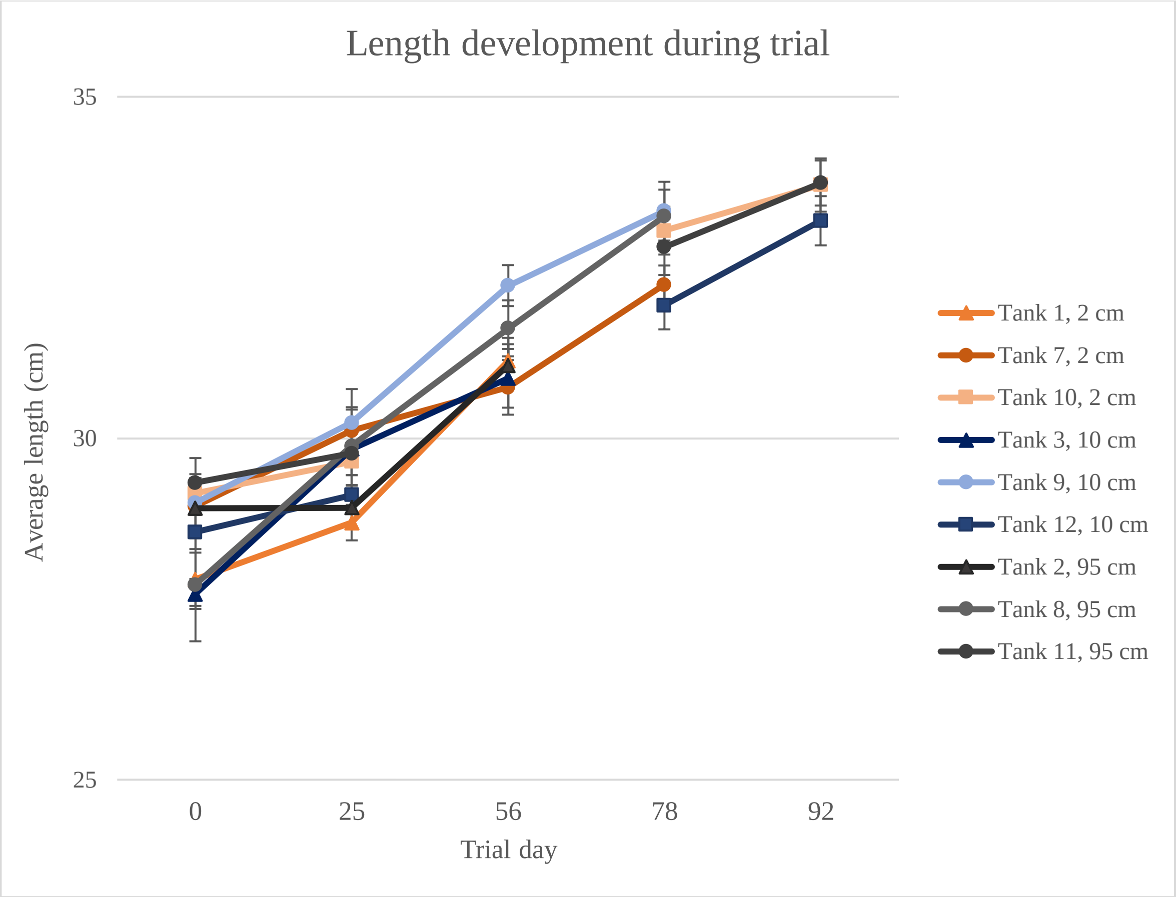


Fig. 4.2: Average length at all samples of each tank. All tanks were measured Day 0, the other samples occurred at different times. Length increased during the whole trial. Weight was not measured for G3 day 56. Weight for G1 was no measured after end sampling day 56, the same counts for G2 (end sampling day 78). Error bars represent standard deviation for the replicate tanks in each group. group. NB: y- axis starts at 25 cm. Dome height groups are represented by shades of orange (2cm), blue (10cm), or grey (95cm).

Table 4.1: SGR of fish in each tank, calculated from prior to dome installation until end sampling.

Treatment	**Tank**	**Experimental period**	**SGR**
2 cm	1	56	0.65
95 cm	2	56	0.21
10 cm	3	56	0.39
2 cm	7	78	0.19
95 cm	8	78	0.29
10 cm	9	78	0.35
2 cm	10	92	0.39
95 cm	11	92	0.38
10 cm	12	92	0.36

4.2 Mortality

A total of 388 fish died across tanks during trial, which is 24 % of the total number of experimental fish; mortality in each tank is listed in Table 7.2 (Appendix). Mortality rates were elevated in the period July 26th (day 20)-August 12th 2020 (day 37) (Fig. 4.3), which constituted 83 ± 2.8 % (average % ± SE) of total mortality. In tank 8, 93 % of total mortality occurred in this period. Most mortalities that occurred outside of this peak window appeared to have wounds that likely contributed to their mortality. Aside from the mortality in tanks, 80 fish in each tank in G1 were sacrificed for samples, and 100 fish in each tank in G2 and G3.

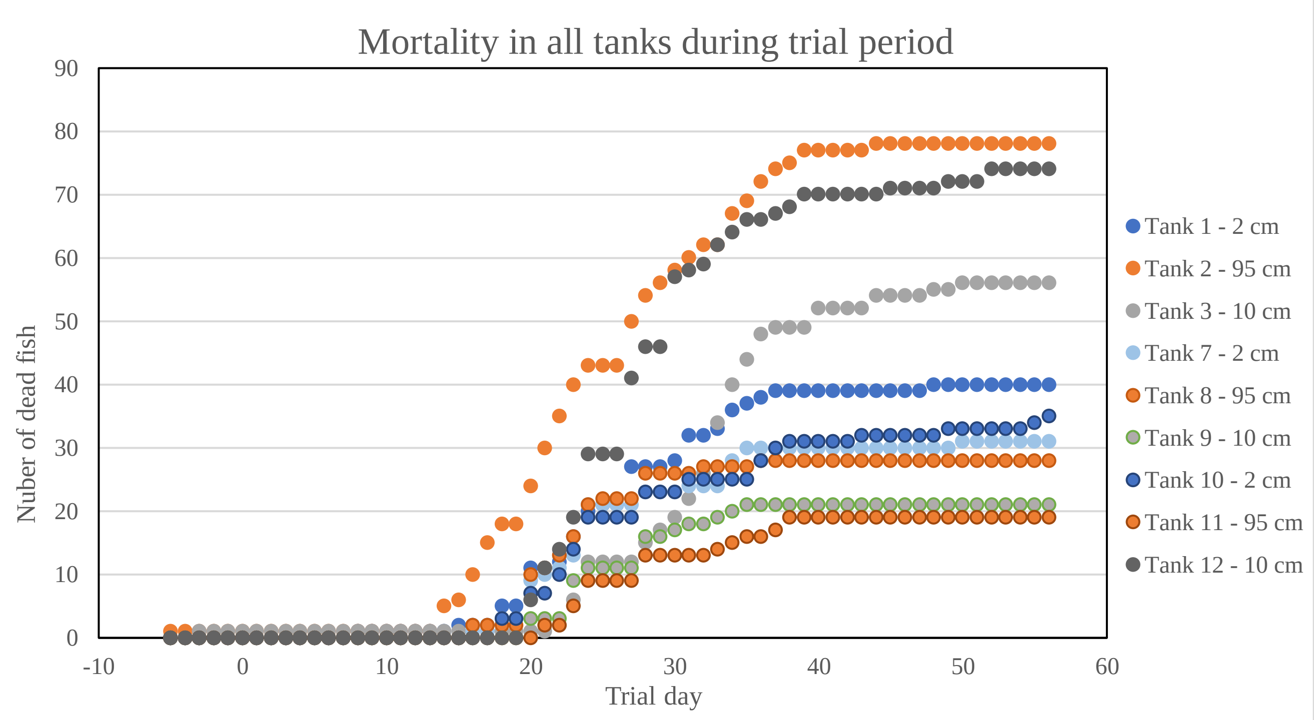


Fig. 4.3: Distribution of mortality during trial period, excluding fish sacrificed for sampling. There were 400 fish in each tank at trial start. An accumulation in mortality was observed from day 20-35, where both numbers of dead fish and frequency of mortality was high. Mortality was highest in tanks 2 and 12. Dome height groups are represented by shades of blue (2cm), grey (10cm), or orange (95cm).

On August 5th, a veterinarian confirmed that fish were infected with bacterial disease, which resulted in all tanks being fed medicine feed (Floraqpharma vet. 2g/kg, Skretting®, with active substance florfenicol) from August 6th- 19th 2020, a period overlapping with the high mortality rates.

4.3 Surface behaviour

Quantitative and statistical analyses are broadly separated into two periods that target the period of acclimating to the dome and learning to use the space (4.3.1 Dome learning period), and the period related to lice infections (4.3.2 Lice response).

4.3.1 Dome learning period

A total of 17 observations per group were conducted during the dome-learning period (DLP), including four observations before domes were installed. Parameters observed were jumps and rolls.

Table 4.2: Results from the ANOVA comparing the null model to the full GLMM model for behaviour data pre- and post-dome installation. The Chi-squared value ($\chi 2$) and p-value for jumping and rolling behaviour full models are reported, with significant differences to the null model indicated (*).

Parameter	**$\chi 2$**	***p***
Jump	8.51	0.037*
Roll	6.98	0.073

4.3.1a Jumping

Total jumps observed during DLP were 401. Distribution of jumps were 90, 191 and 120 jumps min^{-1} for heights 2 cm, 10 cm and 95 cm, respectively. Frequency of jumps were statistically significant with treatment as a factor (Table 4.2). Dome height ($p = 0.004$) was significant for distribution in DLP with average jump frequency min^{-1} 0.12 ± 0.04, 0.24 ± 0.06 and 0.11 ± 0.03 jumps min^{-1} for dome height 2 cm, 10 cm and 95 cm, respectively. Fig. 4.4 illustrates a decrease in jump frequency in all dome types after domes were installed, which were further stabilized at a lower frequency. Jump frequency in the four observations before domes were installed averaged between 0.42 ± 0.05 in tanks with height 2 cm, 0.66 ± 0.03 in 10 cm and 0.29 ± 0.04 in 95 cm. For the 13 observations conducted when domes were installed, dome height 2 cm averaged 0.03 ± 0, 10 cm 0.07 ± 0.01 and 95 cm 0.04 ± 0.01 (Appendix Fig. 7.1).

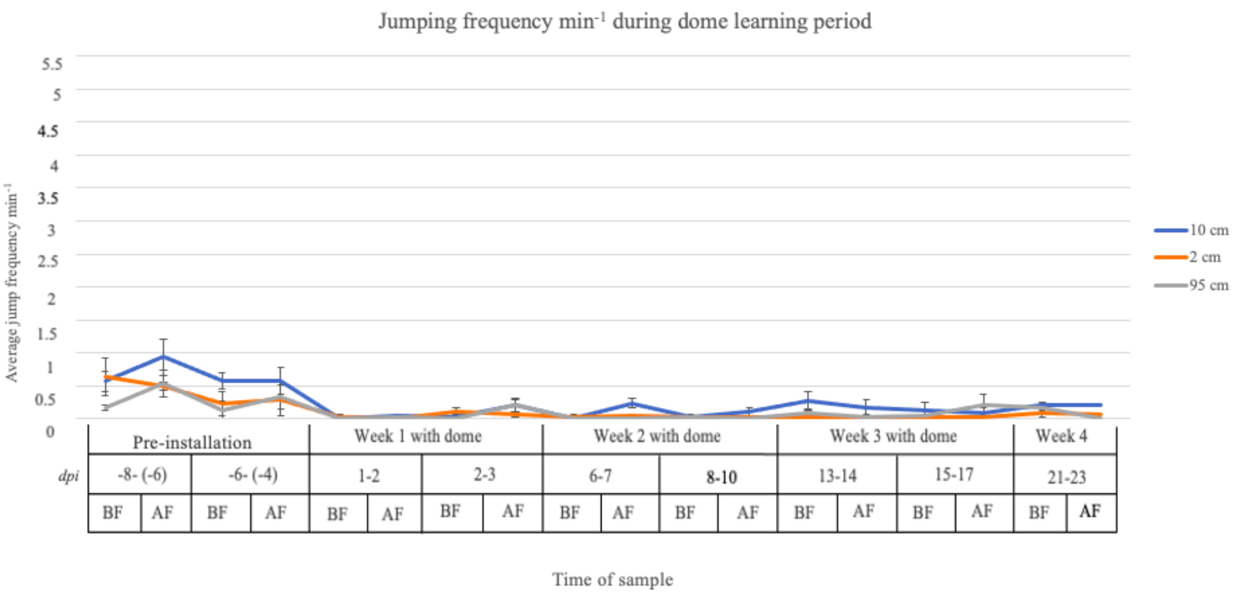


Fig. 4.4: Jump frequency min^{-1} in dome learning period relative to feeding (before/ after). BF= before feeding, AF= after feeding, dpi= days post-installation. Average jumps min^{-1} with standard error bars representing standard error of the mean presented by dome height showing decreased activity level after domes were installed.

4.3.1b Rolling

A total of 1 494 rolls were observed during DLP, distributed between tanks of dome height 2 cm, 10 cm and 95 cm with 593, 536 and 365 rolls, respectively. Although the variability in rolling behaviour was not statistically different from the null model (Appendix Table 7.3), the full GLMM with treatment as a factor indicated a significantly lower frequency of rolling in 95 cm dome tanks (estimate = -0.28, p = 0.017) compared to 2 cm. Average roll frequency min^{-1} in all tanks varied from 0.03-1.09.

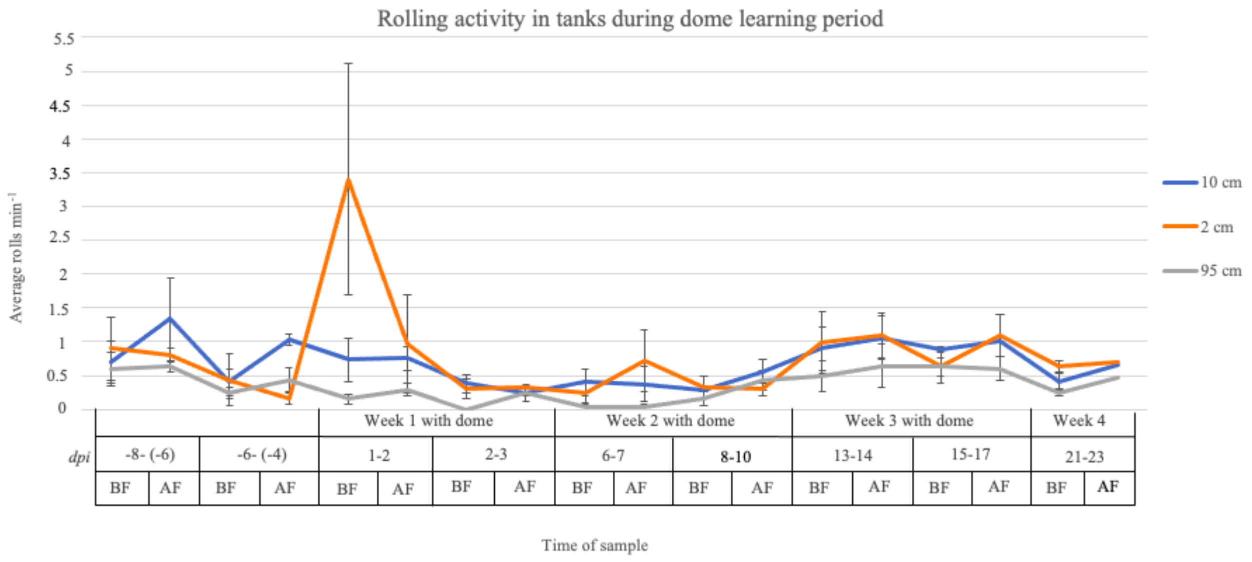


Fig. 4.5: Roll frequency min^{-1} in dome learning period relative to feeding (before/ after). BF= before feeding, AF= after feeding, dpi= days post-installation. Average rolls min^{-1} with error bars representing standard error of the mean presented by dome height. Activity in 2 cm domes peaked on first observation after installation, then frequency stagnated at initial level.

4.3.2 Lice response period

Lice response period (LRP) included analysis of long- and short-term effects of lice infection. Comparing observations pre- and post-infection aimed to reveal how salmon lice infection changes behaviour of salmon (long-term). Comparing observations pre-infection to response during infection (short-term) aim to observe the immediate response of salmon to infective lice. Results from short-term behavioural comparisons are presented in section 4.5.2.

*Table 4.3: Results from ANOVA comparing the full GLMM to the null-hypothesis for each behaviour. Chi-squared ($\chi 2$) and p- value are presented. Significant p-values are indicated with *.*

Parameter	**$\chi 2$**	***p***
Jump	21.34	<0.001*
Roll	16.08	0.0011*
Burst	10.331	0.016*
Twitch	4.16	0.245
Side swimming	53.85	<0.001*

4.3.2a Jumping

During LRP, the full GLMM model was statistically significant from the null model (Appendix Table 7.4), indicating that distribution of jumping behaviour was influenced by treatment and sample. Jumping behaviour was affected by dome height, with highest activity in height 10 cm (estimate = 0.278, $p = 0.001$) and significantly lower frequency in dome height 95 cm (estimate = 0.177, $p = 0.04$). While infected, jump frequency increased in all dome heights with varied frequency between samples, and the same pattern was evident when lice moulted into pre-adult, illustrated in Fig. 4.6.

Sample time (days post infection, dpi) was significant factor for jumping frequency (estimate = 0.019, $p < 0.001$), with increased activity after infection (Fig. 4.6). Behaviour did also differ between groups, with significantly lower frequency in G2 than G1 (estimate = -0.250, $p = 0.05$), illustrated in Fig. 7.2 (Appendix).

