Environmental drivers of Atlantic salmon behaviour in sea-cages: a review

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Abstract

Salmon may sense and respond to a range of environmental variables within sea-cages, including light, temperature, salinity, dissolved oxygen, water currents and certain chemical treatments used during production. Environments within sea-cages are typically highly variable in both space and time, with greatest variation occurring with depth. Preferred swimming depths and densities of salmon are the result of active trade-offs among environmental influences and an array of internal motivational factors such as feed and perceived threats. When preferred levels of multiple environmental cues exist at different depths, behavioural responses to temperature, light, the entry of feed, oxygen levels or the presence of treatment chemicals may dominate and override behavioural responses to all other drivers and determine swimming depths. Behavioural trade-offs in response to environmental drivers typically result in schooling at specific depths within sea-cages at densities 1.5 to 5 times their stocked density, and up to 20 times in extreme cases. Understanding the spatial and temporal variability of key environmental variables within sea-cages and how salmon respond to them may enable modifications to sea-cage environments to improve welfare outcomes, feeding regimes, artificial light management strategies and the efficacy of sea-lice treatments.

Contents

1. Introduction

1.1. Scope and study limitations

The majority of Atlantic salmon production takes place in marine net cages (hereafter sea-cages) where the fish are exposed to a complex natural and artificial environment. Their movements are restricted by the volume set by the net and the surface, wherein they display their preferences and aversions. Behavioural studies of caged Atlantic salmon have revealed that fish rarely distribute themselves randomly in sea-cages, but that their swimming depth and speed is a response to several environmental gradients (e.g. Juell, 1995; Oppedal et al., 2007; Johansson et al., 2007; Korsøen et al., 2009). In general, the metabolic rates of fish are governed by controlling (e.g. temperature) and limiting (e.g. metabolites, food, water and respiratory gases) factors and their preferences have been suggested to reflect behavioural adaptations aimed at optimising their position in the environment (Fry, 1947). Adjustments of management practices to the natural behavioural traits of salmon, utilising their adaptive capacities and avoiding maladaptive behaviours, may improve production efficiency and welfare of the farmed fish.

Salmon behaviours in sea-cages have been extensively studied. However, since the last comprehensive review that synthesised existing knowledge on the behaviour of salmon in relation to efficient cage-rearing (Juell, 1995), diverse new insights have emerged from a range of field and experimental studies (e .g. Oppedal et al., 2001a; 2007; Juell et al., 2003; Juell and Fosseidengen, 2004; Cubitt et al., 2005; Johansson et al., 2006; 2007; 2009; Dempster at al., 2008; 2009a; Korsøen et al., 2009). Approximately 20 experiments have been conducted in industry-scale sea-cages (Table 1). The majority of these studies used the echo-sounder techniques introduced by Bjordal et al. (1993), which have enabled measurement of the detailed vertical distribution of salmon groups in sea-cages with high temporal (seconds) and depth resolution (0.5 m depth increments). In addition to assessing vertical distributions of salmon, many of these studies have manipulated or simultaneously measured a range of environmental and production variables, such as light, salinity, temperature, oxygen, current speeds, feeding regimes and the application of chemical therapeutants, to test the behavioural responses of salmon.

Here, we synthesize the insights generated by these industry-scale trials as to how salmon respond to, and trade-off between, different environmental variables within sea-cages by altering their vertical positioning and modifying other behaviours. Finally, we make recommendations to ensure that the present knowledge is better utilised by the salmon farming industry to improve production parameters such as stocking densities, feeding regimes, artificial light management and the efficacy of sea-lice treatments, and propose new hypotheses regarding the behaviour of salmon in sea-cages that require testing.

2. General overview of modern salmon production in sea-cages

To provide general context, we first provide a brief overview of the extent of salmon aquaculture in sea-cages and typical culturing practices.

2.1. Worldwide production of salmonids

Worldwide, approximately 1.58 million tons of Atlantic salmon and 286 kilotons (kt) of rainbow trout were produced in 2008 (Table 2; reproduced from Kjønhaug, 2009). Production is dominated by Norway and Chile, with Great Britain, North America, the Faroe Islands and Australia also significant producer nations.

2.2. Farm sites and sea-cage sizes

Salmonid farming sites are located in bays, sounds, fjords or scattered amongst islands within archipelagos. Farms in coastal areas typically have relatively homogenous water quality, are subject to a stronger and more variable current regime, and may experience wind-driven upwelling of colder water with lower oxygen saturation levels. Farms located in fjords are less likely to experience upwelling events, but typically experience greater seasonal variation in environmental conditions with strong vertical stratifications variations in salinity, temperature, oxygen and water currents (e.g. Johansson et al., 2007; Oppedal et al., 2007).

Salmon are typically held in either square or rectangular sea-cages of 20-40 m sides, 20 to 35 m deep or circles of 90-157 m in circumference and up to 48 m deep. Cage volumes range from 20000-80000 m^3. Square cages are typically clustered together in a steel platform with between 4-28 cages per site with little distance (2-4 m) between adjacent cages. Circular cages are arranged in mooring grids in single or double rows but with typically greater space between them (>20 m) than square cages.

2.3 Biomasses and stocking densities

Cages may contain up to 200000-400000 individuals at densities typically up to 25 kg m^{-3} (maximum allowable stocking density = 25 kg m^{-3} in Norway; Norwegian Ministry of Fisheries and Coastal Affairs, 2008). In practice, the largest Norwegian sites produce more than 10000 tons of salmon biomass per generation (pers. comm., Trine Danielsen, Marine Harvest) involving more than 2 million individual salmon per site. In 2008, approximately 300 million individual Atlantic salmon and rainbow trout were held in sea-cages in Norway at any given time (Norwegian Fisheries Directorate, 2009).

2.4. Underwater lights, sexual maturation and growth

To arrest and reduce the incidence of sexual maturation, artificial lights are used during winter for both spring- (Hansen et al., 1992; 2000; Oppedal et al., 1997; Porter et al., 1999) and autumn seawater-transferred (Oppedal et al., 2006) Atlantic salmon. Photoperiodic treatment also alters the seasonal growth cycle and larger salmon may be produced in shorter time (Oppedal et al., 1997; 1999; 2003; 2006; Nordgarden et al. 2003). Typical growth rates are in the range of 0.3-2% of the stocked biomass in the cage, depending on season, artificial photoperiod, fish size and water temperature (e.g. Oppedal et al., 2006; Skretting, 2009) with daily feed rations at similar levels.

3. Group and individual behaviours

3.1 Schooling patterns and swimming speeds

Salmonids typically form a circular swimming pattern at daytime and avoid both the innermost part of the cage volume and the cage corners (Sutterlin et al. 1979; Fernö et al. 1988; Juell and Westerberg 1993; Huse and Holm, 1993; Juell et al. 1994; Oppedal et al. 2001a; Dempster et al. 2008; 2009a; Korsøen et al. 2009). While this behaviour is not ‘classical’ schooling, which involves tightly organised synchronised swimming direction and speed (Cushing and Harden Jones, 1968), its semi-organised nature means that it is often referred to as such throughout the literature. Schooling typically leads to packing of the fish in certain areas within the cage at densities 1.5-5 times the stocking density, reaching as high as 20 times in extreme cases (Table 1).

When salmon are held at commercial densities, the cumulative interactions of all individuals in avoiding the sea-cage and other individuals are believed to cause the characteristic circular schooling patterns observed during the day (Juell and Westerberg, 1993; Fernö et al., 1995; Juell, 1995; Føre et al. 2009). Salmon require a certain density in order to form schools; an increase from 30 to 530 individuals in a 500 m^3 cage was required before structured schooling was observed (Juell and Westerberg, 1993). Similarly, schooling was first observed in a group size of 243 individuals in a 2000 m^3 cage, and further pronounced when the group size was increased to 729 individuals (Folkedal, 2006). This schooling pattern was recently verified in an individual-based model by Føre et al. (2009) based on a set of simple rules defining the responses of salmon to other individuals, avoiding the cage and including a stochastic component. The structured behavioural patterns seen at the group level are an ‘emergent property’ of the combined individual behaviours that ultimately create a self-organising school (Føre et al., 2009).

During feeding, circular schooling largely breaks down and fish swim towards the food pellets which are normally distributed in a centralised feeding area (Sutterlin et al., 1979; Huse and Holm, 1993; Juell et al., 1994; Ang and Petrell, 1998) and move back towards the periphery as hunger is reduced (Juell et al., 1994). When fish are continuously fed throughout the day, they form a ring-like structure, characterised by organised foraging (Ang and Petrell, 1998). In contrast, when fed in batches, salmon initially form a spiral-like structure followed by foraging in a disorganised style until feed becomes unavailable. Avoidance of the cage bottom is often observed (Huse and Holm, 1993; Fernö et al., 1995) and could represent anti-predator avoidance, as large piscivorous fish are frequently observed immediately below the cages (e.g. saithe and cod in Norway; Dempster et al., 2009b).

Swimming speeds during the day are typically faster than at night (day: 0.2-1.9 BL sec^{-1}: Sutterlin et al., 1979; Kadri et al., 1991; Blyth et al., 1993; Juell and Westerberg, 1993; Smith et al., 1993; Oppedal et al., 2001a; Andrew et al., 2002; Dempster et al., 2008; 2009a; Korsøen et al., 2009; night: < 0.4 BL sec^{-1} ; Korsøen et al., 2009) as illustrated in Fig. 1 (reproduced from Korsøen et al., 2009). The breakdown in schooling behaviour after sunset may be responsible for this change in swimming speed (Fernö et al., 1988; Juell, 1995, Oppedal et al., 2001a; Korsøen et al., 2009) and may also lead to salmon spreading themselves more evenly throughout the cage on the horizontal plane.