Jumps did most often end in collision with the dome lid for both 2 cm (82.7 % of all jumps) and 10 cm tanks (68.8 % of all jumps) (Table 4.4). 95 cm tanks did not have lid. Total amount of jumps was lowest in 2 cm tanks (375) and highest in 10 cm tanks (837) (Table 4.4).

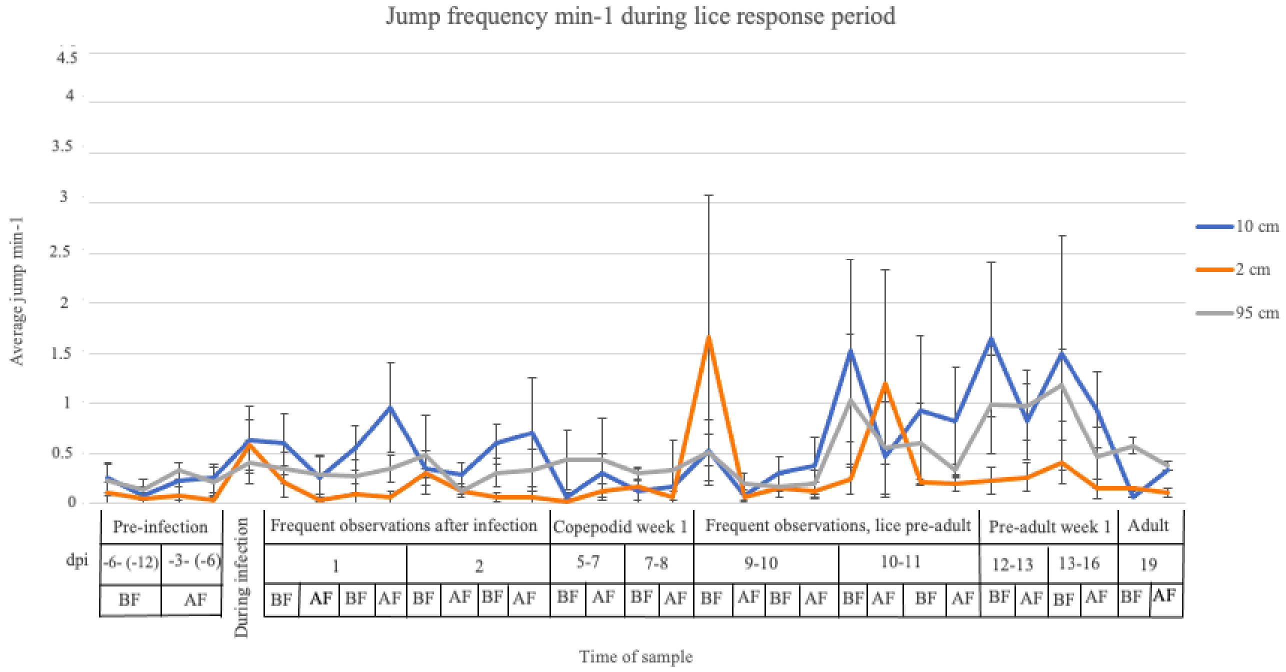


Fig. 4.6: Jump frequency min^{-1} in lice response period relative to feeding (before/ after). BF= before feeding, AF= after feeding, dpi= days post-infection. Presented as average frequency per dome height (jumps min^{-1}± SEM). Graph illustrates increased frequency of activity when lice is introduced in tanks, and also after lice reach pre- adult stage.

Table 4.4: Distribution of jumps during lice response period relative to dome height. Showing total number of jumps, jumps into lid and no lid, also by percentage.

Dome height	**Total jumps**	**Jumps into lid**	**Jumps no lid**	**% into lid**	**% no lid**
2 cm	375	310	65	82,7	17,3
10 cm	837	576	261	68,8	31,2
95 cm	678	-	678	-	100
TOTAL	**1890**	**886**	**1004**	**76 % (excl. 95 cm)**	**24 % (excl. 95 cm)**

4.3.2b Rolling

Initial roll frequency min^{-1} during LRP averaged between 0-1.61. Overall, frequency increased, with 2 cm dome-tanks averaging highest (highest frequency observed being 4.54 rolls min^{-1} on day 10 after infection) while 95 cm dome tanks averaging lowest. Rolls were evenly distributed between into lid (56.8 %) and no lid (43.2 %) (Table 4.5).

Difference in rolling frequencies between treatment groups was statistically significant (Table 4.3). Dome height was a factor that affected behavioural distribution, with dome height 95 cm averaging a significantly lower frequency than 2 cm (estimate= -0.45, $p = 0.002$). Sample time was also a significant factor for roll behaviour (estimate = 0.019, $p = 0.0018$) with increased frequency over time. Although behavioural distribution differed significantly between G1 and G3, response pattern was similar, although at different frequencies (Appendix Fig. 7.3).

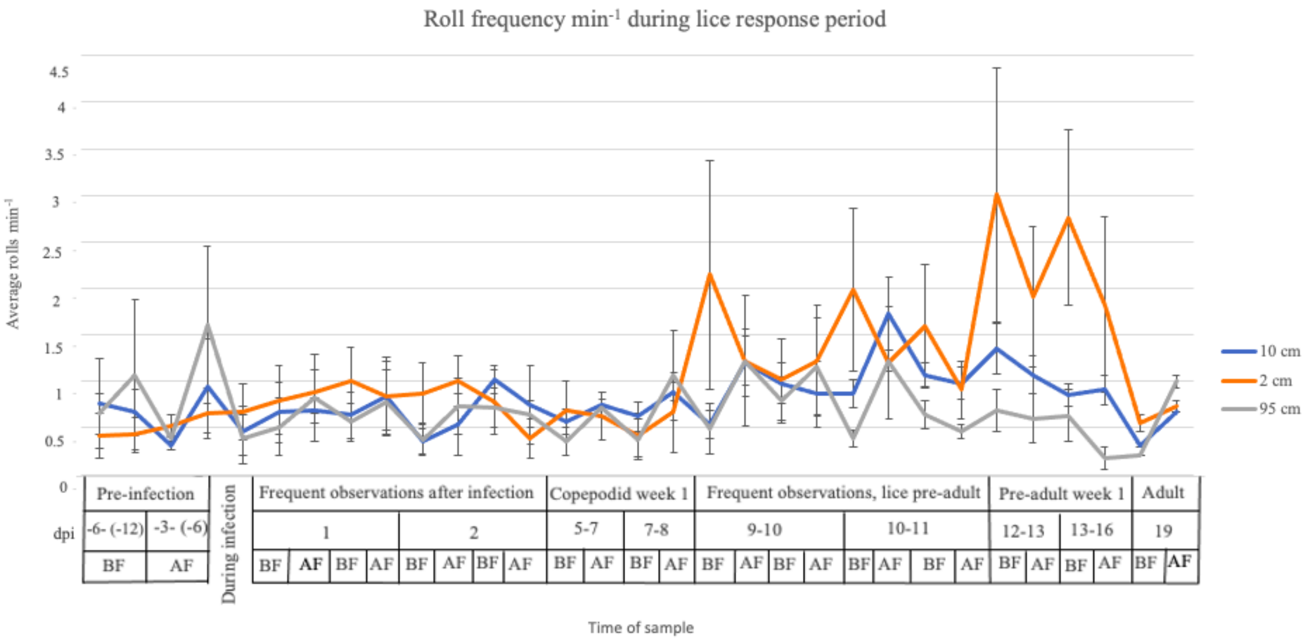


Fig. 4.7: Roll frequency min^{-1} during lice response- period presented by average per dome height (rolls min^{-1}± SEM). *BF= before feeding, AF= after feeding, dpi= days pos- infection. Rolling frequency increased in all tank heights when lice moulted to pre-adult, with 2 cm tanks averaging highest.*

Table 4.5: Total amount of rolls and percentage of rolls into lid and no lid presented by dome height. 95 cm domes had no lid and has therefore 0 rolls into lid.

Dome height	**Total rolls**	**Rolls into lid**	**Rolls no lid**	**% rolls into lid**	**% rolls no lid**
2 cm	1631	926	705	56.8	43.2
10 cm	1244	107	1137	8.6	91.4
95 cm	974	0	974	-	100
TOTAL	**3849**	**1045**	**2804**	**32.7 (excl. 95 cm)**	**67.3 (excl. 95 cm)**

4.3.2c Burst

Adding all observations in all tanks, a total of 279 observations were conducted. 262 of the observations recorded frequencies of ≤ 1 bursts min^{-1}, whereas fish in domes of 2 cm height exhibited 11 samples averaging > 1 bursts min^{-1}. The full GLMM model was statistically significant with dome height as an influential factor for distribution of burst behaviours (Table 4.3), with dome height 95 cm relative to 2 cm (estimate = -0.153, *p* = 0.00035) exhibiting the lowest burst frequencies. Burst swimming was also affected by groups, where activity in G2 (estimate = 0.114, *p* = 0.0089) and G3 (estimate = 0.342, *p* < 0.0001) were higher relative to G1. Response pattern, however, followed the same trend in G1 and G3, although at different frequencies (Appendix Fig. 7.4). Highest observed burst frequency was 4.18 min^{-1} in tank 10 (2 cm) during infection. Elevated frequency was observed in all tanks on this sampling, in response to exposure to infective copepodids (Fig. 4.8).

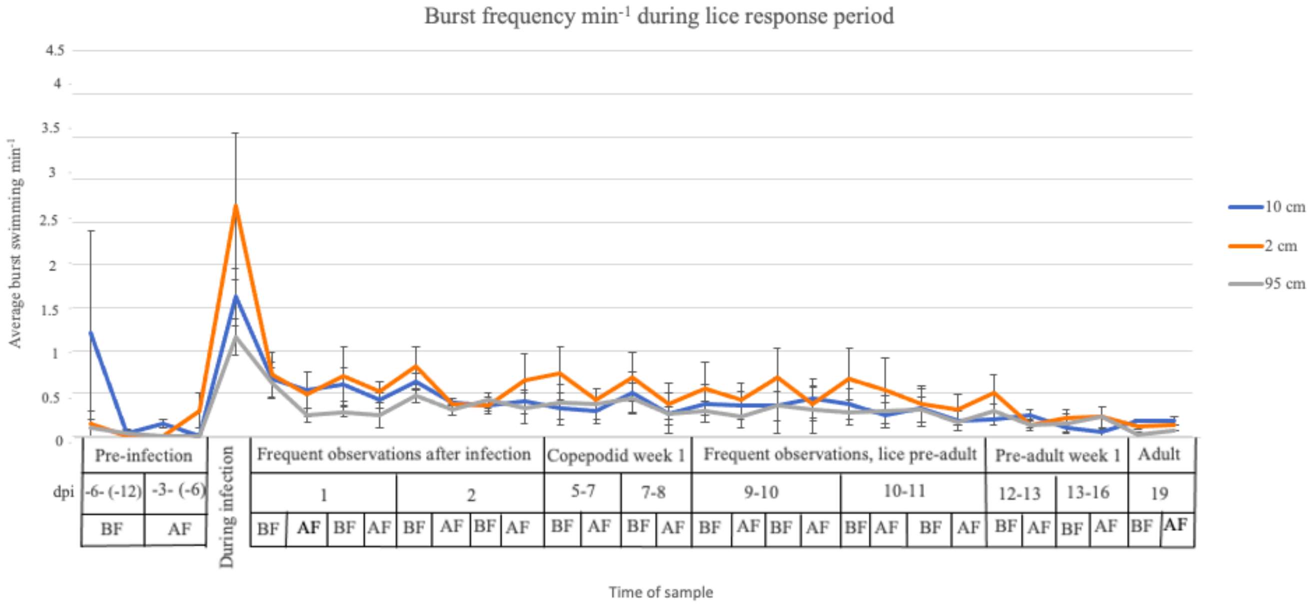


Fig. 4.8: *Burst swimming frequency min^{-1} during lice response-period presented by average per dome height (burst min^{-1}*± SEM). *BF= before feeding, AF= after feeding, dpi= days post-infection. All tanks had increased activity during infection, but burst swimming decreased the following days.*

4.3.2d Twitch

Frequency of twitching behaviour was not significantly affected by treatment of dome height (Table 4.3). There were, however, some difference in activity pattern between groups (Appendix

Fig. 7.5). Initial twitch frequency min^{-1} varied between 0-0.7. In all treatment groups, twitching stabilized at a higher frequency during infection (Fig. 4.9).

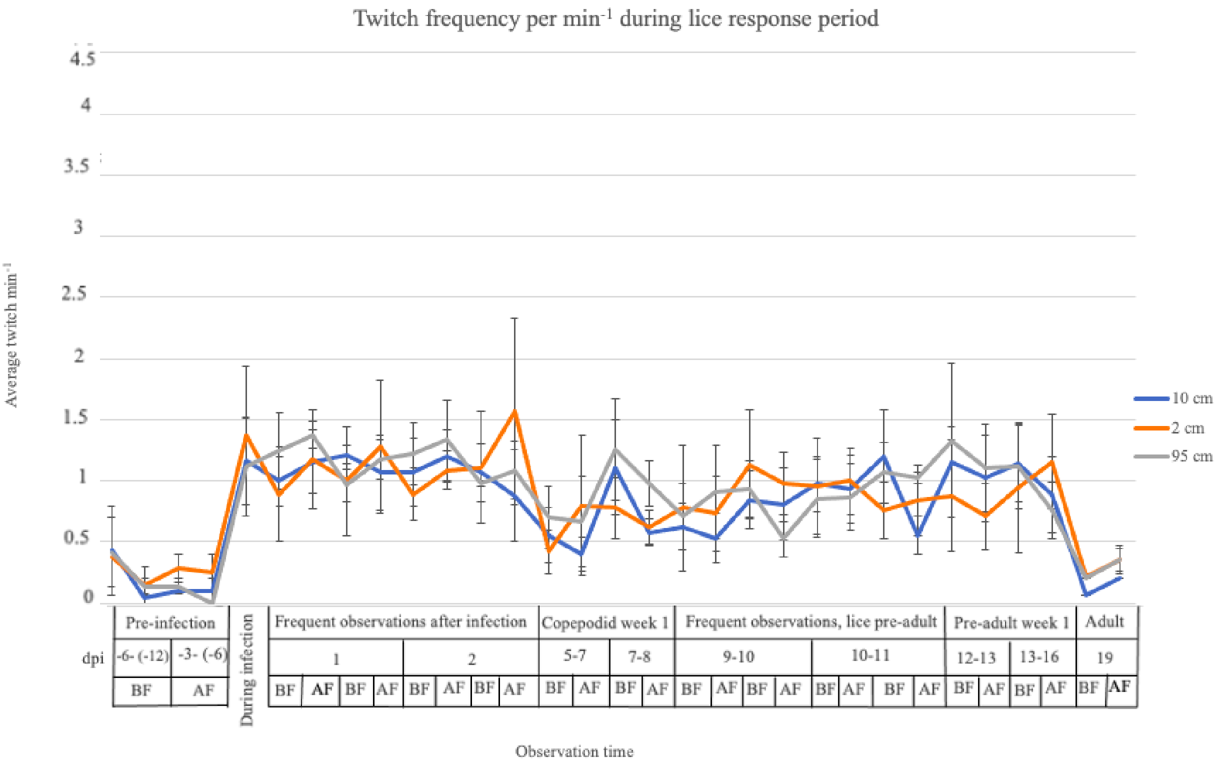


Fig. 4.9: Development of averaged twitch behaviour (twitch $\textit{min}^{-1}$ ± SEM) *during lice response period, distinguished between dome heights. BF= before feeding, AF= after feeding, dpi= days post-infection. Graph illustrates a similar activity level between dome heights, with increased frequency during infection.*

4.3.2.e Side swimming

Distribution of side swimming behaviour was statistically significant with time of sample as a factor (estimate = 0.120, $p < 0.001$) (Table 4.3). Distribution also varied between groups, with G2 (estimate = -0.226, $p < 0.001$) exhibiting a significantly lower frequency than G1 (Appendix Fig. 7.6).

Side swimming was almost absent until lice were introduced in tanks (Table 4.6), and plateaued at a higher frequency with lice in tanks. Activity increased further when lice reached pre-adult 1 stage (Fig. 4.10).

Table 4.6: Average side swimming frequency (average ± SE) per dome height before (4 observations) and after (27 observations) salmon lice were introduced in tanks.

Tank height	**Avg. side swim min^{-1} before lice**	**Avg. side swim min^{-1} after lice**
2 cm	0.02 ± 0.02	0.37 ± 0.06
10 cm	0.03 ± 0.02	0.32 ± 0.04
95 cm	0.01 ± 0.01	0.43 ± 0.04

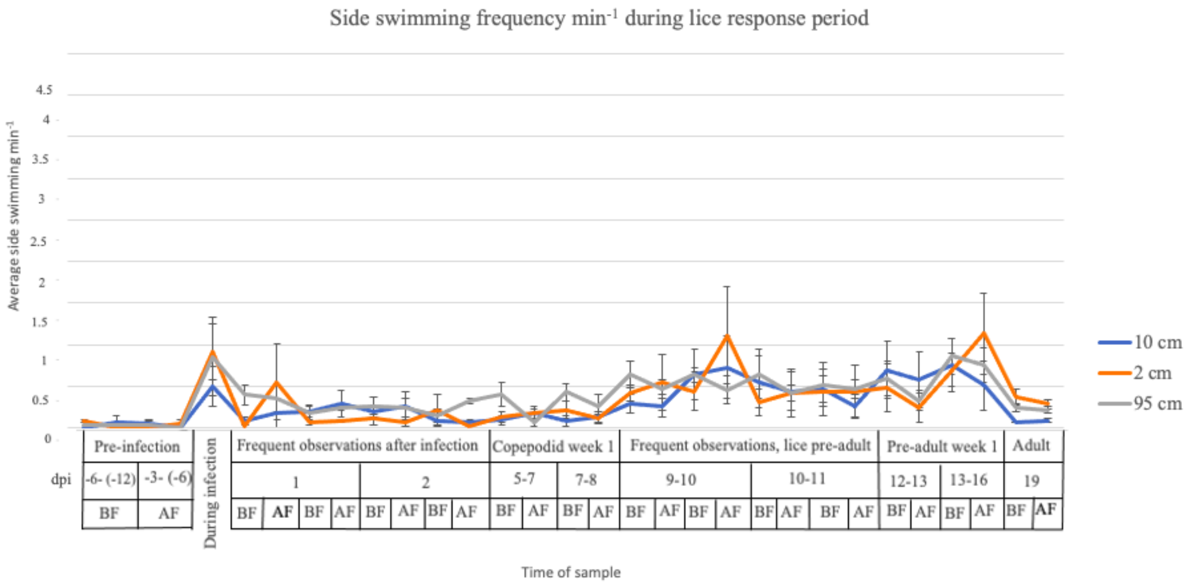


Fig. 4.10: Development of averaged side swimming behaviour (side swimming min^{-1}± SEM) *during lice response period, distinguished between dome heights. BF= before feeding, AF= after feeding, dpi= days post infection. Graph illustrates increased activity over time, showing an immediate increase in all tanks during lice infection.*

4.4 Welfare

4.4.1 Sampling pre-installation

For sampling pre-installation, 20 fish from all tanks were scored using SWIM before domes were installed in tanks. Scores from this sampling were not compared to the other welfare scores, but are considered a basis for welfare evaluation and show the general condition for fish in all tanks.