3.2. Feed and feeding motivation

Salmonids in sea-cages are fed through the distribution of feed at the water surface. As pellets become available in the surface water layer, salmon display a range of horizontal and vertical behaviours in response, such as horizontal movement towards pellets, change in swimming speed and swimming depths (Sutterlin et al., 1979; Huse and Holm, 1993; Juell et al., 1994; Ang and Petrell, 1998). The rate at which fish naturally respond when feed becomes available is principally related to hunger level (e.g. review by Dill, 1983).

Juell et al. (1994) determined that the vertical distribution of caged Atlantic salmon was a good indicator of their hunger level or feeding motivation, with responses to feed input clearer at high compared to low feeding intensities. In essence, salmon ascend to the surface feeding area to feed and thereafter descend gradually in the cage during the course of the feeding period as they become satiated and their feeding motivation declines (Bjordal et al., 1993; Juell et al., 1994; Fernö et al., 1995; Ang and Petrell, 1998; Johansson et al., 2007). Hungry fish remain at the surface in the feeding area after the feeding period and fish fed at high intensities move towards the surface more rapidly than at low intensities (Juell et al., 1994). The response rates of hungry fish correlated with their initial hunger levels. Infrequent, intensively fed fish generally remained deeper than fish fed throughout the day in small batches (Fernö et al., 1995).

An observed rise to the surface during the hour prior to the start of feeding may be interpreted as an anticipatory behaviour related to feeding time and suggests that not only the presence but also the expectation of food has an effect on vertical distribution (Fernö et al. 1995). Several salmon farmers have reported increased surface activities prior to feeding either as responses to feed time, feed boat arrival or start of feeding systems, suggesting anticipatory feed behaviours may be learnt and triggered by unintentional cues such as noise. Recent tank studies have shown that blinking lights can be used to teach salmon to anticipate feeding and respond by moving towards the point of feed entry (Thomassen and Fjæra, 1991; Stien et al., 2007; Bratland et al., 2010; Folkedal, 2010). Fernö et al. (2006) suggest that fishes learn, for example, to associate the footsteps of the farmer or the sound of pellets in the feeding pipes with food and can show strong anticipatory behaviour (e.g. rise to surface and increased surface activity) before the food arrives. The anticipatory behaviour functions as an arousal for appetitive responses and is a positive emotional event that should increase feeding motivation and welfare (Lamb, 2001; Spruijt et al., 2001).

In addition to the immediate pre-feeding period anticipatory response, several studies have hypothesized that the gradual seasonal movement of salmon towards the surface from winter to summer in sea-cages occurs due to a seasonal increase in hunger level (Oppedal et al., 2001a; Juell et al., 2003; Juell and Fosseidengen, 2004). Smith et al. (1993) recorded a surge in appetite in spring, which was independent of temperature, further suggesting that a seasonal movement to shallower depths may be related to increasing appetite. If this is the case, fish will be easily “underfed” when feed-ration calculations are based on temperature alone.

3.3 Group versus individual behaviours

The great bulk of knowledge of the vertical behaviours of salmon in sea-cages (Table 1) is based on average values obtained from measurement techniques that integrate information across large numbers of fish (e.g. echo-sounders; Bjordal et al. 1993), which are often verified by short-term camera observations of random individuals. Individuals are difficult to follow, although ultra-sonic and data storage tags are available and have been used in aquaculture settings (Juell and Westerberg 1993; Bégout Anras et al., 2000; Kristiansen et al. 2004; Cubitt et al. 2005; Rillahan et al. 2009).

Direct comparison of the specific vertical behaviours of individuals and the average group behaviour has been performed on a long-term data set by Johansson et al. (2009), who used individual data storage tags and echo-sounders to investigate swimming depths. Average individual behaviours correlated with group behaviours both in the short (hours) and long term (days to weeks), as illustrated by the similar diel cyclical movement patterns within cages or similar warm and cold water avoidances (Johansson et al., 2006; 2009). While confirming the validity of group-based measurements, the study revealed that a separate level of spatial and temporal variation in displayed behaviours exists at the level of individuals. Only 1 of 23 individuals displayed a cyclical rhythm in swimming depth and temperature across 3 different sub-periods spread over 7 weeks. Behaviours of all other individuals were inconsistent in either swimming depth or temperature rhythm or both between sub-periods. When feeding times were excluded, thereby largely ruling out the effects of the trade-off towards the surface due to feeding motivation, large variation among individuals was still evident during the day, but reduced at night. Johansson et al. (2009) suggested that this variation may reflect a more active environmental sampling by salmon during day than night in order to update information on spatial variation. Such sampling may be difficult to perform at night due to the limited visibility and high number of fish in the cages leading to a high risk of collisions with other fish. Further, the higher daytime variation may reflect a general increase in swimming activity with more trade-offs between different needs during day than night. Taken together, the large intra- and inter-individual variation suggests the existence of unsynchronized variability in the motivational status of individual fish making different and fluctuating multiple trade-offs.

4. Group behavioural responses to environmental variables

4.1. Natural and artificial light

Groups of Atlantic salmon kept in cages generally display a diurnal swimming depth rhythm controlled by natural changes in light intensity. Salmon descend at dawn, swim relatively deep during the day, ascend at dusk and swim close to the surface at night (Bjordal et al., 1993; Fernö et al., 1995; Oppedal, 1995; Hevrøy et al., 1998; Bégout Anras et al., 2000; Oppedal et al., 2001a; Juell and Fosseidengen, 2004; Cubitt et al. 2005; Johansson et al., 2006; 2007; 2009; Dempster et al. 2008; Korsøen et al., 2009). In combination with a slower average swimming speed (Fig. 1), salmon utilise more of the cage volume at night than during the day (Oppedal et al., 2001a; Dempster et al., 2008; Korsøen et al., 2009).

Early studies indicated that salmon avoid high surface light intensities during spring and summer and exhibit preferences for specific light intensities (Huse and Holm 1993; Fernö et al. 1995). However, similar light intensity preferences have not been observed in several subsequent studies (e.g. Oppedal et al., 2001a; 2007; Juell and Fosseidengen, 2004; Johansson et al., 2007). An explanation for this could be either that the higher precision environmental monitoring conducted in the later studies has enabled the role of other environmental factors in vertical distribution to be more clearly distinguished or that light preferences were overruled by temperature.

Distinct changes in the diel and seasonal patterns of vertical distribution of salmon occur when surface mounted artificial lights are applied to sea-cages (Oppedal et al., 2001a). In essence, illumination modifies night time behaviour towards the normal daytime schooling pattern; fish swim at the same depth throughout the diel cycle and maintain daytime swimming speeds. In commercial-scale cages containing 85000 fish per cage, surface mounted lights induced movement of the fish towards the surface and resulted in higher schooling densities and shallower swimming at night compared to the day (Juell et al., 2003). In a different study conducted at similar commercial densities, surface mounted lights also caused the group of salmon to ascend but to a lesser extent compared to salmon in cages with natural dark conditions at night (Juell and Fosseidengen, 2004).

Submerged light sources were developed for the aquaculture industry as they reduce loss of energy from surface reflections, hazards for boat traffic, aesthetic considerations and therefore provide more effective illumination to the fish. Submerged light sources generally expose the fish to a wider depth range with illumination, both above and below the deployed light depth (Juell et al., 2003; Oppedal et al., 2007), compared to surface mounted lights that provide only downwards illumination (Juell et al., 2003).

Salmon display clear attraction to submerged light sources (Juell et al., 2003; Juell and Fosseidengen, 2004; Oppedal et al., 2007; Dempster et al., 2009a; Fig. 2c-e) and school at lower densities compared to sea-cages illuminated with surface mounted lights (Juell et al., 2003; Juell and Fosseidengen, 2004). Night swimming depths suggest that salmon prefer to distribute in highest densities around the depth of the highest light intensity (Juell et al., 2003; Juell and Fosseidengen, 2004; Oppedal et al., 2007; Dempster et al., 2009a). As a direct consequence, lower fish densities occur above and below the depth of peak submerged light intensity, which spreads salmon more effectively throughout the cage volume compared to the higher fish densities observed under surface mounted lights where only half as much volume is available below the peak light intensity (Juell et al., 2003; Juell and Fosseidengen, 2004). Through the choice of light deployment depth, farmers may thus influence salmon swimming depths and densities at night (Juell and Fosseidengen, 2004; Oppedal et al., 2007). This is exemplified by data from a commercial farm (Fig. 2c-e) where the salmon are attracted towards the light depth at night. Behavioural responses to short-term changes in deployment depths and light intensity gradients appear rapid, suggesting that swimming depths and fish densities can be manipulated effectively by selectively positioning underwater lamps (Juell and Fosseidengen, 2004).

Peak light intensity can be stretched over a broad depth range by deploying lights at different depths, thereby dispersing the fish throughout the cage volume (Juell et al., 2003; Juell and

Fosseidengen, 2004). Lamps positioned mid-depth in cages produce a normally distributed light intensity and cause the fish to distribute themselves on both sides of the lamps, while lamps closer to the bottom or surface produce a stronger vertical light gradient, possibly inducing crowding (Juell et al., 2003; Juell and Fosseidengen, 2004; Oppedal et al., 2007).