Table 4.7: Results of POLR analyses of dome height and group effect on welfare scores during sampling pre-installation. P-values are calculated from an ANOVA of the chosen model. Results of post-hoc analyses (pairwise comparisons using lsmeans) of either dome height or group factors are shown for when these are significant in the main model. Note: only results from models when significantly different from the null model (Appendix Table 7.3) are shown.

Welfare indicator	**Model**	**Coefficient**	**t-value**	**p-value**
Eye bleeding	**M0: 1 + Group**			
	Group	13.68		0.001
	Post-hoc – group			
	1-2			**0.005**
	1-3			0.155
	2-3			0.184
Scale loss	**M0: 1 + Group**			
	Group	36		<0.001
	Post-hoc – group			
	1-2			**<0.001**
	1-3			**<0.00**
	2-3			0.639
Fin damage	**M0: 1 + Group**			
	Group	8.776		**0.012**
	Post-hoc – group			
	1-2			0.137
	1-3			**0.008**
	2-3			0.515

4.4.1a Eye status

Eye bleeding (1-6)

The only factor that influenced eye bleeding was group (Table 4.7), where there was a higher appearance of condition in G1 than G2 (estimate = 0.163, *p* = 0.0046). The highest score given for eye bleeding was 4, occurring only on one fish. None were scored 3, and 9 fish were scored 2. Average scores are illustrated in Fig. 4.11A. Scores were, however, evenly distributed between tanks (Appendix Fig.7.8).

Cataract (1-4)

Highest individual initial cataract score was 2, which was given to one fish in tank 2 and two fish in tank 3; the rest were scored 1 (Fig. 4.11B). Because of the low variability in scores, cataract prevalence was not analysed.

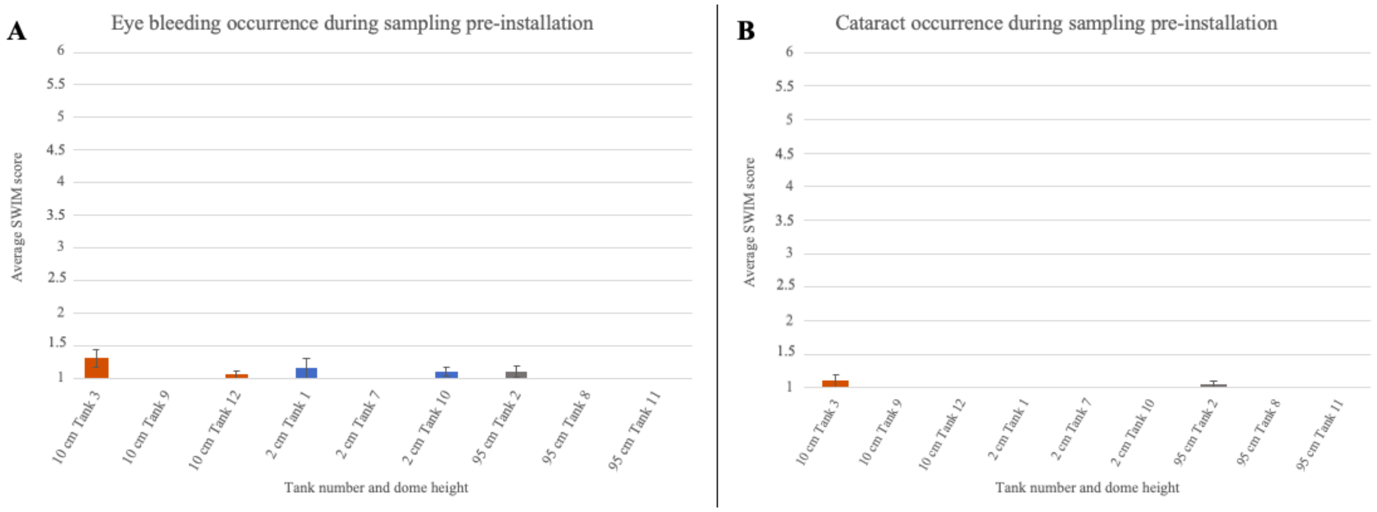


Fig. 4.11: Initial scores for eye status indicators A) eye bleeding and B) cataract on sampling pre-installation. Average score tank^{-1} ± SD.

4.4.1b Skin status

Fin (1-6)

The null model was the best fit, with fin damage occurrence different between groups (Table 4.7), although not strongly significant. One fish from tanks 10, 11 and 12 scored 5. Average score in all tanks are illustrated in Fig. 4.12A.

Scale loss (1-8)

Dome height did not influence the scoring of scale loss, however in the null model, Group as a factor was significant for scale loss condition (Table 4.7). The post hoc test indicated significantly higher scores in G1 relative to G2 and G3 ($p < 0.0001$ for both). The highest score given was 7, occurring in 17 fish, evenly distributed between tanks (Appendix Fig. 7.7). Average score in all tanks ranged between 2.75-5.4 (Fig. 4.12B).

Snout (1-4)

Snout damage averaged between 1-1.05 (Fig. 4.12C), scoring too similar across tanks for any factors to be statistically significant (Appendix Fig. 7.7).

Skin bleeding (1-4)

Initial skin bleeding score averaged between 1.65-2.35 in all tanks (Fig. 4.12D), with 70 % of all fish scoring 2. Different scores were evenly distributed between tanks (Appendix Fig. 7.7) and treatment was considered statistically insignificant.

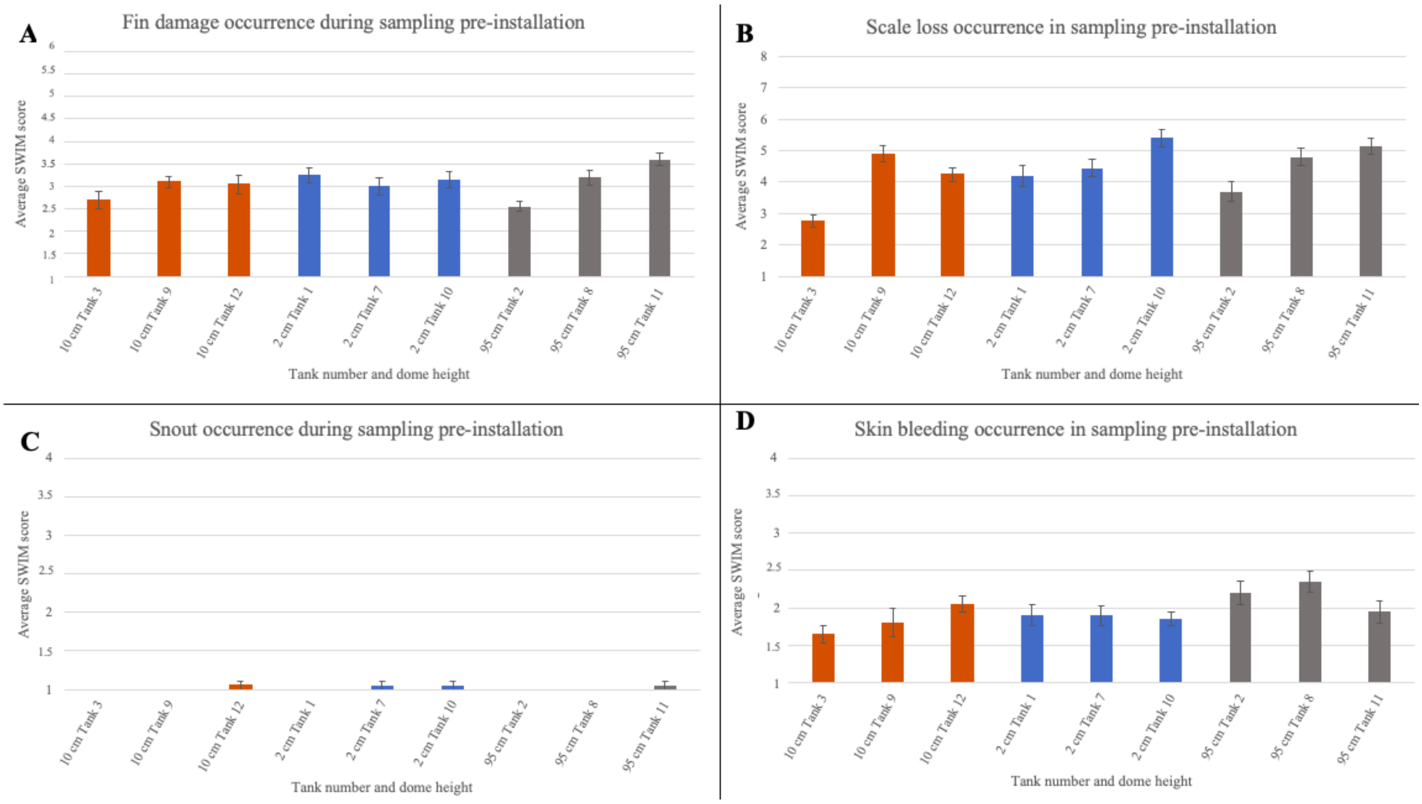


Fig. 4.12: Initial scores of skin status indicators A) fin, B) scale loss, C) snout and D) skin bleeding on sampling pre-installation. Scoring range vary between different indicators. Average score tank^{-1} ± SD.

4.4.1c General condition

Deformity (1-6)

All fish except one scored 1 on deformity (Fig. 4.13A). Deformity as an indicator was not accepted in model because the variability within indicator scores was too low.

Gill damage (1-4)

Gill scores averaged between 1.00-1.15, and variability was too low for any factors to be statistically significant.

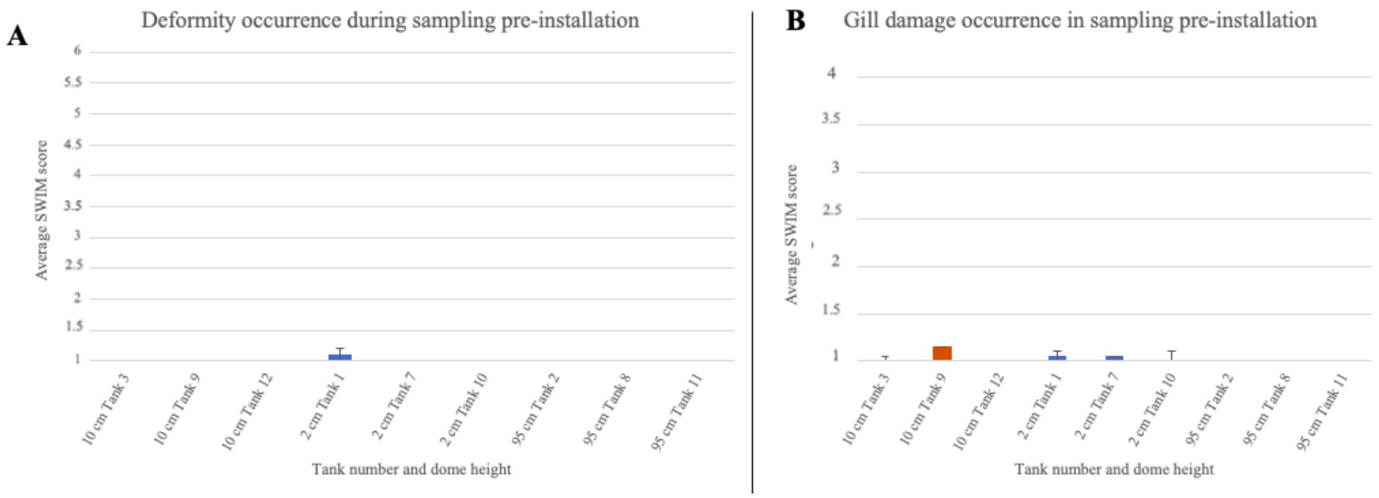


Fig. 4.13: Initial scores of skin status indicators A) deformity and B) gill damage. Scoring range vary between different indicators. Average score tank^{-1} ± SD.

4.4.2 Post-installation, pre-infection and end

During the post- installation period, several losers were observed and wounds on nose (likely from damage from the lid) was observed on sampled fish. At the pre-infection sample, several fish had lost flesh on their pectoral fin, leaving only the fin rays exposed. 75 % of sampled fish in tank 11 (95 cm) had black snouts from colliding into dome wall. In end sampling, 40 fish from each tank were evaluated and black snouts were common in all tank heights in G2 and G3, but black snout was not considered as snout damage. Some fish also had marks from netting on their head, although these were not active wounds (i.e. not bleeding). Wounds from salmon lice grazing was observed frequently, occurring most often in G3, but could not be distinguished to be more severe in any particular dome height. Opercula were observed with tears and appeared to be bleeding in 17.5 % of sampled fish in tank 12 (10 cm) at the end sampling, a state that was not observed in other tanks. Analyses on the following scores only are for pre-infection and end samplings due to the lack of data for G1 at the post-install sampling.

4.4.2a Eye status (scored 1-4)

Eye bleeding

The full model group indicated that distribution of eye bleeding occurrence was influenced by dome height and group (Table 4.8), although not strongly significantly different from the null model (Appendix Table 7.4). Between pre-infection and end sampling, eye bleeding had higher occurrence in 95 cm dome tanks than 2 and 10 cm (Table 4.8). There was a group effect showing lower occurrence of condition in G2 relative to G1 and G3 (Table 4.8), although not a strong effect between G2 and G3. Eye bleeding scores averaged 1.05-1.60 for samples post-installation, pre-infection and end combined (Fig. 4.14A). Few individuals scored high on eye bleeding; seven fish from four different tanks scored 4, distributed between all three samples (Appendix Fig. 7.8), which support that that statistical significance was not biologically important.

Cataract

Scores at pre-infection and end sampling were almost all 1's and therefore could not be analysed due to low variability. Cataract averaged between 1.00-1.25, considering post-installation, pre-infection and end sampling combined (Fig. 4.14B). Some tanks experienced no change in occurrence of cataracts between all three samples.

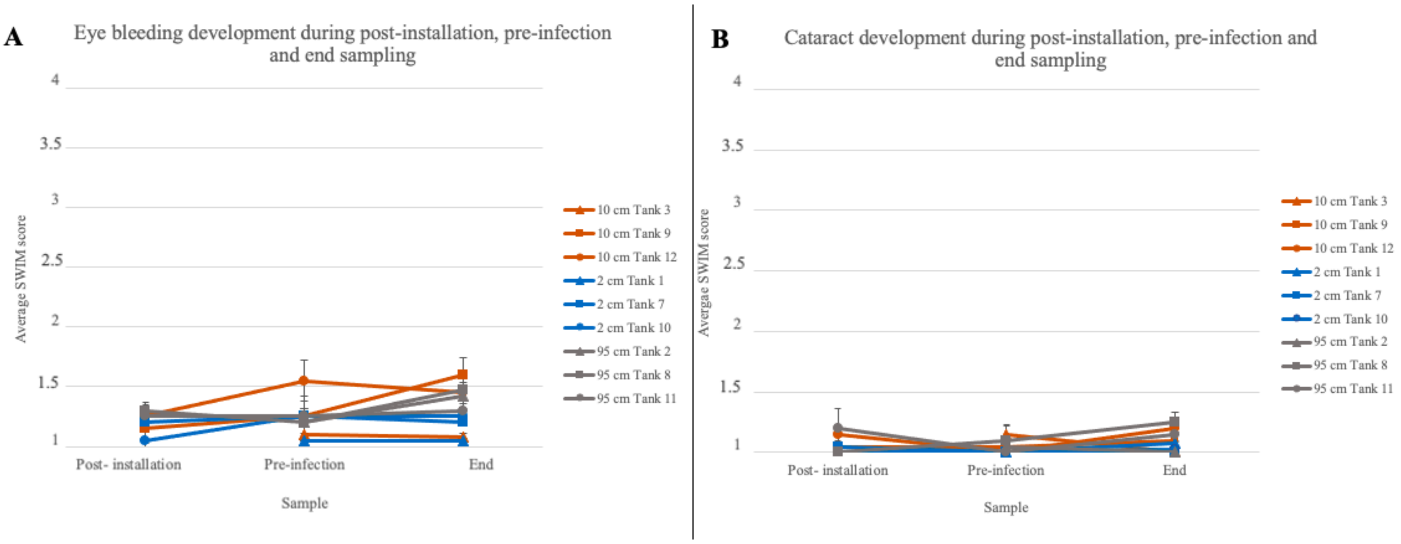


Fig. 4.14: Development of A) eye-bleeding and B) cataract condition during samplings post-install, pre-infection and end based on average indicator score tank^{-1} ± SD *in each tank. Dome height groups are represented by blue (2cm), orange (10cm), or grey (95cm) colour, while groups are represented by triangle (G1), square (G2) or circle (G3) indicator at each sample.*

Table 4.8: Results of POLR analyses of dome height effect and sample time on welfare scores during pre-infection and end sampling. P-values are calculated from an ANOVA of the chosen model. Results of post-hoc analyses (pairwise comparisons using lsmeans) of either dome height or Group factors are shown for when these are significant in the main model. Note: only results from models when significantly different from the null model (Appendix Table 7.4) are shown.