To understand the swimming depth preferences of salmon under artificial lights, the normal diel behaviour of caged salmon proves informative. Salmon school during day, ascend to the surface and reduce swimming speeds in response to the fading natural light at dusk, with an ultimate breakdown of the school structure as light levels fall (reviews; Juell, 1995; Huse, 1998). Schooling behaviour in several pelagic fish species relies on visual contact (Glass et al., 1986). In contrast to mammals, the eyes of fish rely mainly on a relatively slow retinomotor response to adapt to changes in light levels (Guthrie, 1993). For example, Ali (1959) found that adaptation time from light to darkness in Pacific salmon smolts was about 50 minutes. It is thus likely that, at some point during dusk, when the fading natural light is weaker than the artificial light, the salmon actively seek out suitable light levels so they can continue to school rather as a preference to waiting for their eyes to adapt and allowing schooling to break down. Thus, moving towards the artificial light depth maintains their schooling behaviour (Juell et al., 2003; Juell and Fosseidengen, 2004; Oppedal et al., 2007).

4.2. Temperature

Temperatures within sea-cages positioned in surface waters (0-50 m) vary with depth and vertical profiles are normally season-dependent (e.g. Oppedal et al., 2001a; 2007; Fig. 2a). Temperature profiles change from being positively correlated with depth in winter to negatively correlated with depth in summer, with transitional periods where profiles are more variable, but often with highest temperatures at mid-cage depths in fjords (e.g. Johansson et al., 2006; Oppedal et al., 2007).

At stratified sites where temperature and other environmental variables have been measured in high spatial and temporal resolution, salmon clearly positioned themselves vertically in relation to temperature within sea-cages (Johansson et al., 2006; 2007; 2009; Oppedal et al., 2007; Dempster et al., 2008; 2009a; Korsøen et al., 2009; Fig. 2). Seasonal changes in the vertical distribution of salmon have occurred concurrent with temperature shifts, suggesting that salmon prefer the highest available temperature (<14°C) or avoid colder temperatures (Oppedal et al., 2001a).

Johansson et al. (2006) performed a multivariate analysis to determine which environmental variables most influenced the vertical distribution of salmon; temperature emerged as the key environmental factor associated with density and swimming depth. The preferred temperature range was 16-18 °C within a range of 11-20 °C. Salmon individuals and groups displayed both avoidance to water warmer than 18 °C and water at the cold end of the temperature spectrum, indicating active behavioural thermoregulation (Johansson et al., 2006; 2009). In contrast, in reasonably homogenous environments where temperature varies little with depth, temperature does not influence the vertical distribution of salmon (Juell et al., 2003; Juell and Fosseidengen, 2004). Salmon farming is expanding into areas with <4 °C; at present the literature does not describe behavioural effects at this end of the temperature scale.

Results from small-scale experiments in tanks (e.g. review by Beitinger, 1990; Birtwell et al., 2003) provide supportive evidence that temperature strongly influences fish distributions, particularly when a gradient is present. Salmon are known to be highly temperature sensitive (Coutant, 1977; Jobling, 1981). In general, fish presented with thermal gradients occupy narrow ranges of temperatures, defined as their preferred temperatures (e.g. Fry, 1947; Johnson and Kelsch, 1998) and such active behaviour is often referred to as behavioural thermoregulation. Optimising temperature is of great physiological significance for poikilotherm fish; thermoregulation may improve metabolic processes such as circulation, food intake, digestion, growth, bioenergetical re-acclimation processes and scope for activity (e.g. Brett, 1971; Biette and Geen, 1980; Claireaux et al., 1995; 2000). Correlative evidence exists that preferred temperature ranges match optimum temperatures for growth and performance for various species (e.g. Jobling, 1981; Kellogg and Gift, 1983).

4.3. Salinity

Many salmonid farming sites either close to shore, within fjords or near the mouths of rivers are affected by freshwater runoff. Surface waters at these sites may become less saline with development of a distinct halocline with a brackish layer of variable thickness and salinity (but often < 20; Plantalech Manel-La et al., 2009) on top and water with typical marine salinity (> 30) below (e.g. Bjerknes et al., 2003; Johansson et al., 2007).

Newly transferred Atlantic salmon smolts show a distinct preference to distribute at the depth of the halocline, independent of the temperature, for the first 2 months in the sea (Fig. 3). Similar preferences are shown by salmon smolts migrating out from rivers towards the open sea (Plantalech Manel-La et al., 2009). This behaviour might form part of the imprinting necessary for salmon to find their way back to natal rivers as adults or as a strategy to avoid the risk of infection from sea lice (*Lepeophtheirus salmonis*) (Plantalech Manel-La et al. 2009) which avoid salinities of < 20 (Heuch, 1995). Alternatively, this strategy may be beneficial as it reduces the amount of energy required for osmoregulation in saltwater, which is particularly physiologically costly for small salmon (e.g. Smith, 1982).

Sutterlin and Stevens (1992) suggested that salinity preferences may be one of three factors (temperature, salinity and social factors) that regulate the swimming depth of fish in sea-cages in stratified waters. During the return migration of salmon, which normally occurs during spring and summer, it could be expected that salmon develop a lower salinity preference prior to spawning in freshwater (Thorpe, 1988). Thus, observations of salmon gradually ascending towards the surface throughout spring (Oppedal et al., 2001a; Oppedal et al., 2007) or early autumn (Johansson et al., 2006; 2009) could be explained by a lowered salinity preference. However, as the incidence of sexual maturation in the observed groups was < 6%, this behaviour was unlikely to have resulted from a preference for lower salinities driven by the sexual maturation cycle. Evidence exists that salinity does not influence non-migratory salmon (Bakke et al., 1991; Johansson et al., 2006; 2009). In addition, larger fish have greater osmoregulatory ability than small post-smolts due to reduced relative leakage of water as a function of their relatively smaller surface area to volume ratio (e.g. Schmidt-Nielsen, 1990). Accordingly, salinity preferences appear unimportant in determining vertical distributions in sea-cages of > 3 month old, sexually immature post seawater-transferred Atlantic salmon (Oppedal et al., 2001a; 2007; Johansson et al., 2006; 2007; 2009).

4.4. Dissolved oxygen (DO)

Complex spatial and temporal variations in DO levels exist within sea-cages stocked with salmon (Johansson et al., 2006; 2007; Vigen, 2008; Stien et al., 2009). Strong vertical gradients in DO typically coincide with the pycnocline, while fluctuating patterns occur over days to weeks (Johansson et al., 2006; 2007). Severely hypoxic conditions (30% saturation at 12 °C) have been recorded over periods of up to 1 hour in the centre of a commercial cage (Fig. 4; reproduced from Vigen, 2008) and were correlated with periods of low water flow (Vigen, 2008). Seasonal variations in DO levels are also frequently observed at commercial salmon farms (Fig. 5).

Adequate DO levels are a key requirement to ensure fish welfare and development (Kindschi and Koby, 1994; Van Raaij et al., 1996; Ellis et al., 2002). Pedersen (1987) showed that at 15 °C, growth rates of juvenile rainbow trout decreased if fixed levels of DO fell below 7.0 mg O_2 l^{-1} (70% oxygen saturation) and that trout fed less when fixed levels reached 6.0 mg O_2 l^{-1} (60 % oxygen saturation). A recent study with full-feeding Atlantic salmon held in seawater at 16 °C and given fluctuating hypoxic saturation levels of 70% led to reduced appetite; 60% additionally initiated acute anaerobic metabolism and increased skin lesions; 50% additionally initiated acute stress responses, reduced feed conversion and growth; and 40% additionally caused impaired osmoregulation and mortalities (Anon, 2008). Growth rates and condition factors gradually decreased and proportions of fish with skin infections gradually increased in severity as hypoxia levels rose. Lack of energy from aerobic metabolism for fish within the hypoxic groups may have led to down-regulation of energy-demanding processes such as feed uptake, growth and immune function (e.g. review by Wu, 2002). Thresholds levels for the ability to maintain oxygen uptake rates in full-feeding Atlantic salmon of average size 400 g held in seawater were found at approximately 60, 40 and 30 % oxygen saturation at 18, 12 and 6 °C, respectively (Torgersen et al., unpublished data). This very recent work was performed using an adapted protocol from Valverde et al. (2006) with gradually decreasing oxygen levels in an open-respirometry setup. At oxygen levels where fish have problems maintaining homeostasis, stress hormones are released, and fish cannot survive for long if sufficient oxygen levels are not restored.

Despite the importance of DO to production parameters and welfare, little specific information exists to determine how salmon modify their behaviours within sea-cages in response to sub-optimal DO levels. Kramer (1987) classified the response of fish to increasing hypoxic conditions as changes in activity and vertical or horizontal habitat changes. Like most other aquatic animals, fish have the capacity to detect and actively avoid low oxygen levels (DO_{conc} 1-4 mg l^{-1}/ DO_{sat} 15-60% at 25 °C seawater; Wannamaker and Rice, 2000; Wu, 2002) and migrate vertically in the water column to avoid hypoxic zones (e.g. Hazen et al., 2009). However, whether salmon actively avoid depths within sea-cages that have low to intermediate oxygen levels (DO_{conc} 2.5-6 mg l^{-1} or DO_{sat} 30-75% saturation in 15 °C seawater) remains unresolved. In an investigation of the environmental parameters influencing the vertical distributions of salmon at 4 commercial sites, a multivariate analysis indicated that salmon avoided specific depths in the water column where oxygen saturation levels approached 60% at 15 °C (Johansson et al., 2007). However minimum levels of oxygen ranging down to 57% saturation at 14 °C in an experimental study of different stocking densities did not implicate DO as significantly affecting fish densities, possibly due to other environmental factors exerting greater effect on vertical positioning (Johansson et al., 2006). Experimental testing is required to reveal the dynamics and hierarchical effects between hypoxia and other factors.