Welfare indicator	**Model**	**Coefficient**	**t-value**	**p-value**
Eye bleeding	**M1: Dome.height + Group**			
	10 cm dome	0.0534	0.214	**0.043**
	2 cm dome	-0.666	-2.344	

	Group 2	0.847	3.003	**0.010**
	Group 3	0.666	2.303	< **0.001**
	Post-hoc – dome height			
	10 cm – 2cm			0.975
	10 cm – 95cm			**0.048**
	2 cm – 95cm			**0.003**
	Post-hoc – group			
	1-2			**0.006**
	1-3			0.053
	2-3			0.750
Scale loss	**M3: Dome.height + Sample + Group**			
	Dome height	-0.5136	-2.6555	**0.014**
	Sample	-0.5105	-3.0276	**0.010**
	Group	-0.3226	-3.226	< **0.001**
	Post-hoc – dome height			
	10 cm – 2cm			**0.021**
	10 cm – 95cm			**0.929**
	2 cm – 95cm			**0.007**
	Post-hoc – group			
	1-2			**0.041**
	1-3			**0.002**
	2-3			0.609
Skin bleeding	**M2: Sample + Group**			
	Sample	-0.897	-5.169	< **0.001**
	Group	0.083	0.853	0.394
Wound	**M2: Sample + Group**			
	Sample	-1.205	-2.958	**0.012**
	Group	-0.813	-2.921	**0.002**
	Post-hoc – group			
	1-2			0.712
	1-3			**0.007**
	2-3			**0.035**
Snout	**M2: Sample + Group**			
	Sample	0.709	3.891	< **0.001**
	Group 2	0.5624	2.641	< **0.001**
	Group 3	1.605	7.632	
	Post-hoc – group			
	1-2			**0.021**
	1-3			< **0.001**

	2-3			< **0.001**
Fin bleeding	**M1: Dome.height + Group**			
	10 cm dome	0.202	0.990	< **0.001**
	2 cm dome	-0.654	-3.147	
	Group 2	0.005	0.023	0.675
	Group 3	0.158	0.776	
	Post-hoc – dome height			
	10 cm – 2cm			0.583
	10 cm – 95cm			**0.004**
	2 cm – 95cm			< **0.001**
Fin split	**M3: Dome.height + Sample + Group**			
	10 cm dome	-0.48	-1.203	< **0.001**
	2 cm dome	-0.931	-4.500	
	Sample	0.449	2.491	**0.044**
	Group 2	-0.541	-2.639	< **0.001**
	Group 3	-0.781	0.207	
	Post-hoc – dome height			
	10 cm – 2cm			0.450
	10 cm – 95cm			< **0.001**
	2 cm – 95cm			**0.002**
	Post-hoc – group			
	1-2			**0.021**
	1-3			< **0.001**
	2-3			0.423
Fin erosion	**M2: Sample + Group**			
	Sample	-0.872	-4.980	< **0.001**
	Group 2	0.080	0.389	0.285
	Group 3	0.302	0.199	

4.4.2b Skin status (scored 1-6)

Wound

Distribution of wound damage occurrence was significantly affected by group and sample as factors between pre-infection and end sampling, but not influenced by dome height (Table 4.8). G3 scored significantly higher than G1 and G2 (Table 4.8). Wound scores peaked in two tanks of 2 cm height on sampling pre-infection, and overall scores on sampling pre-infection averaged between 1.00-1.65. In samples post-installation and end, score averaged between 1.00-1.15 and 1.08

respectively (Fig. 4.15A). The highest score given was 4, and was observed on one fish in tank 1 and three fish in tank 2 during sampling post-installation.

Scale loss

Distribution of scale loss between tanks was significantly dependent on sample time, dome height and group as factors (Table 4.8). Between pre-infection and end sampling, 2 cm dome height incurred higher frequencies of more severe scores than 10 cm and 95 cm ($p < 0.02$ for both). Scores were different between groups, with G1 higher relative to G2 and G3 ($p < 0.04$ for both) between pre-infection and end. Average scale loss scores decreased from 4.30-5 in post-installation and 3.10-5.15 in pre-infection to 3.20-4.60 in end sampling (Fig. 4.15B). Table 4.11 shows distinguishing of score 6 (highest score) between tanks during the three samplings. All tanks experienced decreased average score from post-install to end sampling except tanks 1 and 2 (Appendix Fig. 7.8). Tanks 7 and 9 (both G2) experienced increased scale loss on sampling pre-infection, while tanks 10, 11 and 12 (all in G3) experienced lowest scores in tanks on the same sampling (Appendix Fig. 7.8).

Table 4.11: Distinguishing of SWIM score 6 (highest score) for scale loss during sampling 2, 3 and 4.

Sampling	**Tank 1**	**Tank 2**	**Tank 3**	**Tank 7**	**Tank 8**	**Tank 9**	**Tank 10**	**Tank 11**	**Tank 12**
Post-install				6	3	-	4	1	4
Pre-infection	1	3	6	6	3	3	-	-	-
End	1	2	-	-	1	-	2	2	2
Total	**2**	**5**	**6**	**12**	**7**	**3**	**6**	**3**	**6**

Snout

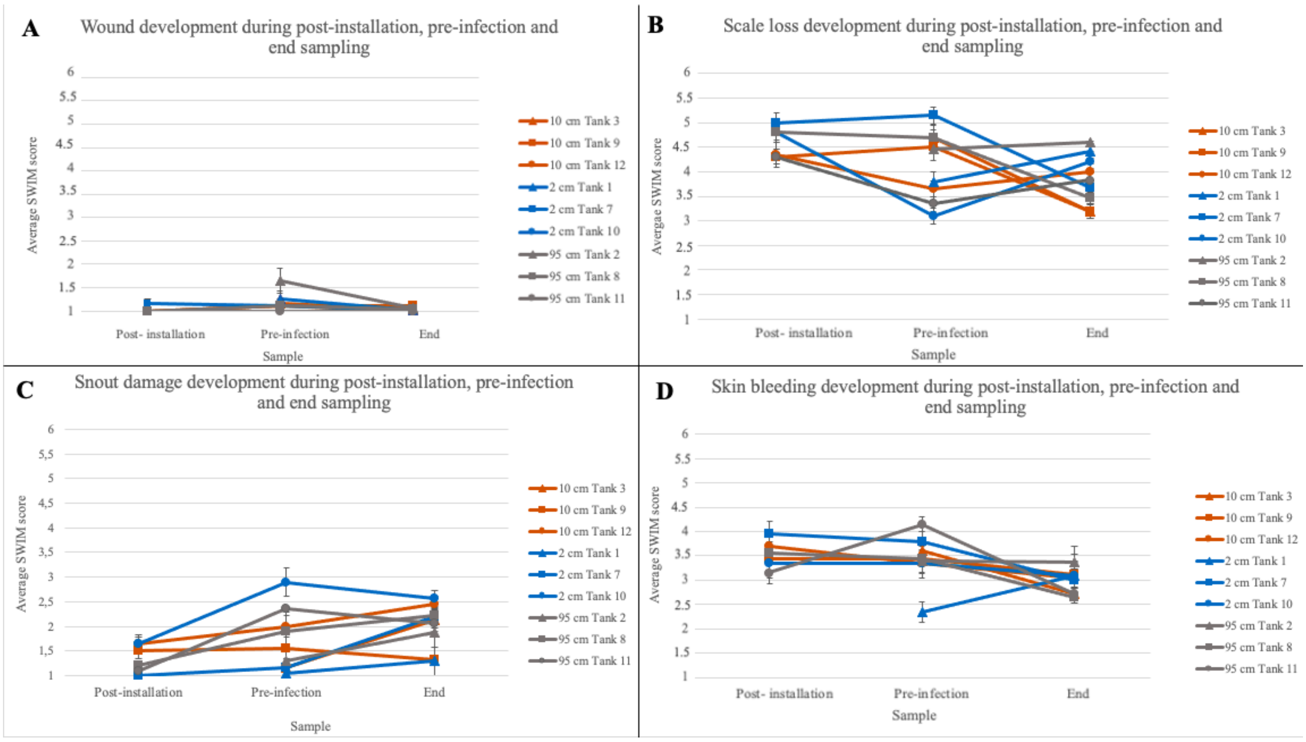
Frequency of snout damage was statistically significant by sample and group (Table 4.8). The post-hoc test showed differences between all groups, indicating higher occurrence of condition in G3 compared to G1 and G2 (Table 4.8). Snout score had an overall increasing occurrence during the three samples, averaging between 1.00-1.70 in post-installation, 1.05-2.00 in pre-infection and 1.00-2.60 in end sampling (Fig. 4.15C). The highest score recorded was 5 and was given to one and two fish in tanks 10 and 11 (both G3) pre-infection, and six fish in five different tanks on end sampling; generally, scores were distributed between all tanks in G3 and in tanks 7 and 9 (G2). Fish from all tanks were given at least one score of 4 on end sampling.

Skin bleeding

Skin bleeding was scored higher in pre-infection than end sampling (Appendix Table 7.4), as the factor was significantly different from the null model (Table 4.8). Skin bleeding scores decreased in each sampling from post-install to end sampling in all tanks except tank 1 (Fig. 4.15D), although with an increase in averaged skin bleeding score in tank 11 on sampling pre-infection (Appendix Fig. 7.8).

Skull wounds

Skull wounds were included in SWIM-evaluation on pre-infection and end sampling (end sampling only for G1). In tanks 3 and 8, all 40 fish scored 1 in end sampling. All other tanks experienced an increase in severity prevalence from pre-infection to end sampling (Fig. 4.15E). For sampling pre-infection, only G2 and G3 were scored on indicator. Condition occurred on 86 fish out of 500 evaluated, and 72 % occurred during end-sample. There was, however, no clear difference between dome heights.



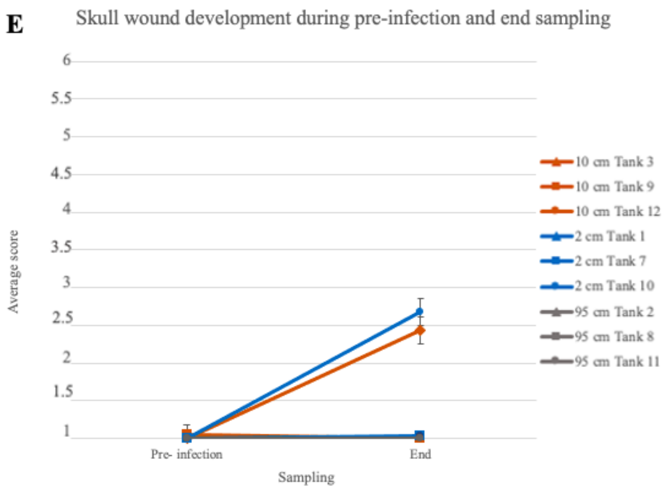


Fig. 4.15: Development of indicator constituting category skin condition presented by average indicator score tank^{-1} ± SD *during sampling post-installation, pre-infection and end (only pre-infecction and end for skull wound). Indicators A) wound, B) scale loss, C) snout, D) skin bleeding, E) skull wound, all with scoring range 1- 6. Dome height groups are represented by blue (2cm), orange (10cm), or grey (95cm) colour, while groups are represented by triangle (G1), square (G2) or circle (G3) indicator at each sample.*

4.4.2c Fin status (scored 1-4)

Fin split

Dome height, sample and group were considered significant factors for affecting distribution of fin split scores (Table 4.8). From pre-infection to end sampling, dome height of 95 cm exhibited significantly higher frequency of severe scores than 2 cm and 10 cm (p < 0.023 for both). Similarly, G1 scored higher than G2 and G3 (p < 0.0213 for both). Fin split scores averaged between 2.15-3.00 for post-installation, pre-infection and end sampling, and all tanks experienced increased in average score from pre-infection to end sampling, except tank 12 (Fig. 4.16A). Highest possible score (4) was achieved by 8, 11 and 27 fish for samples post-installation, pre-infection and end, respectively (Appendix Fig. 7.8). In tank 2, 9 out of 40 fish were scored 4 on end sampling. The lowest score occurred a total of 29 times during all three samples. Fin split scores of 2 and 3 contributed 45 % and 44 % of total samples, respectively.

Fin bleeding

Dome height was a statistically significant factor affecting distribution of fin bleeding scores (Table 4.8). Fin bleeding occurred in higher frequency in tanks of 95 cm domes than for 2 and 10 cm (p < 0.0042 for both) from pre-infection to end sampling.

Scores averaged between 2.15-2.75 at sampling post-installation (Fig. 4.16B). All tanks except tank 11 experienced decreased average scores from post-installation to end sampling (Fig. 4.16B). The most common fin bleeding score was 2, contributing 52 % of all scores from all last three samplings.

Fin erosion

Scores were statistically significant between sample times from the null model for fin erosion (Table 4.8) with higher scores in pre-infection than end sampling (Fig. 4.16C).

Fin erosion averaged between 1.40-2.40 (Fig. 4.16C), with all tanks averaging a higher score at end sample than post-installation, although 4 tanks experienced highest score on sampling pre-infection. Score 4 occurred in highest frequency in post-installation, where 2 fish in all tanks of 2 cm height were scored 4, while only one fish in the remaining six tanks were scored 4 at pre-infection (Appendix Fig. 7.8).

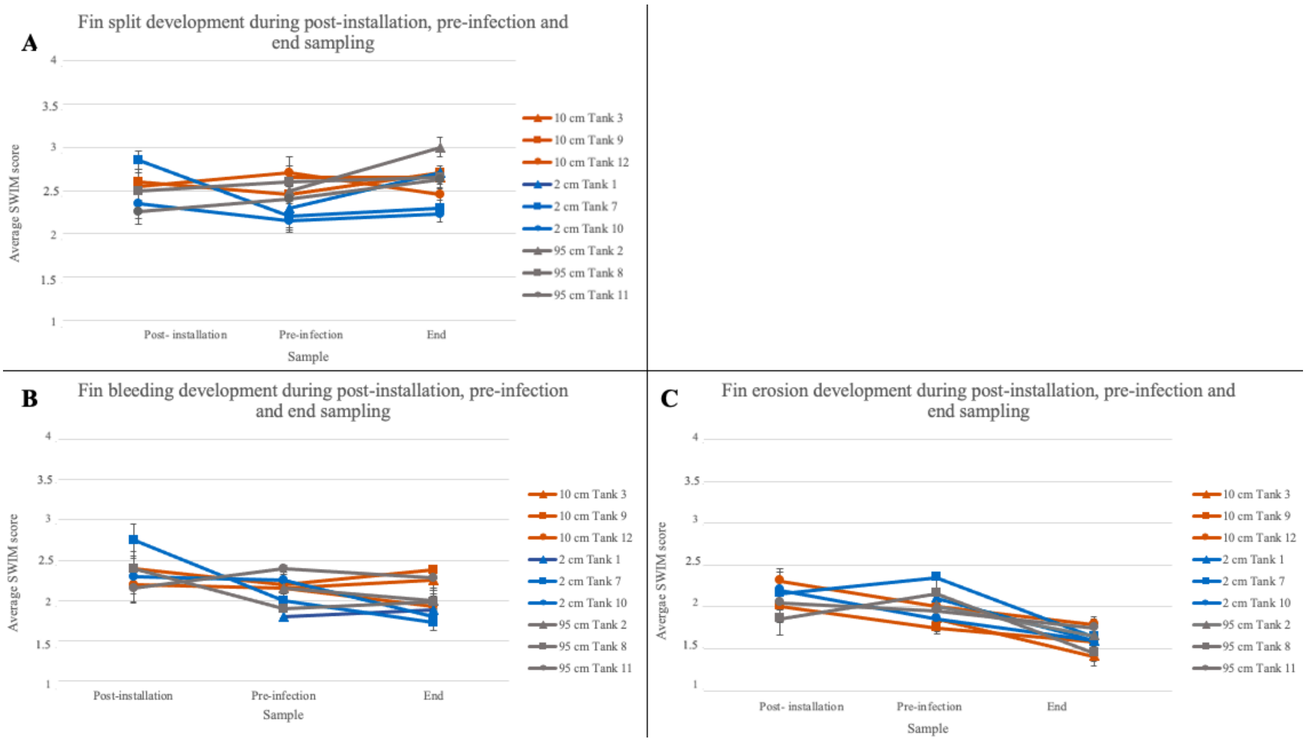


Fig. 4.16: Development of fin status in each tank during samplings post-installation, pre-infection and end. Average score tank^{-1} ± SD *for A) fin split, B) fin bleeding and C) fin erosion. Scoring range 1-4 for all indictors. Dome height groups are represented by blue (2cm), orange (10cm), or grey (95cm) colour, while groups are represented by triangle (G1), square (G2) or circle (G3) indicator at each sample.*

4.4.2d General status (scored 1-6)

Deformity

Deformity score averaged between 1.00-1.10 across all three samplings after domes were installed (Fig. 4.17A), and also was too invariable to analyse. Five fish from four different tanks scored higher than 1, and were generally across all three samples.

Gill damage

Gill scores averaged between 1.00-1.30 across all three samples (Fig. 4.17B). Overall, scores increased from pre-infection to end in five tanks, although scores were frequently 1, and too invariable to analyse. In end sampling, one fish in tank 1 scored 6 which was the highest possible score (Appendix Fig. 7.8).