4.5. Water current velocity

Scant information exists to fully assess the role water currents play in the behaviours of salmon in sea-cages. In a multivariable analysis, extremely turbulent mean current velocities of 5-9 cm s^{-1} measured outside cages did not affect the relative schooling density of salmon (Johansson et al., 2006). Currently, the salmon farming industry is developing into more current-exposed locations (Jensen et al., 2010) and recent development applications in Norway have been made for the establishment of farms at sites where water currents reach a maximum of 0.85 m s^{-1} (F. Oppedal, pers. obs.). Stronger currents may have the potential to influence schooling structure, swimming speeds, directions and ultimately depths, thus their influence on cage-related behaviours requires further understanding.

Swimming capacities of salmon vary with size of individuals, temperature, light conditions and possibly space availability. Estimates of critical swimming velocities (U_{crit}) of ≈3 BL s^{-1} for Atlantic salmon smolts exist (Lijalad et al., 2009) and U_{crit} of 2.2 BL s^{-1} for 800 g postsmolts (Deitch et al., 2006). However, these are derived from swimming tunnels with unfed, individual fish and therefore may not be representative of fully-satiated salmon held under commercial densities. No comparable data exist for larger Atlantic salmon, but Steinhausen et al. (2008) indicate a U_{crit} ≈1.35 BL s^{-1} for adult (2.2-2.9 kg) sockeye salmon caught during their homing migration.

Normal swimming speeds within cages are below these threshold values for critical swimming speeds. During the daytime, salmon typically cruise at 0.3-0.9 body length s^{-1} (BL s^{-1}) (e.g. review by Juell, 1995; Dempster et al., 2008; 2009a) while night speeds are slower at 0-0.4 BL s^{-1} (Korsøen et al., 2009). However, under high current conditions, U_{crit} values may be approached or exceeded. If currents exceed U_{crit} levels, anaerobic capacity is exhausted, swimming ceases, and the fish will be forced into the net wall. Generally, larger fish should tolerate higher current speeds due to their larger body size, with smolts being more vulnerable to high currents despite their higher U_{crit} levels (Fig. 6).

Typically, smolts are set out at 15-25 cm BL (e.g. Oppedal et al., 2006); at these sizes, current speeds of 45-75 cm s^{-1} will cause exhaustion if U_{crit} ≈3 BLs^{-1} (Lijalad et al., 2009). In 800 g salmon of 56 cm, exhaustion will take place at about 120 cm s^{-1} with U_{crit} = 2.2 BL s^{-1} (Deitch et al., 2006). However, in commercial cages lower current speeds probably cause exhaustion as U_{crit} levels will be reduced in fully fed fish or fish held in high densities. If currents approach U_{crit} levels and differential current speeds exist at different depths in sea-cages (see Lader et al., 2008 for an example), we hypothesize that salmon will modify their vertical positioning in cages to depths of suitable current speeds.

Current speeds may also modify vertical behaviour by modifying the cage culture space available for swimming. Sea-cages deform in currents, with a consequent change in sea-cage shape and internal volume (Lader et al., 2008). Current speeds of 0.13 - 0.35 m s^{-1} at two full-scale farms caused cage volume reductions of up to 20- 40% and resulted in the cage bottom being pushed upwards (Lader et al., 2008). The complex inter-relationships between high currents, packing densities and swimming speed ability for fish of different sizes, and the extent of cage deformation, requires resolution to understand the influence of current on the vertical behaviours of salmon and ensure good welfare under high current conditions.

4.6. Sea lice chemotherapeutants

Sea lice (principally the salmon louse *Lepeoptheirus salmonis* but also *Caligus* spp.) infestations are common within sea-cage salmonid farms. Several treatment strategies have been applied to control sea lice levels over the last decades, including the use of a variety of chemotherapeutants (Pike and Wadsworth, 1999; Boxaspen, 2006; Brooks, 2009). Therapeutants may either be administered orally through medicated feed or topically by bathing fish in enclosed net cages or well boats (e.g. Roth, 2000; Telfer et al., 2006).

At present, one of the bathing techniques includes partial or full enclosure of an entire sea-cage *in situ* with a tarpaulin followed by the addition of the chemotheraputant for 35-45 min to kill the sea lice. Recent studies have revealed a clear vertical avoidance reaction to the addition of chemotheraputants (Vigen, 2008; Oppedal and Vigen, 2009). Salmon responded to a controlled experimental addition of cypermethrin (BETAMAX VET, ScanVacc AS, Årnes, Norway) in a 12 m x 12 m cage with the net bottom raised to approximately 4 m and the enclosing tarpaulin hanging down to 6 m depth by crowding at three times the stocking density towards the surface or net-cage bottom when the treatment was added (Fig. 7; Vigen, 2008). The movement and crowding reaction did not appear to be caused by the addition of the tarpaulin, as fish distributed evenly in cages enclosed by a tarpaulin but without chemotherapeutant added (Fig. 7; Vigen, 2008). In a full-scale, commercial bath delousing treatment of a circular cage of circumference 157 m, approximately 35 m deep and tarpaulins set to 15 m depth, salmon again avoided the surface waters and distributed themselves mainly below the depth in the water column where the chemotherapeutant deltamethrin (ALPHA MAX®, PHARMAQ AS, Oslo, Norway) was added and present (Fig. 8; from Oppedal and Vigen, 2009).

Partially effective treatments where salmon are not exposed to correct doses of chemotherapeutants due to their avoidance behaviour may, highly undesirably, increase the speed of development of resistance of sea lice to treatments. As a variety of chemoterapeutants are required to maintain susceptible sea lice populations over time, it is essential that each treatment is carried out optimally (Jones et al. 1992). In general, observations of behavioural monitoring are scarce during delousing treatments, yet preliminary results indicate that without knowledge of the vertical behaviours of salmon, the efficacy of de-lousing treatments may be questionable (Vigen, 2008; Oppedal and Vigen, 2009). We therefore contend that a detailed understanding of avoidance reactions and vertical behaviours of salmon in sea-cages is required to improve the effectiveness of de-lousing techniques and ensure appropriate animal welfare during treatments.

4.7. Other factors

Turbidity has been suggested as a possible directing factor for swimming depth and density. Surface layers of turbid water, colouring produced by runoff, and algal blooms reduce both light intensity and contrast in the water column (Nyquist, 1979). These properties can reduce the susceptibility of fish to surface predators (Guthrie and Muntz, 1993) and therefore possibly change the surface avoidance trade-off. However, to date no evidence exists to suggest turbidity modifies vertical behaviours of salmon in sea-cages. In contrast, the behaviours of groups of salmon held under low artificial light and natural light intensity in Oppedal et al. (2001a) suggested that turbidity was unimportant in swimming depth selection.

Forced submergence in sea-cages modifies both horizontal and vertical behaviours as salmon compensate for a loss of buoyancy due to depleted swim bladder volumes. When they cannot access the surface to refill their swim bladders, salmon increase their swimming speeds up to 1.6 times normal levels and school more tightly (Dempster et al., 2008; 2009a; Korsøen et al., 2009).

5. Behavioural trade-offs to multiple environmental variables

Environments within sea-cages are typically characterised by highly fluctuating levels of multiple factors in both space and time. Vertical positioning of salmon therefore stems from active trade-offs among these multiple environmental influences and an array of motivational factors such as feed and perceived threats. When many fish prefer the same depth strata within a cage, crowding and social factors must also be taken into account. Salmon must therefore continuously update and make trade-offs of preferred swimming depths and densities. The trade-offs made will likely differ among individuals, as their environmental preferences, motivations and social interactions clearly differ (Sutterlin and Stevens, 1992; Claireaux et al., 2000; Johansson et al., 2009). As a result, no single strategy is necessarily optimal or can be expected at any given time, either for individuals or the entire group of fish (Johansson et al., 2009). Here, we describe and explain the dynamics of trade-offs among multiple environmental influences from existing examples (Table 1).

5.1. Surface avoidance and feeding motivation

Vertical distribution of salmon in sea-cages can often be explained by a trade-off between light-induced surface avoidance and attraction to food (Juell et al. 1994; Fernö et al. 1995). Many fish species migrate downwards as a response to increased light levels at day or with season (e.g. Fernö et al., 1995). This has been suggested as an evolved trait for avoidance of surface predators (e.g. birds) and possible avoidance of damaging UV-light in surface waters (Bullock, 1988; Fernö et al., 1995). However, surface feeding induces a shift in vertical positioning towards the surface (see Section 3). The degree of response is largely dependent on feeding motivation, with salmon initially close to the surface at the beginning of a feeding period followed by a descent away from the surface as feeding progresses. The level of feeding motivation seems to be traded-off against the light avoidance both during feeding and after or between meals. Further, several long-term studies indicate that the trade-off between surface light avoidance and swimming depth is modified by a seasonal increase in feeding motivation, with fish positioning themselves at shallower cage depths as appetite increases (Fernö et al., 1995; Oppedal et al., 2001a; Juell et al. 2003; Juell and Fosseidengen 2004). With a regression tree analysis, Johansson et al. (2007) determined that higher fish densities close to the surface were strongly related to feeding time itself, but traded-off outside feeding hours. Overall, a clear trade-off exists between surface avoidance and surface feeding motivation.

5.2. Temperature and natural light

Salmon trade-off between light and temperature in sea-cages when preferred levels exist at different depths. Temperature often dominates the light-temperature trade-off, presumably because the physiological benefits of maintaining a position in a preferred temperature range outweigh those associated with optimal light levels. A multiple regression analysis on the influences of surface light, temperature at 0.2 m and visibility range on fish density in the 0-1 m depth interval indicated that an increase in temperature was the main factor affecting the ascent in spring, overruling the surface light avoidance (Fernö et al. 1995). Further, Oppedal et al. (2001a) documented that temperature overruled responses to other factors when surface waters were warmest, with salmon gathering at the surface, regardless of the typical avoidance of the high light intensities at the surface in spring and summer during the day. At night in winter, movement upwards toward the natural low light levels is overruled by the avoidance of cold surface water (Oppedal et al., 2001a; Korsøen et al., 2009). In both abovementioned studies, salmon ascended towards the surface at night within the relatively homogenous temperature layer below the thermocline, but did not ascend further through the thermocline into the colder overlying waters. These vertical behaviours can be interpreted as temperature overruling the avoidance of the surface due to high light levels during the day, and attraction to the surface at night as light levels fall. Finally, Oppedal et al. (2007) observed that salmon expressed an increasingly stronger temperature preference as the temperature range in sea-cages increased, displayed as higher swimming densities in the depth layer of optimal temperature. This trade-off between thermo- and photoregulatory behaviour may derive from the fact that temperature has more direct impact on physiology with respect to growth, while schooling may be maintained at a wider range of light intensities.

5.3. Temperature and artificial light

The underlying drivers governing trade-offs between thermo- and photoregulatory behaviour are likely to be similar whether natural of artificial lights are used. However, the outcome of trade-offs in terms of where fish position themselves in cages may differ markedly due to the ability artificial light sources give to manipulate light levels either at the surface or sub-surface. In studies using surface mounted lights, salmon in coastal waters with homogeneous temperatures throughout the water column responded at night by attraction towards the artificial illumination of < 10% of normal daylight intensities (Juell et al., 2003). In contrast, fish in thermally stratified fjord waters responded by swimming in the deep warmer water in winter and gradually ascended towards the surface as temperatures peaked in shallower waters as summer approached (Oppedal et al. 2001a). Clearly, this suggested that temperature modified the effect of artificial surface light. In a following study by Oppedal et al. (2007), where submerged lights were positioned randomly at 1, 5 or 10 m depths for 2 weeks during winter, spring and summer, the multiple trade-offs between temperature and light were elegantly illustrated: i) when warmest temperature (<14°C) and illumination where at the same depth, salmon swimming depth remained at this depth throughout the diel cycle; ii) when slightly warmer temperature was at a different depth than illumination, the salmon preferred the depth with warmest waters during the day and moved towards depths with greatest illumination at night or iii) displayed a bimodal distribution with some fish preferring illumination at night while others preferred depths where warmest waters occurred but all fish still preferred depths with warmest waters during the day; iv) when the vertical temperature gradient was strong (7 °C), the warmest water was preferred through the diel cycle, completely overruling illumination. Salmon contained in standard sea-cages with submerged lights at 7 m depth in late spring/early summer behaved similarly to group ii) in Oppedal et al. (2007), with a vertical preference for temperature (1-2 °C difference) during the day and vertical migration to the depth with greatest illumination at night (Dempster et al., 2009a).

Salmon followed over a production cycle in larger commercial cages display similar patterns (Fig. 2). When lights were switched on at 7 and 15 m depths, fish avoided the colder surface area both day and night. Artificial lights at these depths overruled the typical night ascent as the depths with illumination matched the depths with warmest water. During the spring rise in temperature at the surface layer, fish choose the warmest temperature during the day and the illuminated, but slightly colder, deeper waters at night. In summer, the bimodal distribution of fish during the day indicates that individual fish make different trade-off choices, preferring either highest temperature or illuminated waters during the day, while all fish prefer illumination in the short night of summer.

5.4. Multiple trade-offs

During a 50 hr period, a shift in the trade-offs salmon made among differing environmental influences was documented within two replicate commercial cages (Fig. 9, reproduced after Figs. 2 and 8, site 4 of Johansson et al., 2007). Temperature was relatively homogenous among depths at approximately 15 °C. During the afternoon of day 254, salmon predominantly swam deep in the cage, avoiding light at the surface. From dusk of day 254 and through the night, salmon distributed relatively evenly throughout the water column with a proportion of the salmon moving towards and staying close to the surface. This may be interpreted as a reduction in the importance of the daytime surface light avoidance as the illumination attenuated. On the morning of day 255, the fish descended away from the high light levels at the surface, but this trade-off was overruled when feeding started as fish responded to pellets delivered at surface by moving into surface waters (see Section 2.2). When the hunger level was reduced, the salmon again moved downwards in the water column to avoid surface light (see Section 2.3). At dusk of day 255, the salmon again distributed evenly as per the previous night, but after midnight all fish descended and avoided the hypoxic conditions (DO < 70%) which occurred from 0-7 m depth. A strong movement towards the surface in response to feed occurred when the hypoxic conditions were moderate at day 256 with fish moving downwards as feeding terminated. This example illustrates the complex outcomes of trade-offs made by salmon under conditions where light and DO levels fluctuate against short periods of strong feeding motivation when feed become available. Feeding motivation overrode light levels and drove vertical behaviours when DO levels were moderate (> 85%), while hypoxia (< 70%) overrode behaviour driven by low light intensity at night.

6. Conclusions, future research and recommendations for practical implementation of knowledge to date

6.1 Need and recommendations for measuring environmental variables in sea-cages

Given the clear environmental driving of salmon behaviour in sea-cages summarised in this review, we recommend the establishment of environmental monitoring protocols. Without knowledge of their production environment, farmers will have no capacity to adaptively manipulate cage environments to improve production. Environmental monitoring requirements have recently been included in Norwegian legislation (Norwegian Ministry of Fisheries and Coastal Affairs, 2008) and must be implemented by the Norwegian industry. Salmon farming industries elsewhere in the world should enact similar guidelines.

Ideally, continuous, whole of the water column, real-time monitoring would provide farmers with the best information on environmental conditions in cages. Whole of the water column monitoring technologies are under development and may be widely available to the industry soon (e.g. welfare meter; http://www.imr.no/welfaremeter/). In the meantime, as a minimum environmental sampling strategy for sea-cages, we recommend continuous monitoring of a temperature and salinity profile at each farm. Temperature and salinity should be monitored at a minimum of 4 depths in the cage, to adequately capture the top layer, the position of the thermocline or halocline and the bottom layer within cages. Dissolved oxygen levels should be measured continuously at a reference point outside of the farm and inside the farm within the most susceptible cage for low DO levels. Such a cage would be positioned between other cages, where the least current flow occurs and/or in the cage with highest stocked biomass. DO measurements should be taken a minimum of one third of the way into the cage and ideally at the same 4 depths as temperature and salinity. The depths measured must be chosen depending on the behavioural trade-offs fish exhibit towards environmental variables (principally feeding, light and temperature preferences) and modified according to seasonal changes in the outcomes of behavioural trade-offs.

6.2. Documenting the effects of sporadic events on vertical behaviours and environmental trade-offs in sea-cages

Numerous sporadic, short-term events dramatically alter conditions in sea-cage over time scales of hours to weeks. Such events include storms (high surface turbulence combined with increased currents), and jellyfish (e.g. Sammes and Greathead, 2004) and phytoplankton blooms (e.g. Johnsen and Sakshaug, 2000). Salmon may modify their vertical behaviours in response to these events and the nature and outcome of trade-offs towards environmental variables may in turn change. Some very limited evidence exists that suggests salmon move away from the surface and swim deep within cages during stormy weather (Bégout Anras et al., 2000), and that this behavioural response overrides vertical preferences towards other environmental variables such as temperature and light. While salmon are known to feed poorly during phytoplankton blooms and suffer increased mortality in both phytoplankton and jellyfish blooms, no data exists to assess how or whether salmon adapt their vertical behaviours or trade off decisions to cope with the modified conditions these blooms create. Thus, documenting the effects of sporadic events on behaviour should be a priority area for future research. Such information may provide farmers with the ability to modify the cage environment to enable salmon to engage in greater coping behaviours.

6.3. Welfare perspectives

Fish that experience a wide range of salinity, temperature and DO values may be better prepared to meet short-term changes and thus spatial variation may not necessarily be negatively correlated with fish welfare (Johansson et al., 2007). However, environmental variation might induce a stress response that incurs a physiological cost for the fish. Changes in environmental conditions will generally lead to a mismatch between physiological states and the environment, causing reduced maximum oxygen uptake rate and increased oxygen consumption. For example, temperature variation induces an extra energetic cost measured as increased oxygen consumption for individuals, with acclimation rates of 20-25 % per day towards the new temperature (Torgersen et al., 2009). Further, a negative psychological and physiological impact occurs in salmon exposed to an acute increase in temperature from 8 to 14 °C (Folkedal et al., 2010), as indicated by weaker conditioned responses to the anticipatory signal of a blinking light to indicate the commencement of feeding (see section 3.2).