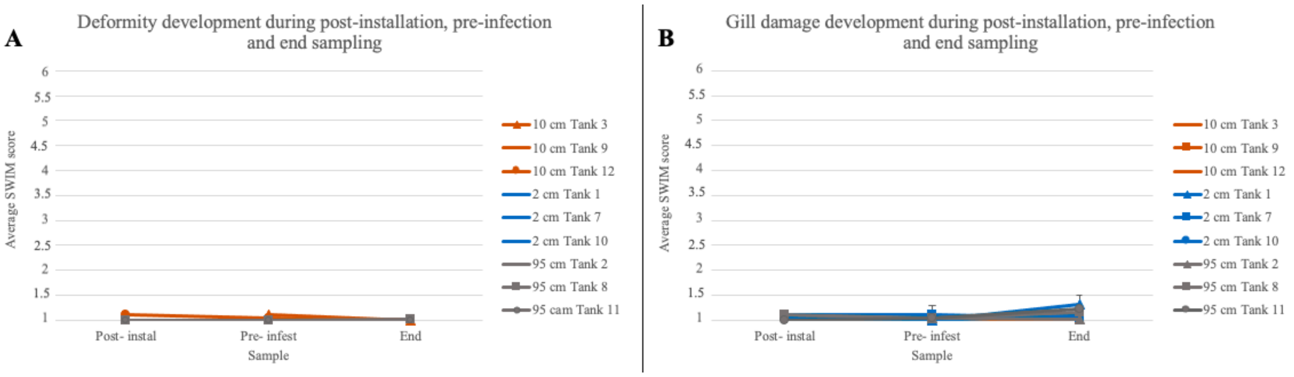


Fig. 4.17: Development of indicators A) deformity and B) gills in each tank during samplings post-installation, pre-infection and end. Average score tank^{-1} ± SD *are presented. Score range 1-6. Dome height groups are represented by blue (2cm), orange (10cm), or grey (95cm) colour, while groups are represented by triangle (G1), square (G2) or circle (G3) indicator at each sample.*

4.5 Salmon lice

Salmon lice were introduced to tanks 38, 56 and 79 days after dome installation for G1, G2 and G3, respectively. Long-term effects of salmon lice are discussed in section 4.3.2, while this section focus on behaviour during infection.

During infection, behaviours jump, burst, twitch and side swimming increased in trial tanks. Frequencies for twitch and burst behaviour were significant between groups, but no behaviour was significantly affected by dome height.

4.5.1 Salmon lice infection and development success

Salmon lice were counted on 40 fish in each tank at the end sampling. Infection and development success varied between groups, G1, G2 and G3 averaging 5.5, 2.5 and 14.4 lice fish^{-1}, respectively (Fig. 4.18).

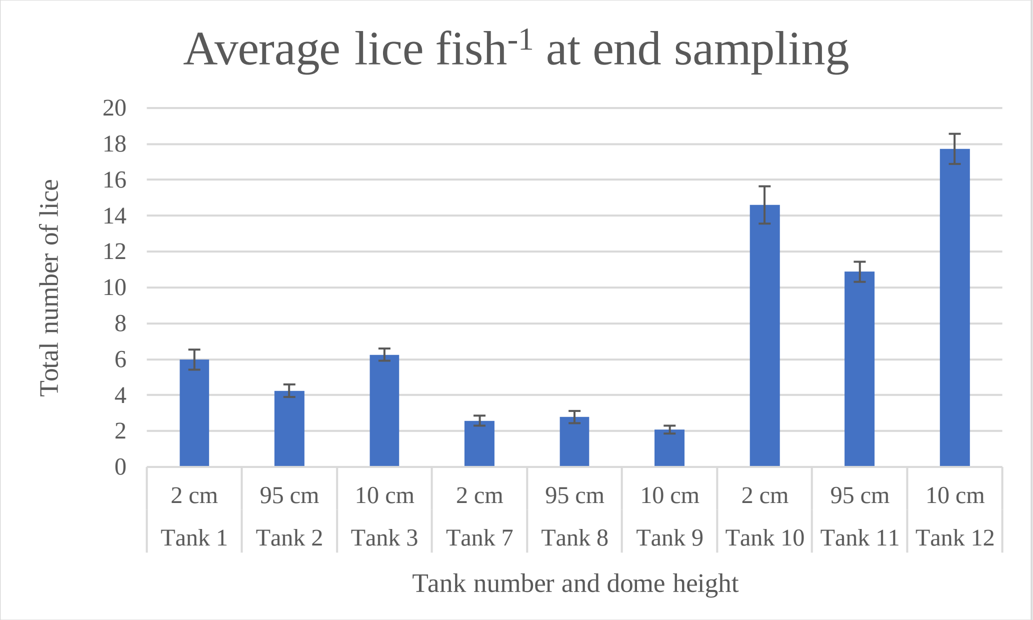


Fig. 4.18: Average lice numbers fish^{-1} ± SD *21 days after infection in tanks, distinguishing between tanks. Lice were counted on 40 fish in each tank.*

4.5.2 Surface behaviour during exposure to salmon lice copepodids

Surface behaviour can indicate salmon lice infection success. Comparison of four observations before infection and one observation during infection form the basis of immediate behavioural response to salmon lice infection. This is not to be confused with lice response period (Section 4.3.2), considering four observations pre infection and 31 observations after.

Table 4.12: Results from ANOVA comparing the full GLMM to the null- model for jumping and rolling. When results are statistically significant, null- hypothesis is rejected and the full model tested. Significant p- values are indicated with *.

Parameter	**$\chi 2$**	***p***
Jump	16.74	0.002
Roll	2.28	0.68
Burst	65.6	<0.001*
Twitch	62.62	<0.001*
Side- swimming	41.32	<0.001*

4.5.2a Jump

Jumping behaviour was significantly affected during exposure to infective copepodids (Fig. 4.12). The GLMM showed no significant difference between dome heights ($p > 1.78$ for both heights) or groups ($p = 0.49$), but time of sample affected distribution of jumping (estimate = 0.402, $p < 0.001$), indicating that all tanks increased jumping behaviour during exposure to infective lice. Fig. 7.2 (Appendix) illustrate the increased jumping behaviour when infected with lice, although at different frequencies between groups.

4.5.2b Rolls

Roll behaviour was not affected by either sample time, dome height or group, illustrated in Fig. 4.7 showing no behavioural change during lice infection.

4.5.2c Burst

Frequency of burst swimming was statistically significant with treatment as a factor (Table 4.12), with burst frequency being significant between groups (estimate = 0.28, $p = 0.002$). The GLMM indicated that sample period affected burst behaviour (estimate = 1.66, $p < 0.001$), which is illustrated in Fig. 4.8, showing a peak in activity observed during lice infection.

4.5.2d Twitch

Distribution of twitch behaviour was statistically significant (Table 4.12). The GLMM indicated that twitch behaviour was highly affected by the addition of lice to the tank (Table 4.13) compared to pre-infection frequencies ($p = 0.0001$), visualized in Fig. 4.9. Results showed differences in twitch behaviour between Groups (estimate = 1.042, $p < 0.0001$), but dome height did not have a significant effect ($p > 0.3$).

Table 4.13: Average twitch frequency min^{-1} for four observations before and one observation during infection. Presented as observations distinguished between tank heights.

Dome height	Avg twitch min^{-1} before infection	Avg twitch min^{-1} during infection
2 cm	0.27 ± 0.05	0.91 ± 0.06
10 cm	0.17 ± 0.09	0.87 ± 0.06
95 cm	0.17 ± 0.09	0.96 ± 0.06

4.5.2e Side swimming

Difference in distribution of side swimming was statistically significant with treatment as a factor (Table 4.12), with sample period as significant factor for behaviour (estimate = 0.737, $p < 0.0001$), as illustrated in Table 4.14.

Side swimming behaviour did not differ significantly between groups ($p = 0.9$), although pattern of difference between before and after exposure to lice was the same among groups, only with highest frequency in G3, thereafter G2 and G1, respectively (Appendix Fig. 7.9). Behaviour did not differ significantly between dome heights ($p > 0.34$ for both 10 cm and 95 cm domes).

Table 4.14: Average side swim frequency min^{-1} before and after salmon lice were introduced in tanks distinguished by tank height. Results show that side swimming was almost absent until lice were introduced in tanks.

Dome height	Avg twitch min^{-1} before infection	Avg twitch min^{-1} during infection
2 cm	0.02 ± 0.02	0.37 ± 0.06
10 cm	0.03 ± 0.02	0.32 ± 0.04
95 cm	0.01 ± 0.01	0.43 ± 0.04

Considering long term observation of behaviour during LRP (see section 4.3.2), jumping and rolling frequencies when lice reached pre-adult were highest in the group with the highest lice levels (G3) and lowest in group with lowest infection (G2) (Appendix Fig. 7.2 and 7.3, respectively). This indicates that jump and roll frequency is directly linked to infection success, suggesting that pre-adult stage of salmon lice initiate increased jump and roll frequency, as suggested by Furevik et al. (1993).

5 Discussion

Experimental salmon experienced limited surface access through a surface based air-dome (Ø = 1 m) in indoor tanks (Ø = 3 m). Three different dome heights were tested (2 cm, 10 cm, 95 cm) to observe if dome height affected behaviour and welfare. The hypothesis suggested a lower dome height to reduce welfare and inhibit the salmon´s possibility to express natural behaviour. Considering the technical challenges with constructing counterweight for an air-dome of a great volume, aim was to find minimized dome height where salmon can express normal behaviour and welfare is ensured. To provoke natural behaviours, salmon lice were introduced in tanks.

Overall, observations indicate that jumping and rolling behaviour was affected by dome installation as activity in all tanks decreased immediately after installation. Only jumping behaviour was significantly affected by a particular dome height, with lowest frequency in tanks with 2 cm domes.

After lice infection, dome height as factor was statistically significant for behaviours jump and burst, with 2 cm tanks ranging highest only for burst swimming while 10 cm had highest frequency of jumps. Response pattern to lice infection are, however, comparable between tanks for most behaviours, indicating that dome height has little influence on behaviour.

Welfare samples showed that the indicators of eye bleeding, scale loss, fin bleeding and fin split were statistically significant between dome heights. However, only scale loss occurred in highest frequencies in tanks with 2 cm domes. For eye- and fin bleeding indicators, 2 cm tanks scored lowest, while 95 cm tanks scored highest. Results suggest that difference between dome heights are not crucial as much as the presence of a dome construction for welfare.

5.1 Growth

The three groups were held in tanks for different time length. G1 were in tanks for 56 days, G2 for 78 days and G3 for 92 days, which is an explanation why growth rate was higher in G3. For all groups, weight was, however, lower at sampling post- than pre-install. Sampling post-installation (pre-infection for G1) was conducted at 31.07.2020 for all groups, which overlapped with the ongoing bacterial infection in tanks. Thus, this infection could have affected growth in all tanks. Length increased in all tanks during the trial, and as with weight, length increased most in G3 and least for G1. Considering both weight and length, growth seem to vary randomly between dome heights and therefore no correlation between growth and treatment was apparent.

Initial fish weight of trial fish was 279.34 ± 8.28 g (mean ± SE). SGR varied between 0.19-0.65, with 55 % of tanks recording an SGR between 0.35-0.39. This is comparable to research conducted by Korsøen et al. (2012) who found SGR = 0.22 after 30 days submergence. Oppedal et al. (2020) recorded SGRs = 0.69, 0.94 and 1.23 based on 100 randomly netted fish (averaging between 0.5-0.8 kg) after 41 days of submergence. Despite higher growth potential in smaller fish, SGR was higher in trial conducted by Oppedal et al. (2020), holding bigger fish. Fjelldal et al. (2020) reported an SGR of 0.42 for fish infected with salmon lice, which was higher than SGR in 8 out of 9 tanks in this trial. Compared to both dome studies and lice studies, SGRs in this trial are overall poor. Since there was no control group lasting the whole trial period, it is not clear how domes affected growth under these experimental conditions. Results, however, suggested little difference between dome heights, which indicates that other factors must have affected growth. Hand feeding may have reduced growth potential, and bacterial infection may have stagnated growth (Pettersen et al. 2015).

5.2 Mortality

Total mortality was 24 %, excluding fish euthanised for sampling, which is high, especially for a trial lasting for 56-92 days. Research suggests that a salmon's swim bladder will be emptied after 22 days of submergence (Dempster et al. 2009; Korsøen et al. 2009). 22 days after domes were installed was July 28th, which overlapped with the period with highest mortality rates (July 26th-August 12th 2020, trial day 20-37). Fish who did not learn to refill swim bladder in the dome could possibly suffer during this period. Dead fish found during this time looked weak and had wounds on the sides, which indicated that they were sick. Veterinarian checks concluded a bacterial infection on August 6th, and one may assume that the infection affected mortality rates for a period before infection was identified. How long infection had been present in fish groups before diagnosed by the veterinarian is unknown, and whether some fish died as a result of not adapting to refill in dome is therefore uncertain. The veterinarian report suggested that the bacterial infection was caused by handling of the fish during transfer into the experimental tanks, and was not likely to be a result of trial set up (i.e. presence of domes).

An important find was, however, that a cage structure like in this trial will not give sick fish the opportunity to heal or recover, and will affect a weak fish negatively. In commercial surface-based sea cages, it is recommended to minimize equipment for the fish to potentially come in contact with. Submerged cages will, however, require equipment that can be a threat for salmon in the cage. In addition to the dome itself, the fish is surrounded by net, even at cage top, which leads to increased risk for damaging skin and fins, and increasing scale loss as they search for surface access. Since the purpose of submerging a sea cage is to avoid certain welfare threats, e.g. salmon lice, it is not practical to bring submerged sea cages to the surface to check welfare status of the fish manually. Submerged farming therefore has a critical requirement for equipment that ensures monitoring and reporting of welfare and lice counting in submerged position, throughout production cycle or for as long as welfare state allows it.

5.3 Behavioural observations

5.3.1 Dome learning period (DLP)

During the dome learning period (DLP), four observations were conducted before dome were installed, and 14 observations after, all distinguished between jumps and rolls min^{-1}. Additional observation relevant for behaviour was also reported.

After domes were installed in tanks, jump frequency decreased immediately, and stagnated at a lower level for the remainder of this period (Fig. 4.4). Fish with 95 cm domes exhibited the least jumps, while 2 cm tanks had highest frequency of jumps. Considering 95 cm domes have the most space, this might indicate that a lower dome height stresses the fish, who starts jumping as a response. Increased jumping and rolling activity are observed as a stress response by Furevik et al. (1993), and can suggest why this activity was observed after domes were installed.

Initially, roll frequency averaged 0.48-0.87 rolls min^{-1}, distinguished by dome heights. First observations after domes were installed, fish in 2 cm dome tanks averaged 3.40 rolls min^{-1}, while 10 and 95 cm averaged 0.73 and 0.15, respectively. Furevik et al. (1993) observed roll activity in surface cages (3 000 fish cage^{-1}) and suggest 4.53 rolls min^{-1} as normal frequency, which is higher than all individual roll observations conducted during DLP in this trial. Rolling is referred to as refilling behaviour, and considering observations of tilted swimming and increased swimming speed (both behaviours observed strategies in species for compensating for negative buoyancy (Huse and Ona 1996)), on trial day 2, roll frequency can indicate insufficient refilling success in domes at this time. Tilted swimming was, however, not observed after 17 days with domes.

Subsequently after installation, 2 cm dome tanks exhibited a decreased roll frequency in the following observations. The large standard error on average roll frequency in 2 cm tanks highlights the large variability within the same dome height (Fig. 4.5). 2 weeks after installation, roll behaviour increased in all tanks, suggesting that fish were successfully adapting to dome, and the frequency of roll behaviour was restored to initial levels. There was no significant difference between dome heights, suggesting that different dome height does not affect roll activity as much as the presence of a dome considering that normal frequencies as suggested by Furevik et al. (1993) is much higher than in this trial.

Observations showed that even one day after installation of domes, fish in 2 cm domes showed a controlled swimming behaviour towards the dome area, slowing down when getting closer. This behaviour was then observed regularly throughout the trial, exclusively in 2 cm tanks, and might indicate that fish can adapt to a limited dome height and control behaviour accordingly. Despite this observation, 2 cm domes had the highest percentage of jumps into lid; this was somewhat expected since jumping and rolling behaviours represents different needs (surface searching and swim bladder refilling, respectively) which likely cannot be replaced by each other. Although highest percentage of jumps into lid was observed in 2 cm tanks, the most severe jumps were observed in 10 cm tanks. This suggests that domes with 10 cm height allows fish to execute normal jumping behaviour without hitting lid, while some jumps are more powerful and will lead to fish colliding into the roof. The transparent roof on the dome might have been more difficult for the salmon to distinguish and identify, resulting in fish not recognizing the presence of a lid and mistakenly executing full distance jumps. This less controlled behaviour could lead to more physical damage than in a 2 cm dome.

On the second day after installation, one fish looked frustrated, swimming against the dome and conducting aggressive behaviour against the lid (dome roof), like actively hitting the lid, was observed. Movement was repeated 5-7 times in a row, and looked like aiming to break the lid. First observation of this behaviour overlapped with observation of tilted swimming in tanks. Throughout the trial, this behaviour was observed once in 10 and 2 cm dome tanks. This desperate movement could indicate that fish were frustrated and seeking wider surface access. This behaviour has, however, not previously been reported for submerged or air-dome cage studies.

Four days after installation, fish were observed to break surface in the dome area with their dorsal fin and tail. Behaviour was observed twice in 95 cm tanks and once in 2 cm tank during DLP. Since behaviour occurred in low frequency, suggestion is that behaviour also was conducted in 10 cm tanks, although not whilst behavioural observation was conducted in tank of respective dome height.

The same behaviour has been observed by Korsøen et al. (2012), referred to as environmental scanning.

By the end of DLP, disoriented fish were observed in tanks of all dome heights. Within the same period of time, weak fish were observed to swim in dome area without interacting with the surface (i.e. swim bladder refilling behaviour), also looking disoriented. One weakness considering this observation is the uncertainty whether behaviour was a result of treatment or disease. However, mortality did not accumulate before July 26th (trial day 20), and indications are that bacterial infection is an important contributor for mortality.