Recently, several studies have indicated that stressful rearing conditions, including environmental stressors such as temperature and oxygen, are correlated with increased susceptibility to diseases and suppressed cytokine expression in fish (Wedemeyer, 1997; Metz et al., 2006; Fridell et al., 2007; Ndong et al., 2007; Fast et al., 2008; Perez-Casanova, 2008). For example, outbreaks of pancreas disease caused by the salmonid alpha virus may be stress related (McLoughlin and Graham, 2007). These findings emphasize that monitoring protocols for environmental stress are required during salmonid farming in sea-cages to identify when remedial actions should be taken.

6.3.1. Site-specific environments require specific stocking density limits

Maximum allowable stocking densities are a common tool used to regulate production (e.g. Norway: 25 kg m^{-3}; Norwegian Ministry of Fisheries and Coastal Affairs (2008)). Stocking density limits have also been discussed in the context of setting limits to ensure acceptable welfare (FSBI, 2002; Turnbull et al., 2005; Adams et al., 2007; Huntingford and Kadri, 2008; Turnbull et al., 2008). However, recent reviews have argued that the use of stocking density alone is insufficient to ensure welfare of farmed salmon (Huntingford and Kadri, 2008; Turnbull et al., 2008). Stocking density *per se* may not be the overriding factor limiting production. Instead the underlying consequences of low or high levels of social interactions associated with changes in stocking density or, more importantly, the degradation of water quality with increasing density may ultimately limit production. A better approach may be to develop husbandry systems that maximise welfare through monitoring water quality and observing fish behaviour (Huntingford and Kadri, 2008). Reinforcing this conceptual line of argument, Dawkins (2004) states that the behavioural patterns of animals will indicate their social choices and likes or dislikes about their physical environment. Changes in such patterns with stocking density or degree of crowding will be particularly important in identifying whether animals want and require more space.

A greatly underestimated aspect of the discussion regarding fish welfare in sea-cages is the actual swimming density of the fish and how it is affected by stocking density. Salmon rarely disperse evenly throughout the water column and instead congregate at certain depth intervals in densities from 1.5-20 times the stocking density (Table 1). Deriving generalisations from studies that have investigated the effects of stocking densities will prove difficult as the temporal and spatial variability of environmental variables that drive swimming densities to completely different levels than stocking densities will likely have been present yet unmeasured. Nevertheless, the great variation in vertical distributions in sea-cages induced by a changing environment identified in this review demands that preferences and aversions must be a component in establishing appropriate stocking densities.

Competition for depths based on the trade-off preferences of salmon may be one way in which adverse welfare effects manifest at high stocking density in sea-cages (Ellis et al. 2002). The severity of the effects would then depend on environmental heterogeneity, with increased severity where heterogeneity limits the volume of preferred space available (Johansson et al., 2006). For example, normal (7-11 kg m^{-3}) compared to high (18-27 kg m^{-3}) stocking densities allowed a greater proportion of caged salmon to occupy the more favourable, but restricted volume above the pycnocline (Johansson et al., 2006). Thus, high stocking densities may force more fish into sub-optimal environmental conditions, such as waters with high temperatures or low DO. Generally, a homogeneous sea-cage environment will have a higher production capacity compared to a heterogeneous environment, as long as environmental variables remain within thresholds. However, if threshold limits are approached, salmon will be better off in environments where they are able to choose based on their preferences.

In summary, better welfare outcomes for salmon in sea-cages could be achieved through establishing site-specific biomasses and stocking densities linked to the prevailing environmental conditions at individual sites and revising these between each production cycle. For such measures to be effective, modern monitoring protocols must be developed and included within “simple to use” management tools.

6.3.2 Manipulating vertical distributions through feeding regimes and artificial lights

Feeding intensively at the surface to rapidly satiate salmon leads to fish swimming deeper at preferred depths throughout the day instead of the shallower swimming typically seen in fish that are hungrier for longer when fed in small batches throughout the day (see Section 3.2).

Similarly, fully fed fish swam deeper compared to those fed in a restricted way. A combination of intensively fed and satiated fish thus leads to greater avoidance of the surface waters, which generally experience more variable and sub-optimal environmental conditions and may also lead to fish perceiving a sustained predation risk. Feeding regimes that provide the fish with the longest possible periods at their preferred environments (Dawkins, 2004) deeper in the cages may thus improve welfare.

Several studies indicate that light deployment depth may be used as a powerful management tool to attract the fish to optimal depth layers or disperse them to utilise more of the cage volume (see Section 4.1). Submerged artificial lights are superior to surface mounted artificial lights in this regard, as surface lights may induce crowding of the fish at night compared to submerged lights. Acute or chronic crowding may reduce the welfare of the fish through increased fin erosion (e.g. Latremouille, 2003; Person-Le Ruyet et al., 2008; 2009) or exposure to periods of suboptimal oxygen levels. Further, deployment of lights to specific depths may attract the fish away from potential depth-related harmful environmental conditions such as aluminium toxicity in freshwater runoff, algal and jellyfish blooms, suboptimal temperatures and oxygen, algae or parasitic infections such as sea-lice (reviewed by Dempster et al., 2009a).

6.3.3 Development of a behaviour-based operational welfare index (OWI)

The development of operational welfare indices (OWIs) to measure fish welfare has been a focus of the fish farming industry for the last decade (see review by Branson, 2008), yet few functional OWIs currently exist. Norway, the largest producer of Atlantic salmon (Table 2), has recently legislated that OWIs must be introduced (The Norwegian Animal Welfare Act, 2004). Despite this, in 2008, approximately 300 million individual Atlantic salmon and rainbow trout were held in sea-cages in Norway at any given time (Norwegian Fisheries Directorate, 2009) without any proper measure of their welfare status. Proxy measures of welfare, based on normal growth rates, the absence of disease outbreaks and low mortalities, are used as indirect measures. However, these measures (mortality and poor growth rates in particular) only allow recognition of episodes resulting in poor welfare after the fact and provide little or no ability for farmers to detect and react to the onset of conditions that lead to poor welfare. Disease outbreaks are often initiated by poor environmental conditions, indicating that a more immediate, early-warning OWI could provide a mechanism to implement cage management strategies to avoid disease (e.g. WEALTH; http://wealth.imr.no/).

OWIs must be easy for farmers to use and measurement should be simple or remote. Recent attempts to use indirect OWIs based solely on environmental measurements (e.g. temperature, oxygen) appear promising (e.g. welfare meter; http://www.imr.no/welfaremeter/). However, these environment-based measures of welfare are still indirect or rely on measurements of condition after the event. A new, instantaneous behaviour-based OWI could be based on the motivations, preferences or aversions of fish.

Using the comprehensive knowledge of preferred behaviour of Atlantic salmon in sea-cages now gathered in this review (Table 1) and Juell et al. (1995), we propose that an OWI based on modelled preferred vertical behaviours and deviations from these behaviours could be developed. The foundation of the OWI would be swimming depth preferences and packing densities of fish in sea-cages compared to expected preferred distributions. Normal cage behaviours at the group- and partly individual-level have been studied in detail (Table 1) and some of this behaviour has been modelled (Alver et al., 2004; Føre et al., 2009); combined, these studies provide a solid basis for establishing preferred behaviours under differing environmental conditions. If an unexpected packing density is observed, then the fish are choosing to avoid an area of the cage due to an undesirable environment. Calculation of an index based on deviation from expected behaviour could be used as a welfare index. In preliminary work, Oppedal et al. (2007) developed an index of preference displaying the avoidance/preference towards variable environments observed in cages. Further work in this area could result in the development of a real-time OWI that would allow farmers to respond to the onset of conditions through cage management techniques.

6.4. Comparing trade-off decisions between surface-based and submerged feeding

Preferred ranges of key environmental variables often occur at conflicting depths in sea-cages, forcing salmon to make trade-off decisions in their vertical positioning. For example, light conditions may induce fish to remain at depths where temperature or oxygen conditions are sub-optimal for growth relative to other depths. In such cases, control over salmon behaviour may prove beneficial as it enables the farmer to reduce the impact of detrimental culture conditions. As the addition of food to cages significantly influences salmon behaviour (see Section 3.2), altering food insertion depths and the time and duration of feeding events may represent ways in which to steer the fish both in time and space.

In all previous studies, feeding motivation has been based on surface feeding and trade-offs made by the fish have always been towards the surface (see Section 3.2). Submerged feeding at depths corresponding to the normal swimming depth preferences of salmon, for example in response to temperature, will likely drive the trade-off towards the environmental factors salmon themselves choose to be of most importance. Changing the depth position of the fish towards its preference should therefore enable better welfare (Dawkins, 2004). Keeping the fish away from the surface may increase growth, as indicated by Thomassen and Lekang (1993) and may also reduce sea lice infestations (Hevrøy et al., 2003). Therefore, we contend that studies at commercial-scale with submerged feeding are required to understand the importance of feeding and depth of feed entrance into sea-cages on the trade-off decisions made by salmon.

6.5. Manipulating the swimming depths of salmon to reduce encounters with sea lice

Sea lice are a perpetual problem for the salmon farming industry as they impose costs through reduced growth rates and treatments (Costello, 2009a), and they have been implicated in declines of wild stocks in Europe and North America (Ford and Myers, 2008). The salmon louse (*Lepeoptheirus salmonis*) is primarily responsible for infesting farmed salmon, although *Caligus* spp. epizootics can also occur (Costello et al., 2009b).

The biology and genetics of sea lice has been recently reviewed (Boxaspen, 2006). The infective copepodid stage of the salmon louse is pelagic, strongly phototactic (Bron et al., 1993), and typically occurs in greatest abundances at shallow depths in coastal waters (Johannesen, 1978; Costelloe et al., 1996; 1999; McKibben and Hay, 2004). Lice copepodids in large enclosures in the sea amassed near the surface during the day and dispersed into deeper layers at night (Heuch, 1995). Larvae actively avoid low salinity waters (Heuch et al., 1995), resulting in reduced lice abundances on farmed fish in low salinity areas (Revie et al., 2003; Jones and Hargreaves, 2007; Heuch et al., 2009). Depth, light and salinity preferences of sea lice larvae provide opportunities for active manipulation of the vertical distributions of salmon to reduce levels of infestation.

Salmon held in 20 m deep cages had approximately 50% less lice coverage compared to salmon held in 6 m deep cages at the same site, probably as a result of fish swimming in deeper waters in the 20 m cages away from peak lice abundances in the top few metres (Huse and Holm, 1993). Manipulative trials where salmon were held in submerged cages at 10-20 m depth compared to surface cages held from 0-10 m depth (Osland et al., 2001) and in small submerged cages at 4-8 or 8-12 m depth compared to surface controls at 0-4 m depth (Hevrøy et al., 2003) also resulted in significantly lower sea lice infestation at the deeper depths. While infestation rates were increased in small groups of salmon exposed to surface mounted artificial lights compared to fish held in control cages subject to natural light (Hevrøy et al., 2003), as part of a longer and larger study (Oppedal et al., 2001a) found that the preferred swimming depths of salmon were more important than the artificial surface light in determining lice infestation levels (Hevrøy et al., 2003).

Combined, the existing evidence suggests that an opportunity exists to steer fish away from surface waters where sea lice are in highest abundances. Today's use of submerged artificial lights, which attract salmon to the deployed light depth, may decrease infestation rates as salmon avoid the surface layer. Similarly, deployment of lights well below any steep halocline will also pull fish away from this area of concentrated sea lice larvae and likely reduce infestation levels. However, whether a phototactic locomotory response will also initiate vertical movement of larvae to depths at which artificial lights are deployed at, particularly at night, are unknown. If this were the case, actual infestation rates may be similar or increased. Rigorous testing is required to determine best light deployment practices.

Submerged feeding may also enable salmon to be encouraged away from the surface to depths where sea lice larvae occur in reduced abundances. Salmon at commercial densities have been observed to feed effectively through a submerged feeding system with feed input at 6 m depth (Dempster et al., 2008; 2009a) and 15 m depth (Korsøen et al., 2009). For such a technique to be effective, however, the trade-offs between both light, feeding motivation and temperature preferences must be addressed and taken into account so fish are not forced away from preferred light or temperature levels.

6.6. Climate change impacts on salmon aquaculture

Ocean temperatures have risen over the last century (Domingues et al., 2008) and various scenarios predict global rises in water temperature over the next century of 1-3 °C (e.g. IPCC, 2007). If such rises eventuate, longer periods of sub-optimal warm temperatures must be expected, with higher peak levels than normally seen today. Consequently, many of the current optimal salmonid farming regions (e.g. southern Norway, U.K., Tasmania, and the Chiloe Sea, Chile) will be exposed to a range of higher surface water temperatures above optimal thresholds in the summer months (> 20 ºC). Concurrently, sites to the north or south of these farming regions will become optimal and warmer winter temperatures may lead to marginally increased growth rates throughout winter.

Despite salmonids being among the most intensively investigated fish, temperature thresholds for large Atlantic salmon and rainbow trout in seawater are poorly known. For salmon smolts in freshwater, lethal thresholds of 24-32 ºC have been determined depending on acclimation temperatures (Elliott et al., 1991). Similarly, the lethal range for small rainbow trout in freshwater is 27-29.5 °C (Beitinger et al., 2000). Lower temperature thresholds are likely for larger fish; a summary of laboratory studies indicated that extended exposures to temperatures of 21-22.2 °C are lethal for migrating adult salmon in the Columbia River (Gray, 1983). During short periods of high temperature, thermal stress builds-up and if recovery periods are insufficient, tolerable cumulative stress levels will be exceeded (Bevelhimer and Bennet, 2000). Well below these critical threshold levels, rises in sea-surface temperatures are likely to significantly modify production parameters such as growth. The optimum temperature range for growth of Atlantic salmon in seawater ranges from 14-18 °C (e.g. Johansson et al., 2009). Field data from the large growth database of Skretting (2009) indicate that growth declines by 20-25% when temperatures increase from 16 to 20 °C in Atlantic salmon farms worldwide, while no data above 20 °C is available. Data from Tasmania indicate more severe effects with negative growth rates above 18 °C (Fig. 10).

Increased temperatures will likely increase periods of hypoxia within sea-cages, resulting from higher demand from the fish and lower solubility of oxygen in warmer water. Hypoxia will change the nature of environmental trade-offs, driving vertical avoidance behaviours. During periods of high temperature, fish in thermally stratified waters will move vertically and crowd in denser schools (e.g. Johansson et al., 2006), possibly escalating hypoxia problems. Within homogenous waters, fish will be equally exposed to unsuitable temperatures. If hypoxia results, poor welfare will ensue, resulting in a combination of increased disease susceptibility, poor growth, feed conversion and generally impaired performance. We therefore contend that future research on temperature thresholds for both individuals and groups of large salmonids in seawater is needed for improved site selection and farm management under a changing climate scenario.

6.7. Individual-based measurements

To increase our understanding of the preferences of salmon in sea-cages, future studies should include a greater focus on individual measurements. This will result in a better understanding of the coping and motivational mechanisms with environmental cues that drive the behaviour of fish in production environments (e.g. Sutterlin and Stevens, 1992; Juell, 1995; Johansson et al., 2007; Johansson et al., 2009). Such parameters would, if possible, include individual feed intake, growth, physiological status, sex, maturity, swimming speeds, horizontal movements, and parameters that describe the multiple environments they experience including depth, temperature, salinity and oxygen at high temporal and spatial resolution. This may in turn be used to better inform studies that rely on group-based measurements, improve production management and assist in ensuring acceptable welfare across the wide behavioural range exhibited by individuals within sea-cage production units of tens to hundreds of thousands of fish.

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Table 1. Factors affecting swimming depth and densities of Atlantic salmon (*Salmo salar*) in sea-cages. Upper-case letters indicate strong effects, lower-case letters indicate weak effects.

	Factor										Method				Environment/remarks
Reference	Feed	Light	Temp	Sal	DO	SD	Season	Sub	OFD /SD	Prac. Imp.	Fish size kg	no. fish	SD kg m^{-3}	Volume m^{3}	
Huse and Holm, 1993	f	NL					S			P	1.2-2.5	900	0.5-3	726 2420	4-14 °C at 0.2, 2 and 55 m; Sea lice infestation
Bjordal et al., 1993	F	nl								P	0.4-1.0	3×30000	7-17	1800	6-12 °C
Juell et al., 1994	F	nl								P	0.3	2×4300	1.3	1000	Feeding intensity;
											1	2×4000	4	1000	Restricted feeding
Fernö et al., 1995	F	NL	t				S		5x	P	0.35	2×3475	1.2	1000	4-14 °C at 0.2 and 2 m
Oppedal, 1995^{a}	f	NL/LL	t				s		2x	P	1-2.7	4×4962	3-8.5	1584	0-9 °C at 0-10 m
Juell, 1995 (review)	F	NL	t				s			P					
Hevrøy et al., 1998		NL/LL					S	Sub		P	1.8	6×10	0.2	100	Sea lice infestation;
											1.8-4	4×2300	2-5	2000	3-14 °C at 0-14 m
Bégout Anras et al., 2000	F	NL							2x	P	1.5	6000	15	1150	Strong and calm wind
Oppedal et al., 2001	f	NL/LL	T	s			S		10x	P	1.8-4	4×2300	2-5	2000	3-14 °C at 0-14 m
Juell et al., 2003		LL	t				s		20x	P	0.5-1.1	4×85000	2-7	12500	5-11 °C at 1-15 m
Juell and Fosseidengen, 2004	f	NL/LL	t				s		13x	P	0.2-0.7	4×200000	4-7	17500	5-16 °C at 1-25 m
Johansson et al., 2006		NL	T	s	DO	SD	S			P	1.7-2.3	3×8800	7-10	2000	11-20 °C at 0-12 m
											1.5-2.2	3×24700	18-27		
Oppedal et al., 2007		LL	T	s			S		10x	P	0.3-1.4	3×15000	2-9	2000	2-14 °C at 0-14 m
Johansson et al., 2007	f	NL	T	s	DO				10x	P	1.3-4.8	8×50000	8-16	12500-21875	8-16 °C at 0-20 m
Dempster et al., 2008		NL	t					SUB	10x	P	1.7-4.4	4×500	0.7	1100	6-14 °C at 0-10 m
Dempster et al., 2009		LL	t					SUB	10x	P	0.4-0.6	4×3800	1-2	1800	
Vigen, 2008		NL			DO				3x	P	2.5	7000	31	576	Delousing treatment
Korsøen et al., 2009		NL	t					SUB	3x	P	3.5-4.6	6×2300	5-7	2000	3-11 °C at 0-25 m
Johansson et al., 2009^{b}		NL	t			SD				P	1.5	23	6-32	2000	11-20 °C at 0-12 m

Temp: temperature; Sal: salinity; DO: dissolved oxygen; SD: stocking density; Sub: Submergence; OFD: Observed Fish Density; Prac. Imp.: practical implications; NL: natural light; LL: continuous artificial light; Volume = experimental sea-cage volume.