5.3.2 Lice response period (LRP)

Lice response period (LRP) started at different times since all groups were infected at different times. G3, being infected last, experienced the longest lasting trial (92 days), and potential damages from tank and tank set up would be more prominent in G3 and G2 than G1. LRP started with four observations before lice were introduced in tanks, and 27 after infection. Observations distinguished between jumping and rolling (into lid/ no lid) and twitching, bursting and side swimming min^{-1}.

Jump frequency increased in all tanks when lice were introduced and averaged between 0-1.2 jumps min^{-1} over the 30 minute infection period. Same behaviour with comparable frequencies was observed by Bui et al. (2018b; 2018c) with frequencies 0.14-0.58 and 1.2 jumps min^{-1}, respectively, for domesticated salmon. All groups experienced a peak in frequency when lice reached pre-adult stage, as observed by Furevik et al. (1993), and activity levels did not recover over the different lice stages (Fig. 4.6). Jump frequencies were significantly higher in 10 cm dome tanks throughout the period, and lowest jump frequency was observed in 2 cm dome tanks. 82 % of all jumps in 2 cm tanks ended in collision with the lid, and 62 % in 10 cm, suggesting that both dome heights are too low for the fish to express their natural behaviour. There are, however, no indications that welfare indicators were worse in 2 cm domes compared to 95 cm domes, indicating that fish in 2 cm dome tanks can adapt to a limited dome height and be able to control jump behaviour accordingly.

Rolling frequency was stable comparing activity before and during infection, but activity increased overall when lice reached pre-adult. This observation was expected, as salmon lice moulting to pre-adult is stated to cause stress reaction in salmon (Grimnes and Jakobsen 1996), which respond with increased surface activity (Furevik et al. 1993).

After lice reached the mobile stages, overall roll frequency was highest in 2 cm and lowest in 95 cm dome tanks (Fig. 4.7). Rolling was probably more prevalent in 2 cm domes because the dome height limited their capability for jumping, suggesting that rolling behaviour partly replaced jumping behaviour (referred to as surface searching). According to Fig. 4.6, fish do, however, jump despite the limited area in the dome. Group was a significant factor for rolling behaviours, although all three groups showed same response pattern of increased rolling activity when lice reached pre-adult (Appendix Fig. 7.3). Highest frequencies were observed in G3 and lowest in G2.

Distribution of twitch behaviour was statistically insignificant, although frequency varied between groups (Appendix Fig. 7.5) with G2 showing lowest activity. Observations, however, suggest salmon lice infection to affect twitch behaviour, as frequency for all dome heights increased after infection (Fig. 4.9), which is also observed in other trials (e.g. Bui et al. 2018b).

Increased burst swimming is suggested to be a strategy to reduce lice attachment (Bui et al. 2018a). Response pattern observed in this study show increased frequency during infection (Fig. 4.8), average frequencies ranging between 0.9-2.7. Results are comparable to domesticated salmon in normal tanks, averaging with 2.3 and 5.6-6.8 bursts min^{-1} (Bui et al. 2018b; 2018c). Burst swimming frequency was significantly different, although not strongly, for domes of different heights with highest frequency in 2 cm tanks.

Burst swimming recovered one day after infection (Fig 4.8), and plateaued at a slightly higher level than initial frequency. Frequencies for all dome heights during pre-adult and adult stages of the lice were comparable to results reported by Bui et al. (2018a), averaging at 0.2 bursts min^{-1} for non-manipulated and 0.8 bursts min^{-1} for behaviourally-manipulated salmon.

Side swimming occurrence is also apparent to be highly affected by lice infection (Appendix Fig. 7.6) as frequency increased both during exposure to infective copepodids and again when lice reached pre-adult (Fig. 4.10). Side swimming behaviour is, however, not observed in other trials.

5.4 Welfare

A random sample of 5-12 % of total fish (20 or 40 individuals) were evaluated using SWIM (Stien et al. 2013) or an adapted version of SWIM in each tank per sampling. Evaluating >5 % of randomly netted fish is an indicator for general welfare in tank. When counting lice in commercial production, where each cage holds up to 200 000 fish, it is required by law to count lice on at least 20 randomly netted fish in each cage at the farm (Forskrift om lakselusbekjempelse, Attachment 1, 2017), thus is a far smaller percentage of the total biomass. One can therefore suggest >5 % fish a representative sample when highlighting the importance of random selection.

Welfare scores from sampling pre-installation were used as control and were not compared to results from the following three samples as scoring range differed. Initial welfare scores were evenly distributed between tanks (Appendix Fig. 7.7). Results, however, showed suboptimal condition of fins, scale loss and skin bleeding, averaging between 2.5-3.6, 2.8-5.3 and 1.6-2.4, respectively.

After sampling pre-installation, fin damage was divided into three subcategories, scoring both fin erosion, -bleeding and -split. This change made sampling pre-installation not suited for comparison to the following three samplings. Change was, however, considered to be more pragmatic, as a more detailed scale would be more comprehensive and give more functional results. During samplings post-installation, pre-infection and end sampling, fin condition improved, although fin split increased in severity (Fig. 4.16A). Findings from Korsøen et al. (2009) suggest air-dome construction and roof net to cause increased fin damage as fish swim into them searching for surface access. Comparison between post-installation and end sampling, however, show improved condition within dome heights (Fig. 4.16). Developmental improvement of condition is observed in previous research on submerged cages with air-dome (Oppedal et al. 2020) and in snorkel cages (Stien et al. 2016), indicating that salmon adapt to limited surface area and are not constantly searching for surface. Statistical comparison between sampling pre-infection and end, however, suggest dome height as an influential factor for the development of fin split-and bleeding, with highest frequency in 95 cm dome tanks for both indicators. When considering fin condition, presence of the dome structures was more relevant for fin damage than the dome height.

Scale loss scores were initially high at the pre-installation sample (averaging between 2.8-5.4, scale ranging 1-8) (Fig. 4.15B). Score range was changed from 1-8 to 1-6 for the last three samplings, meaning comparison between initial and end scores was not possible. Changes were, however, considered to be necessary for scoring accuracy of condition. Comparing sampling pre-infection and end, dome height was found to be statistically significant in affecting condition, 2 cm domes scoring highest. Significance was, however, not very strong between 2 and 10 cm domes ($p = 0.02$), suggesting that at a dome-height where lid is necessary, there is greater surface for the salmon to crash into, which cause more scale loss. Notably, initial scale loss scores were high across tanks prior to dome installation, and lack of change in scores in subsequent samplings suggest that being held submerged with air-omes does little to facilitate recovery in fish. Scale formation is an important phase of healing, and has approximately normal function 36 days after scale loss (Rydal Sveen et al. 2019), which indicate that no healing of scale loss in this trial is connected to construction.

Skin bleeding was initially prevalent in fish just after transfer into the experimental tanks, but occurred in decreased frequencies in the last three samplings. This indicator was not affected by dome height, and scores decreased at the end sampling suggesting that lice infection did not aggravate severity and frequency of skin bleeding appearance. Generally considering skin status, Oppedal et al. (2020) observed no negative affect on skin status from a 3 m diameter dome for 5-7 weeks submergence. Results might indicate that a smaller dome diameter affect skin condition negatively, although the poor initial scale loss and skin bleeding condition in this trial must be considered an influencing factor.

Prevalence of deformity, cataracts and gill damage were generally not observed throughout the study, suggesting that air-domes and dome heights does not affect or induce these indicators.

Snout damage was considered statistically insignificant between treatments, although condition got worse from post-installation to end sampling (Fig. 4.15C). Results was not fully covered by analysis comparing only result from pre-infection and end sampling. Group and sample time did, however, significantly impact snout condition. Snout damage occurred in highest frequency in G3 relative to G1 (estimate = -0.799) and G2 (estimate = -0.565, $p < 0.001$ for both). Results indicate that time spent in tank with dome affected snout injuries and severity, which was also found by Korsøen et al. (2012, 2009) in submerged sea cages with air-domes. The same condition is observed in snorkel cage trials (e.g. Stien et al. 2016), suggesting that salmon damage themselves from the roof net or dome/snorkel installation when searching for surface. Research by Macaulay et al. (2020), however, observed no snout injuries on fish that were introduced to domes in freshwater tanks then transferred to submerged sea cages with same dome size (i.e. in dome-acclimated fish compared to dome-naïve fish). Further research on dome-height should focus on early introduction to rearing environment, proposing that young salmon better can develop behavioural adaptation to environment (Salvanes et al. 2013; Braithwaite and Salvanes 2005).

Eye bleeding was initially observed in low frequencies, and analyses revealed statistical differences between groups at the first sampling; however, this difference was negligible and represented little biological significance. Over the trial duration, the occurrence of eye bleeding increased. Considering increased occurrence of both dorsal fin damage and snout injuries, it is possible that surface searching salmon scrape against net roof, which affected eye bleeding occurrence. Comparing scores pre-infection and trial end, negative condition occurred in the highest frequency in 95 cm domes, indicating that occurrence of eye bleeding did not increase with lowered dome height. G1 experienced significantly higher frequencies of condition in first sample, but lower frequencies in last sample, indicating that group (time spent in trial tanks) was not relevant for occurrence of eye bleeding.

Wound was included as indicator after first sampling since this condition was observed on several fish. Prevalence of negative scores in sampling post-infection was, however, low and averaged between 1.00-1.15. Group was an influential factor in wound scores between sampling pre-infection and end, with G3 slightly more severe than G2, indicating that wounds are less likely to heal in tanks with domes, but instead becomes worse over time. However, fish were diagnosed by the veterinarian to be infected with bacterial disease during trial. Considering wound as an indicator for disease, observations of wound at sampling pre-installation indicates that fish were weak already before domes were installed in tanks.

Previous research suggest stocking density relevant for welfare and suggest ideal stocking density to be 22 kg m^3 (Turnbull et al. 2005). Lower density is proposed to lead to increased physical damage and reduced growth (Jørgensen et al. 1993). Based on these results, stocking density in trial tanks was too low during the whole trial (14.31 kg m^3 initially) considering that fish regularly were killed for welfare evaluation as growth increased with time.

Feeding regime is also suggested as important factor for welfare (Huntingford et al. 2006), with ration size (Cañon Jones et al. 2010) as potential influencing factor in this trial. Unpredictive feeding can result in increased aggression among individuals, and therefore affect welfare negatively (Huntingford et al. 2006). Aggression was not observed between individuals, but could still have happened as observations normally were only conducted 1 hour per 96 hours. Aggressive behaviour was, however, observed against the dome construction, although this is suggested as a response to the presence of a dome with lid, limiting their jumping

General condition of fish, considering both behaviour and welfare, appears to be affected by the bacterial infection when present. This adds an uncertainty as to whether the infection or treatment provoked different reactions in the fish, however all fish experienced bacterial infection and provides less of a confounding factor when interpreting results of dome height treatment. Considering welfare concerns, there are no indications that a higher dome is more optimal than a lower dome, proposing that 2 cm domes are sufficient for behaviour expression and welfare. Further research with low domes should be tested at a larger scale and in sea cages where natural environmental conditions are likely to influence behaviour and welfare in other ways.

5.5 Salmon lice response

Infection success was different between groups 1, 2 and 3, averaging 5.5, 2.5 and 14.4 lice fish^{-1}, respectively (Fig. 4.18). Comparing four behavioural observations before and one during infection, behavioural observation during lice infection suggests potential behavioural changes as an immediate response to infection.

Behavioural changes were altered by infection, jumping, bursting, twitching and side swimming behaviours different to pre-infection levels. These observations are supported by previous literature reporting that salmon initiate a behavioural response to lice infection (Bui et al. 2018a). Salmon were observed to be irritated, and looked like trying to shake off the irritation in desperate movements, an observation that occurred particularly during exposure to infective lice, independent of dome height (Furevik et al. 1993).

Distribution of side swimming behaviour was suggested as significant only considering time of sample (before/ after infection). Occurrence of side swimming increased with increased group number, proposing that longer time spend in tank can result in higher frequency (Fig. 4.10), but side swimming is not observed in previous trials considering behavioural development during lice infection (e.g. Bui et al. 2018b; 2018c; Furevik et al. 1993).

Long-term observations during DLP suggest jumping and rolling behaviour to be directly linked to lice abundance, since activity occurred in highest frequencies in tanks with highest infection success. All groups experienced increased frequencies when lice reached pre-adult, as suggested by Furevik et al. (1993).

Behavioural observations during lice infection in submerged sea cages are important as lice are also found at 10 m depth (Olafsen et al. 2019; Olafsen and Tjølsen 2020), therefore submerged fish are likely to still acquire infections, although theoretically, less intensely than standard cages. During lice infection, there was no statistical difference in behaviours between dome heights, indicating that fish with all three dome heights responded naturally when infected with lice. This find is relevant since it is statutory to ensure that dome constructions allow the farmed salmon to execute normal behaviour always (Dyrevelferdsloven §23, 2018), also when introduced to a stressor i.e. salmon lice. Considering welfare evaluations pre-infection and at trial end, there was no clear difference between dome heights, and 2 cm domes is therefore suggested to be sufficient height for salmon in submerged sea cages.

5.6 Commercial relevance

Increased challenges connected to surface-based aquaculture, with salmon lice as major contributor (Taranger et al. 2015), has led research to increasingly focus on preventive measures against lice. Complex constructions aiming to reduce encountering with salmon and salmon lice have been developed, e.g. skirts (e.g. Grøntvedt et al. 2018; Stien et al. 2018), snorkels (e.g. Geitung et al. 2019; Oppedal et al. 2017) and submerged cages with air-domes (e.g. (Korsøen et al. 2012; Macaulay et al. 2020; Olafsen and Tjølsen 2020). Denying surface access in submerged cages incurs a requirement for salmon to be able to regulate their buoyancy using alternative methods than through surface access . Studies suggests that farmed salmon can adapt to refilling in air-domes (Korsøen et al. 2012; Macaulay et al. 2020), and this is supported by surface behaviour observations in this study. Behavioural observations indicated that salmon can adapt to refill in 2 cm domes, suggesting that 2 cm dome height is sufficient for conducting normal behaviour.

Olafsen et al. (2019) submerged fish to 15 m depth with air available from a tarpaulin air-dome in center of cage, kept stable by tubes made out of PE plastic (EgersundNet et al. 2020). Results, however, showed salmon lice in all stages at trial end, indicating that lice is present at 10 m depth (Olafsen et al. 2019; Olafsen and Tjølsen 2020). Presence of lice at these depths, sets requirements for fish to be able to express behavioural responses to infection. In the current study, 2 cm domes were sufficient for salmon to express stress behaviour without reduced welfare compared to higher domes. However, considering the potential for lice to adapt to chemical treatments (Ljungfeldt et al. 2017; Igboeli et al. 2012), there is also a rising concern for resistance to non- chemical control methods (Coates et al. 2021). Considering the adaptation capacity of lice, one should not introduce them to the depth of submerged sea cages, which would create risk of high infection pressure there as well. Ideally, salmon should be submerged immediately after being transferred to sea. One potential solution is to grow smolts bigger before transferring them to sea water, and minimizing production cycle in sea water. Further research is needed on how to best avoid lice infection pressures with fluctuating distributions (i.e. changing halocline depths) in submerged sea cages.

From a construction perspective, results indicating that 2 cm dome height is sufficient for conducting normal behaviour is a positive outcome. Domes with greater height also have greater volume, generating more buoyancy. Increased buoyancy leads to a need for increased size of counterweights to maintain stability in the water column. After first production cycle of fish in Atlantis cage, farmers reported that the air-pockets (Ø = 2 m, H = 30 cm) were too heavy, in terms of handling with available equipment, which resulted in challenges connected to HMS (Olafsen et al. 2019). Results from the current trial indicating that 2 cm height of dome is sufficient for refilling could lead to a potential reduction in counterweight from 0.94 m^3 for a dome height 30 cm, to 0.063m^3 for 2 cm dome height. For a dome with Ø = 1 m, weight would be 2 kg and 231 kg for dome heights 2 cm and 30 cm, respectively. Construction implemented by Olafsen et al. (2019) is relatively uncomplicated, and if functional while ensuring production of salmon with good welfare, it can thus be practical for several locations. A reduced dome height might not set as high requirements for equipment and machinery for maintaining and manipulating submerged cages.

6 Conclusion

Based on behavioural observations and welfare evaluations, results do not clearly indicate whether salmon could successfully refill their swim bladder. Tilted swimming, which is a clear indicator for negative buoyancy, was not observed after 17 days with domes. Rolling behaviour was, on the other hand, observed in lower frequencies than suggested as normal and could indicate inadequate refilling. Results do, however, suggest that fish in a 2 cm dome can express natural behaviour when being exposed to stressors in the same frequency as in 95 cm domes. During salmon lice infection, increased activity was observed, which was not affected by dome height. These results are relevant since salmon lice are suggested to be present at 10 m depth and deeper, thus likely to be occasionally affecting salmon in submerged cages.

During this trial, welfare condition was likely to be affected by bacterial infection during dome learning period, although only short-term as most welfare indicators did not increase in severity after bacterial disease was treated. The only indicators with increased occurrence towards trial end were snout and fin split, which is also observed in previous research on depth-based principles (e.g. Stien et al. 2016; Korsøen et al. 2012), and is therefore not linked to bacterial infection. Increase in fin split scores was significant from pre-infection and end sampling, but a worsened condition between samplings was, however, not observed in all tanks. Decreased snout condition was strongly significant pre-infection to and, and is suggested to be affected by dome, but not by dome height. Considering both behaviour and welfare, the limiting factor for salmon in submerged cages with an air-dome is rather the presence of a dome-construction than dome height.

Results from this trial indicate that 2 cm dome is sufficient for fish to express normal behaviour. It is, however, suggested to conduct similar small-scale trials with healthy fish to reveal potential affects the bacterial infection had on welfare- and behavioural results. It is also suggested to increase fish density in further research to ensure that potential negative effects from low density are revealed. Further research should observe if early introduction to air-domes in freshwater tanks can improve refilling behaviour in a low dome once transferred to sea.

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7 Appendix

Table 7.1: Overview over previous studies using air-dome in submerged sea cages. Dome areas are used as basis for calculations in Fig. 2.1.

Area	Authors	Air-dome dimension
0.28 m^2	Macaulay et al. (2020)	Cylindric. Ø = 0.6 m
0.8 m^2	Nilsson et al. Unpubl.	Cylindric. Ø = 1 m
3.1 m^2	Nilsson et al. Unpubl	Cylindric. Ø = 2 m
4.9 m^2	Olafsen and Tjølsen (2020)	Cylindric. Ø = 2.5 m
7.1 m^2	Nilsson et al. Unpubl. Oppedal et al. (2020)	Cylindric. Ø = 3 m Octagonal. Ø = 3 m
12.6 m^2	Nilsson et al. Unpubl.	Cylindric. Ø = 4 m
***50.25* m^2**	EgersundNet et al. (2020)	Cylindric. Ø = 8 m

*Table 7.2: Mortality in all tanks during trial period. Marks * indicate that 20 or 40 fish were sacrificed for welfare sampling.*

Dato	**Tank**									**Total**
	1	**2**	**3**	**7**	**8**	**9**	**10**	**11**	**12**	
01.07.2020		1								1
02.07.2020										0
03.07.2020			1							1
04.07.2020										0
05.07.2020										0
06.07.2020*	20	20	20	20	20	20	20	20	20	180
07.07.2020										0
08.07.2020										0
09.07.2020										0
10.07.2020										0
11.07.2020										0
12.07.2020										0
13.07.2020										0
14.07.2020	1									1
15.07.2020										0
16.07.2020										0
17.07.2020										0
18.07.2020										0
19.07.2020										0
20.07.2020		4								4
21.07.2020	1	1								2

22.07.2020		4		1	2					7
23.07.2020		5								5
24.07.2020	3	3		2			3			11
25.07.2020										0
26.07.2020	**6**	6		6	**8**	3	4		6	39
27.07.2020		6		1	1			2	5	15
28.07.2020	1	5	1	1	2		3		3	16
29.07.2020	4	5	4	2	3	**6**	4	3	5	36
30.07.2020	4	3	6	**8**	5	2	**5**	**4**	10	47
31.07.2020*	21	20	20	20	21	20	20	20	20	182
01.08.2020										0
02.08.2020	**6**	**7**							**12**	25
03.08.2020		4	3	2	4	5	4	**4**	5	31
04.08.2020		2	2							4
05.08.2020	1	2	2			1			11	17
06.08.2020	4	2	3	1		1	2		1	14
07.08.2020		2	4		1				1	8
08.08.2020	1		**8**			1		1	3	14
09.08.2020	3	5	6	4		1		1	2	22
10.08.2020	1	2	4	2		1		1	2	13
11.08.2020	1	3	4		1		3			12
12.08.2020	1	2	1				2	1	1	8
13.08.2020		1					1	2	1	5
14.08.2020		2							2	4
15.08.2020			3							3
16.08.2020										0
17.08.2020										0
18.08.2020							1			1
19.08.2020		1	2							3
20.08.2020									1	1
21.08.2020										0
22.08.2020										0
23.08.2020	1		1							2
24.08.2020							1		1	2
25.08.2020			1	1						2
26.08.2020										0
27.08.2020									2	2
28.08.2020										0
29.08.2020										0
30.08.2020							1			1

31.08.2020*	40	40	40	20	20	20	1			181
01.09.2020										0
02.09.2020						1				1
03.09.2020										0
04.09.2020										0
05.09.2020										0
06.09.2020										0
07.09.2020										0
08.09.2020										0
09.09.2020										0
10.09.2020										0
11.09.2020										0
12.09.2020										0
13.09.2020										0
14.09.2020										0
15.09.2020										0
16.09.2020										0
17.09.2020										0
18.09.2020										0
19.09.2020										0
20.09.2020										0
21.09.2020				1			2			3
22.09.2020*				40	40	40	21	20	20	181
23.09.2020										0
24.09.2020										0
25.09.2020										0
26.09.2020										0
27.09.2020										0
28.09.2020										0
29.09.2020										0
30.09.2020										0
01.10.2020										0
02.10.2020										0
03.10.2020										0
04.10.2020										0
05.10.2020										0
06.10.2020										0
07.10.2020										0
08.10.2020										0
09.10.2020							1			1
10.10.2020										0
11.10.2020										0

12.10.2020										0
13.10.2020*							40	40	40	120
Total	**120**	**158**	**136**	**132**	**128**	**122**	**139**	**119**	**174**	1228
Mortality excluding SWIM	***40***	***78***	***56***	***32***	***28***	***22***	***39***	***19***	***74***	***388***

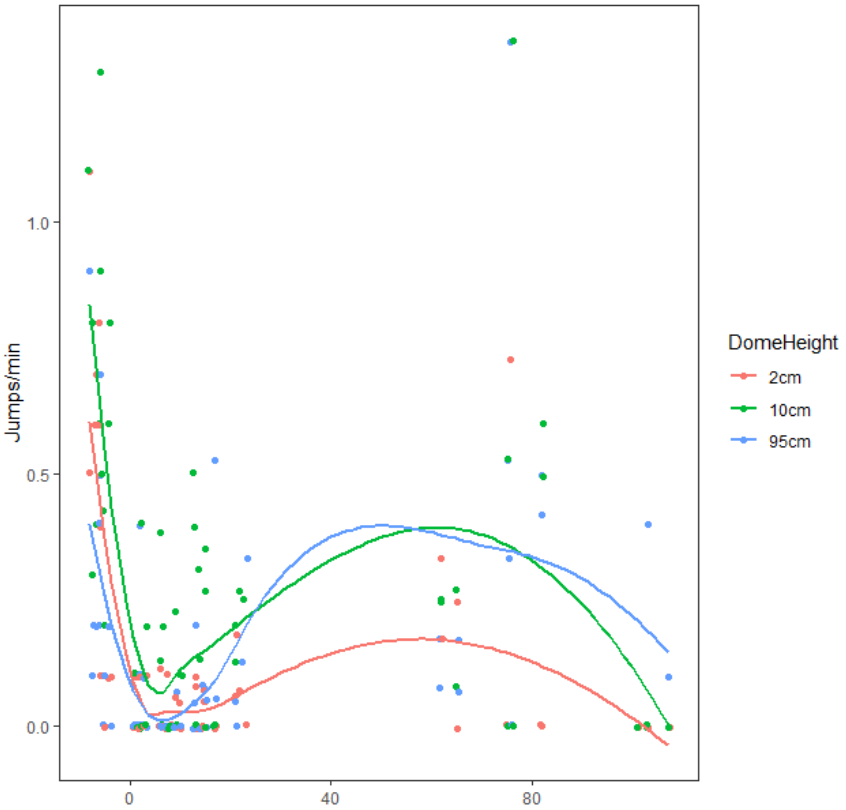


Fig. 7.1: Average distribution of jumps min^{-1} distinguishing between dome heights only. Domes were installed on day 0. Response pattern between heights are comparable, although at different frequencies.

Table 7.3: Results of the POLR model versus the null model for welfare indicators in sampling pre-installation. Analysis doesn´t work for indicators deformity, snout, cataracts, skin bleeding and gills because the scores are so similar. Deformity, snout, cataracts and gills initially scored low.

Welfare indicator	**Model**	**AICc**
Eye bleeding	**M0: 1 + Group**	**89.45**
	M1: Dome.height + Group	89.88
Scale loss	**M0: 1 + Group**	**418.98**
	M1: Dome.height + Group	420.96
Fin	**M0: 1 + Group**	**418.98**
	M1: Dome.height + Group	420.96

Table 7.4 Results of the POLR models versus the null model for welfare indicators in pre-infection compared to end sampling. Analysis doesn´t work for indicators deformity, cataracts and gills because the scores are so similar, all four indicators initially scoring low.

Welfare indicator	**Model**	**AICc**
Eye bleeding	M0: 1 + Group	712.90
	M1: Dome.height + Group	**708.78**
	M2: Sample + Group	714.32
	M3: Dome.height + Sample + Group	719.20
Scale loss	M0: 1 + Group	1560.91
	M1: Dome.height + Group	1554.84
	M2: Sample + Group	1554.23
	M3: Dome.height + Sample + Group	**1547.62**
Skin bleeding	M0: 1 + Group	1444.91
	M1: Dome.height + Group	1448.66
	M2: Sample + Group	**1419.66**
	M3: Dome.height + Sample + Group	1423.43
Wound	M0: 1 + Group	1444.91
	M1: Dome.height + Group	1448.66
	M2: Sample + Group	**1419.66**
	M3: Dome.height + Sample + Group	1423.43
Snout	M0: 1 + Group	1323.74
	M1: Dome.height + Group	1323.51
	M2: Sample + Group	**1310.12**
	M3: Dome.height + Sample + Group	1310.34
Fin bleeding	M0: 1 + Group	1169.45
	M1: Dome.height + Group	**1154.65**
	M2: Sample + Group	1170.33
	M3: Dome.height + Sample + Group	1155.56
Fin split	M0: 1 + Group	1120.08
	M1: Dome.height + Group	1102.17
	M2: Sample + Group	1116.19
	M3: Dome.height + Sample + Group	**1097.93**
Fin erosion	M0: 1 + Group	1201.77
	M1: Dome.height + Group	1204.54
	M2: Sample + Group	**1178.76**
	M3: Dome.height + Sample + Group	1180.99

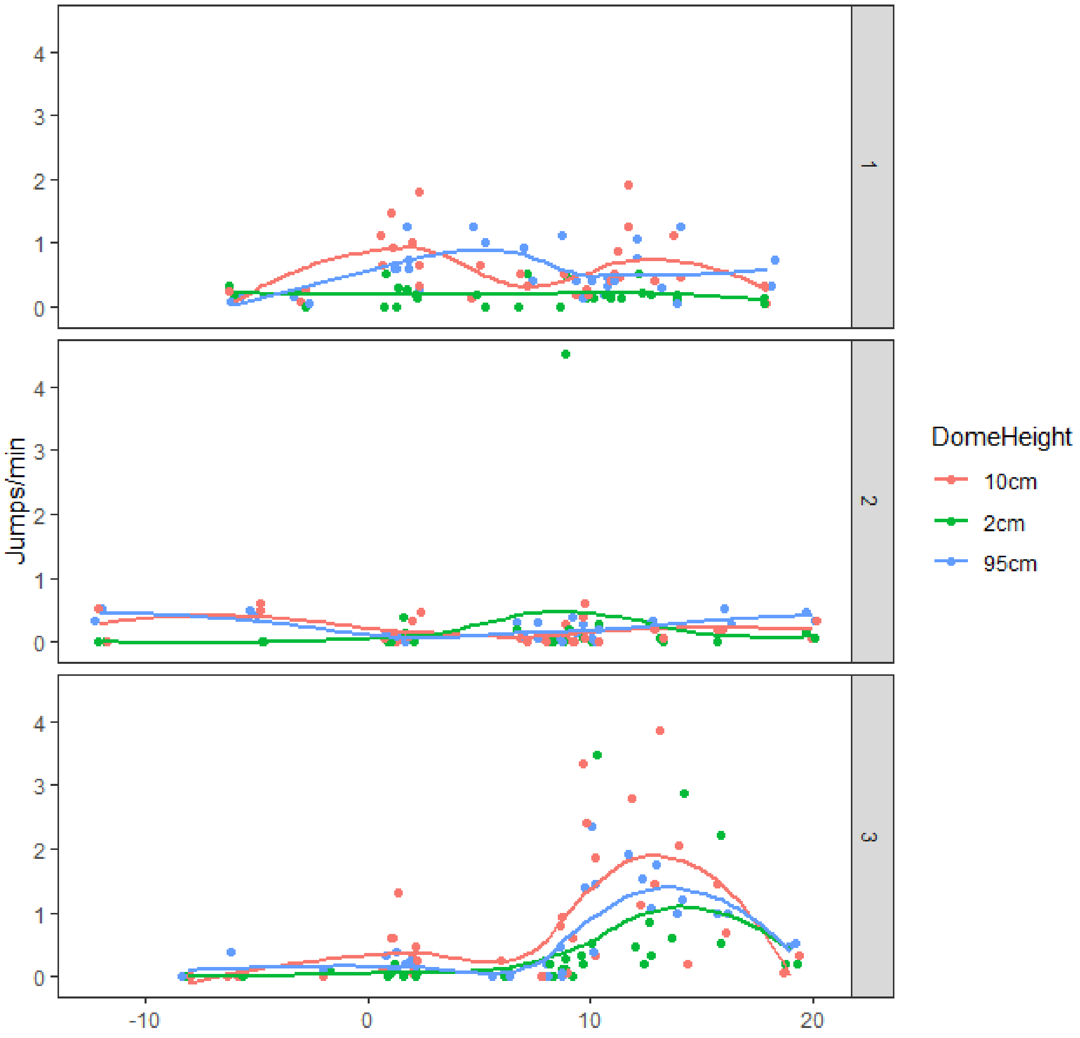


Fig. 7.2: Distribution of jump frequency min^{-1} during LRP. Lice were introduced at point (day) 0. All groups show increased activity when lice reached pre-adult stage (from day 9).

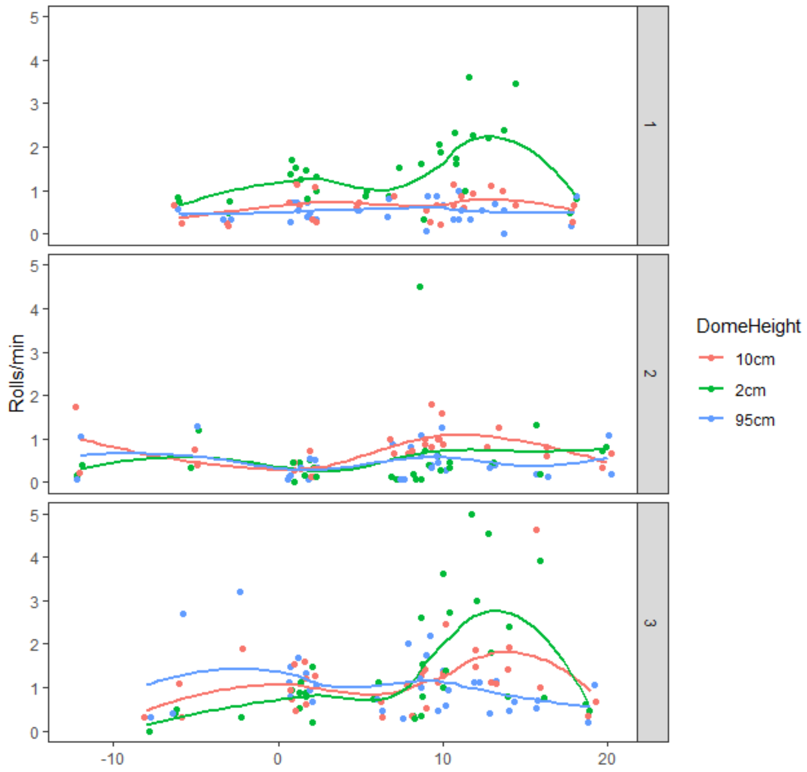


Fig. 7.3: Distribution of roll frequency min^{-1} during LRP. Lice were introduced at day 0. Activity increased in all tanks during infection and again when lice reached pre-adult (day10-11).

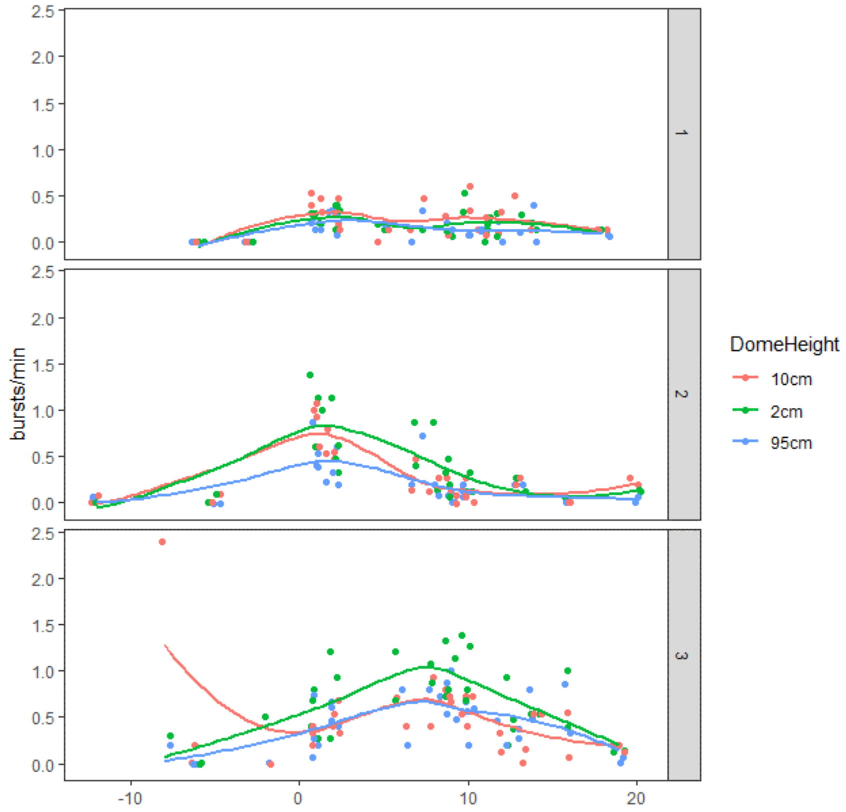


Fig. 7.4: Distribution of burst frequency min^{-1} during LRP. Lice were introduced at point (day) 0. Showing increased activity when infected with lice, although at different frequencies between groups, as G1 has overall lower frequencies.

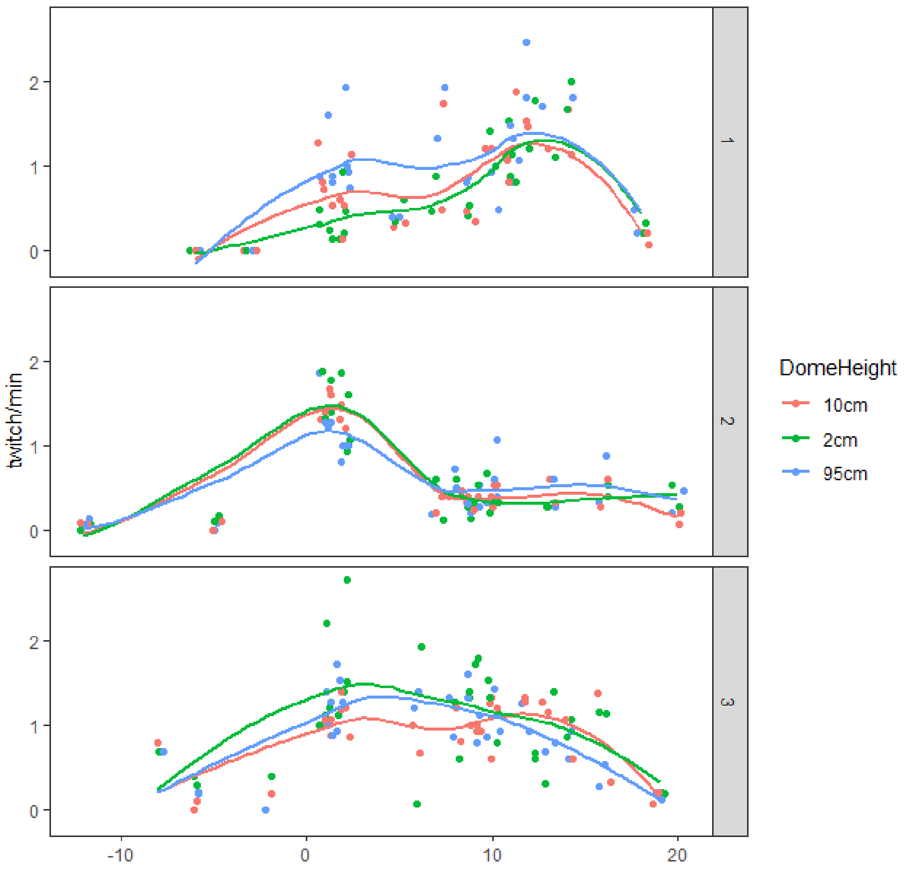


Fig. 7.5: Distribution of twitch frequency min^{-1} during LRP. Lice were introduced at point (day) 0. Overall, groups experienced increased activity for two 1-2 days after infection (0) and again when infected with lice reached pre-adult (10).

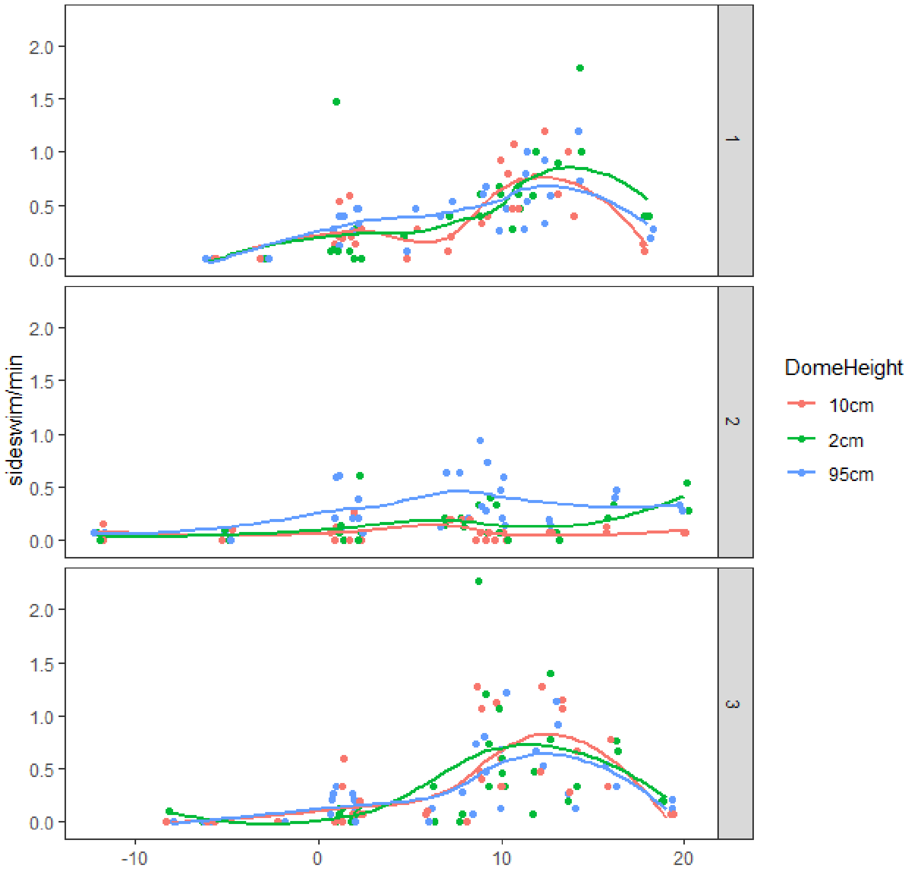


Fig. 7.6: Distribution of side swimming frequency min^{-1} *per group during LRP. Lice were introduced at point (day) 0. Activity accumulating at higher frequencies in all groups during lice infection (0) and when lice reach pre-adult stage (from day 9).*

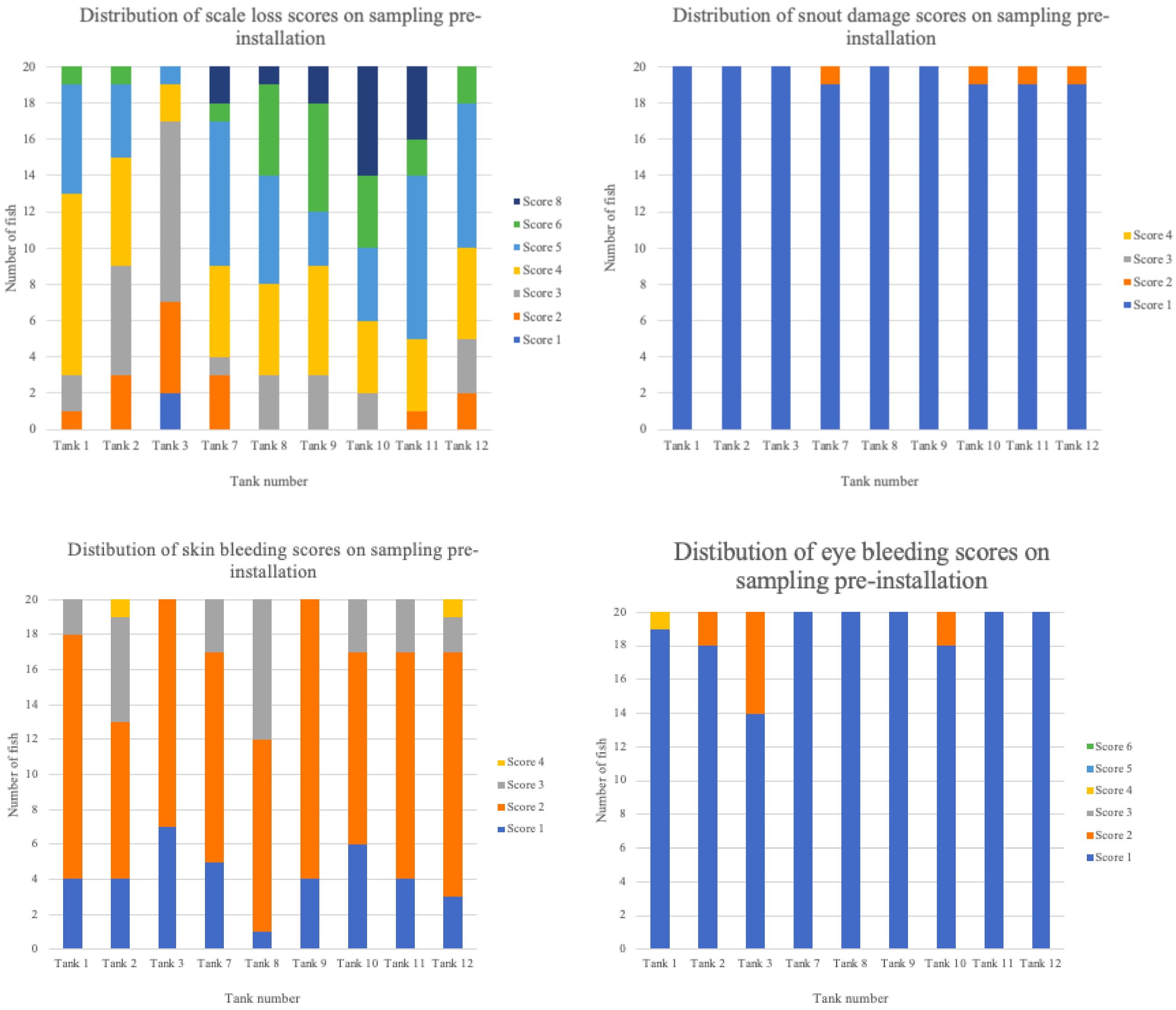
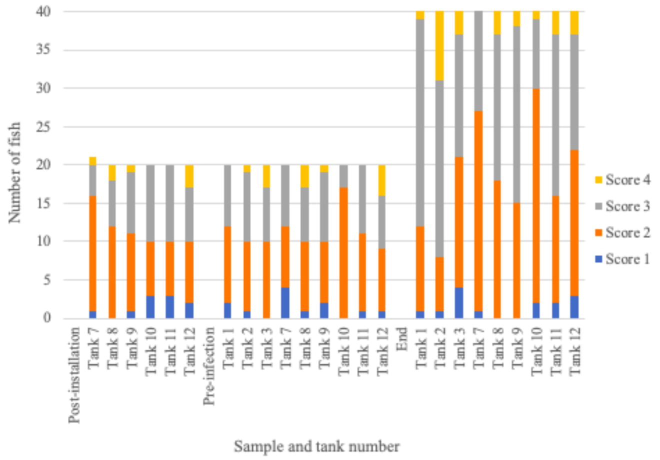
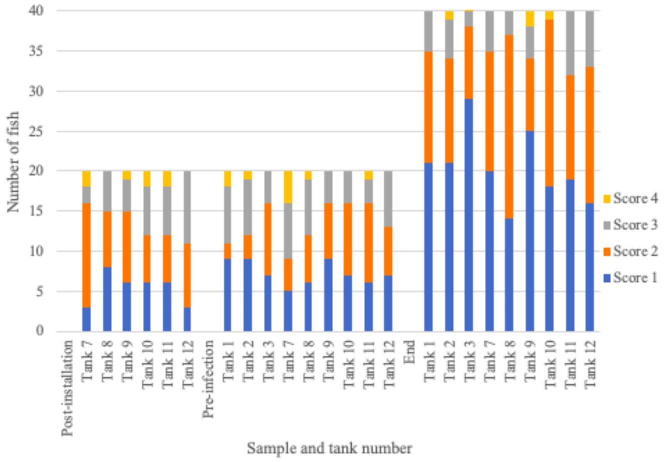


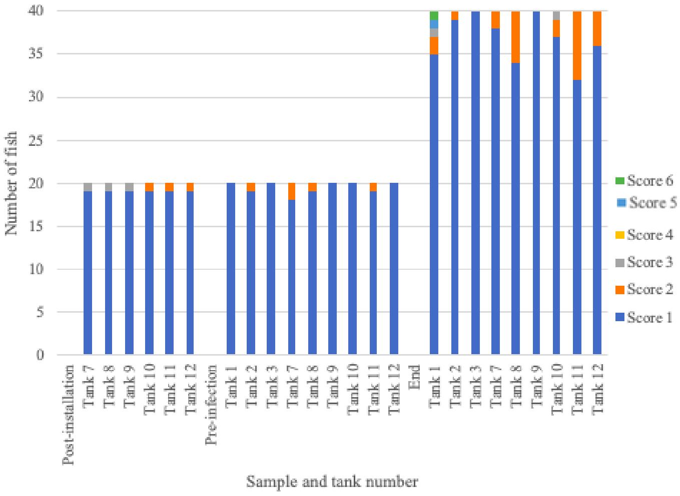
Fig. 7.7: Distribution of score on welfare indicators eye bleeding, skin bleeding, scale loss, snout damage and skin bleeding during sampling pre-installation.



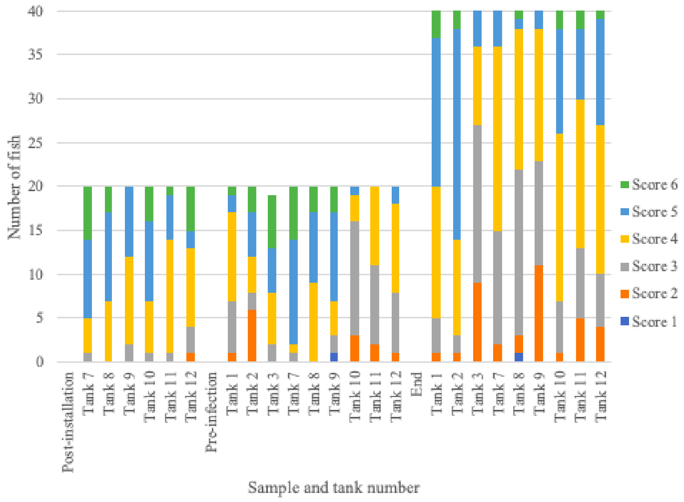
Distribution of fin split scores during samplings post-installation, pre-infection and end



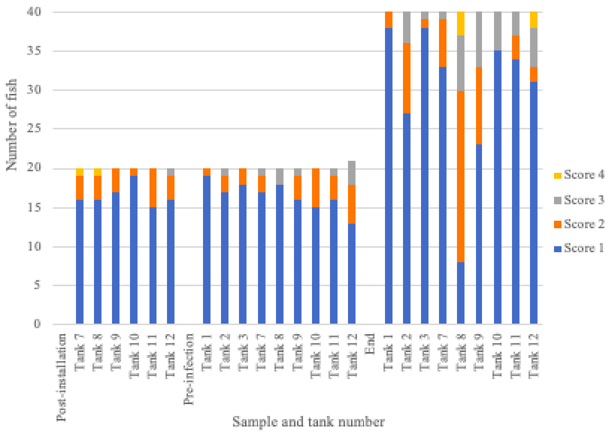
Distribution of fin erosion scores during samplings post-installation, pre-infection and end



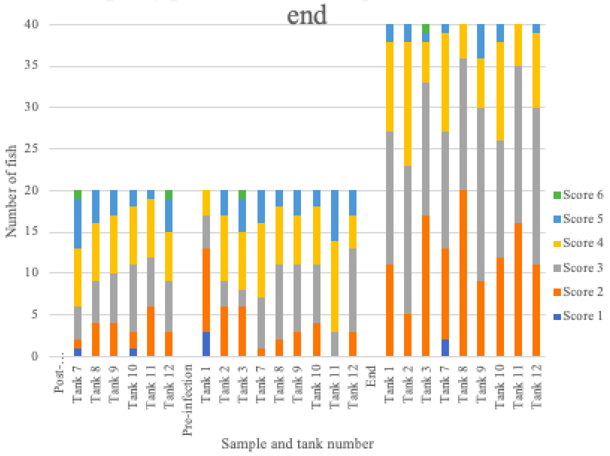
Distribution of gill scores during samplings post-installation, pre-infection and end



Distribution of scale loss scores during samplings post-installation, pre-infection and end



Distribution of eye bleeding scores during samplings post-installation, pre-infection and end



Distribution of skin bleeding during sampling post-installation, pre-infection and end

Fig. 7.8: Distribution of scores on welfare indicators fin split, fin erosion, gill damage, scale loss and eye bleeding during samplings post-installation, pre-infection and end. Only G2 and G3 sampled post-installation.

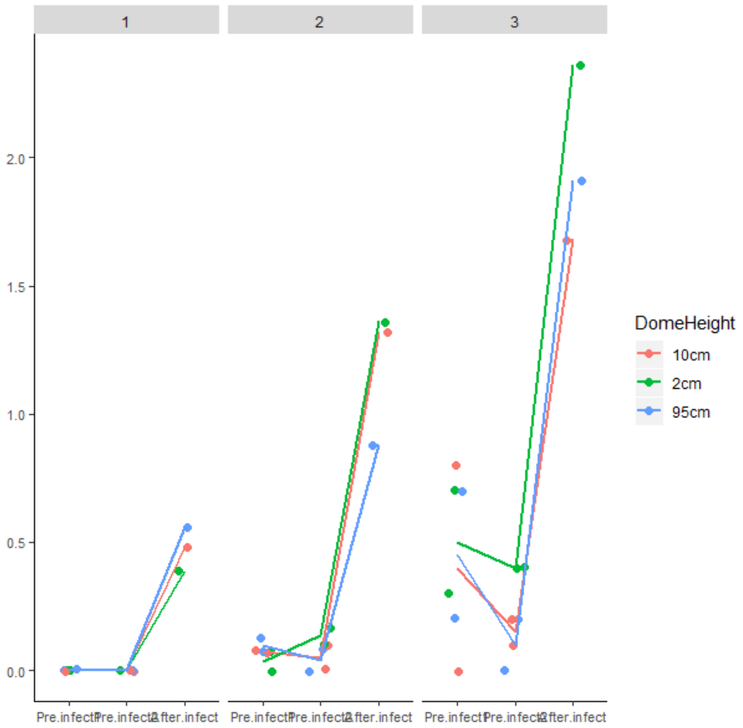


Fig. 7.9: Distribution of side swimming behaviour distinguishing between groups and dome heights before, during and after infection. Difference in distribution are statistically significant, response pattern is, however, comparable between groups, although frequencies increasing with increasing group number.