^{a} rainbow trout; ^{b} study on individuals

Table 2 . Worldwide production of salmonids (Atlantic salmon; *Salmo salar* L., and rainbow trout; *Onchorhynchus mykiss*) in sea-cages in 2008 (numbers in kilotons live biomass) within major production areas. Live body mass recalculated from Kjønhaug, 2009.

Country	*Salmo salar*	*O. mykiss*
Norway	797	92
Chile	429	194
Great Britain	146	
North America	145	
Faroes	39	
Australia	28	
Total	1584	286

Figure captions

Figure 1. Example of variations in mean group swimming speed (body lengths per sec; BL sec $^{-1}$) with time of day for Atlantic salmon (*Salmo salar* L.) held in sea-cages during December and January. Night is indicated by the dark bar at the top of the figure. Measurements were made using underwater cameras and infra-red light sources. Average swimming speeds per cage are shown with standard deviations. Data were taken from three 2000 m^3 cages in the control group of Korsøen et al. (2009).

Figure 2. Temperature from 10 August 2007 to 30 June 2008 (a) and group schooling densities in 5-day periods (b-e) from a representative, commercial salmon cage at Centre for Aquaculture Competence in Rogaland, southern Norway, illustrating some of the behavioural drivers discussed within the review. Data reproduced from Stien et al. (2009). The cage held 68 000 Atlantic salmon (*Salmo salar* L.) of average size 70 g in May and grew to 5.3 kg at harvest in November the year after. Cage size was 24 × 24 m wide, 20 m deep until January and 35 m deep thereafter. Stocking densities increased from 1.7 to 7.8 kg m^{-3}. Continuous artificial underwater light sources were applied at 7 and 15 m depth from 20 December until 12 June. A normal seasonal temperature pattern with warmest water in the surface layer during summer and coldest during winter was observed (a). In August (b), the salmon were attracted to the surface for feeding combined with a subgroup deep down that avoided the strong surface light. At night, all fish swam close to the surface where temperatures were most favourable. In December (c), a strong diurnal rhythm was observed with salmon choosing the slightly warmer deep water and avoiding high surface light intensities during the day and ascending towards the surface at night. Following the onset of continuous light, the rhythm disappeared and ‘daytime’ behaviour was observed continuously. In April (d), a reversed diurnal rhythm was evident with salmon in the 2-3 °C warmer surface layer during the day and descending down to the artificial light sources at night. In June (e), the larger salmon (>2.5 kg) avoided the high surface temperatures. The highest observed fish densities (2.6 × stocking density) were seen in April and resulted from a temperature preference and possibly high hunger motivation in spring.

Figure 3. Halocline preference in Atlantic salmon (*Salmo salar* L.) post-smolts held in sea-cages at Institute of Marine Research, Matre, southern Norway, one month after sea transfer distinguishable as peak fish biomass in the middle of the halocline and not at peak temperature. Data reproduced from Oppedal et al. (2001b). The vertical biomass distributions (% of biomass with depth) are based on echo-sounders in 4 replicate 12 × 12 × 14 m deep cages with approximately 4 × 7800 salmon with a mean weight of 113 g at sea-transfer on May 3. Distributions are means ± S.E. of two-hour periods before (June 2, am), during (June 2, pm and June 3) and after (June 5) strong freshwater runoffs. Corresponding temperature and salinity profiles are taken within the two hour period. Similar halocline preferences were still seen in August (not shown).

Figure 4. Extreme oxygen variation in September within a commercial sea-cage compared to outside reference (from Vigen, 2008). Cage size was 24 × 24 × 15 m deep and most of the 110 000 post-smolt Atlantic salmon (*Salmo salar* L.) of ca. 700 g (77 tons) swam in the upper 10 m at 7 to 15 kg m^{-3}. The severe hypoxia is correlated to slack water conditions.

Figure 5. Oxygen fluctuations through a year exemplified by data inside a commercial Atlantic salmon (*Salmo salar* L.) cage from 1 March 2008 to 1 March 2009 in the archipelago of Austevoll in Hordaland, Western Norway. Data reproduced from Kristiansen and Stien (2010). White areas indicate missing data. The cage held approximately 90600 Atlantic salmon at smolt transfer at end of October 2007 (55 g) and the salmon grew to 4.3 kg at start of June 2009 when they were

harvested. Cage size was 25 x 35 m wide and 20 m deep. Periods of oxygen super-saturation (>100%) occur during the spring algae bloom, while in the autumn there are periods of very low oxygen saturation (<50%). Oxygen saturation varies with time and depth.

Figure 6. Fish body length versus water current speed, indicating that smaller fish must swim faster (higher body lengths per second) than larger fish to maintain their position in a sea-cage during current flow.

Figure 7. Atlantic salmon (*Salmo salar* L.) attempt to avoid delousing chemicals by crowding in the 1-m surface water layer compared to an even distribution in a control group with only the de-lousing skirt present (reproduced from Vigen, 2008). Observed Fish Density (OFD) based on echo sounders are given on the colour scale. Skirts were completely set 15 min before (-15 on x-axis) the chemical was applied (time 0 min) and removed 45 to 51 min after treatment commenced. The control cage (skirt only) had the skirt set at time 0 and removed after 95 min. A commercial dose of cypermethrin (BETAMAX VET, ScanVacc AS, Årnes, Norway) was added within 5 min to the treatment volume (12 × 12 × 4 m deep) enclosed by the 6 m deep skirt which surrounded the sea-cage. The stocking density with net bottom lifted to approximately 4 m during the treatment was 30 kg m^{-3} (7000 fish of 2.5 kg).

Figure 8. Atlantic salmon (*Salmo salar* L.) avoid the volume in a sea-cage where a delousing chemical is present (reproduced from Oppedal and Vigen, 2009). The colour scale gives Observed Fish Density (OFD) based on echo sounders used during a bath treatment with deltamethrin (ALPHA MAX®, PHARMAQ AS, Oslo, Norway) in a commercial cage of circumference 157 m, 35 m deep using two skirts of 90 m length × 15 m deep. Total biomass was approximately 999 tons (196000 fish of 5.1 kg) giving a stocking density of 15 kg m^{-3}. The cage net was not lifted during treatment. Salmon were starved for 2 days prior to treatment. Feeding started 17 min prior to treatment application (-17 on x-axis) to attract the fish towards the surface and into the treatment volume. Skirts were set at -65 to -20 min and removed 38 to 85 min after the treatment was applied. The deltamethrin treatment was added from 0 to 1 m depth from time -12 to 0 min. Salmon swam deeper in the cage during setting of the skirt. Thereafter, a large proportion of the caged population were attracted to the surface when feeding commenced. Following chemical distribution, the salmon swam at depths below the treatment volume enclosed by the skirt. After skirts were removed and water flow through the sea-cage returned, salmon returned to the surface to feed.

Figure 9. Oxygen conditions and observed fish density (OFD) during a 50-hour period in a sea-cage (25 × 25 × 25 m deep) containing 146 tons of Atlantic salmon (*Salmo salar* L.) (reproduced from Johansson et al., 2007). The vertical distributions show an example of multiple behavioural trade-offs made by the salmon between surface light avoidance during the day, surface feed and feeding motivation attraction during the day and avoidance of depths in the sea-cage where hypoxia occurred during the second night and morning.

Figure 10. The effect of ambient water temperatures on the specific growth rate (SGR) of Atlantic salmon (*Salmo salar* L.) illustrated by data from the Skretting growth performance database of commercial farmers worldwide (closed squares; Skretting, 2009) where the cold temperature data mainly represent East Canada, and Finnmark and Agder in Norway. Growth data from Tasmania are shown for temperatures above 14 °C (open triangle). Fish size used for illustration is 1.5 kg while negative effects of high temperatures are more pronounced in large compared to small fish. The more severe negative effects of high temperature in the Tasmanian data is due to long-term (>3 months) experience of warm water at water depths experienced by the fish. In comparison, the worldwide data set is dominated by short-term high temperature experiences in combination with

unknown temperatures below 6 m depth and to what degree the fish occupy these or the measured temperatures.

Figure 1.

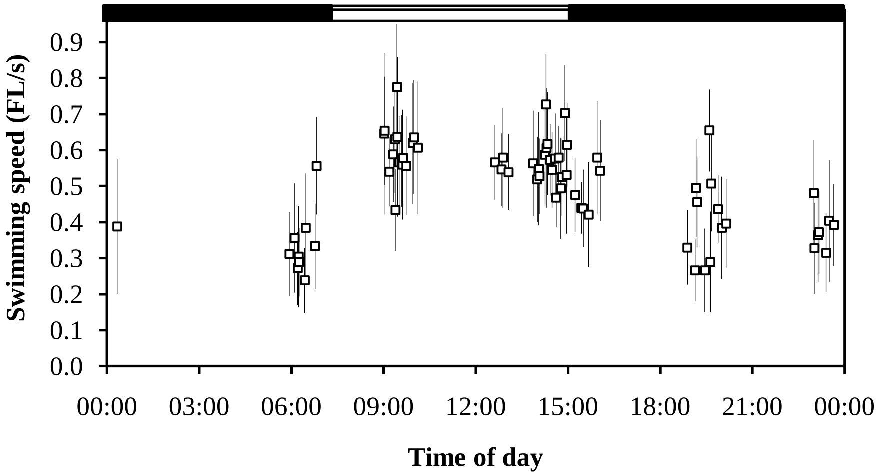

0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
Swimming speed (FL/s)
00:00
03:00
06:00
09:00
12:00
15:00
18:00
21:00
00:00
Time of day

Figure 2.

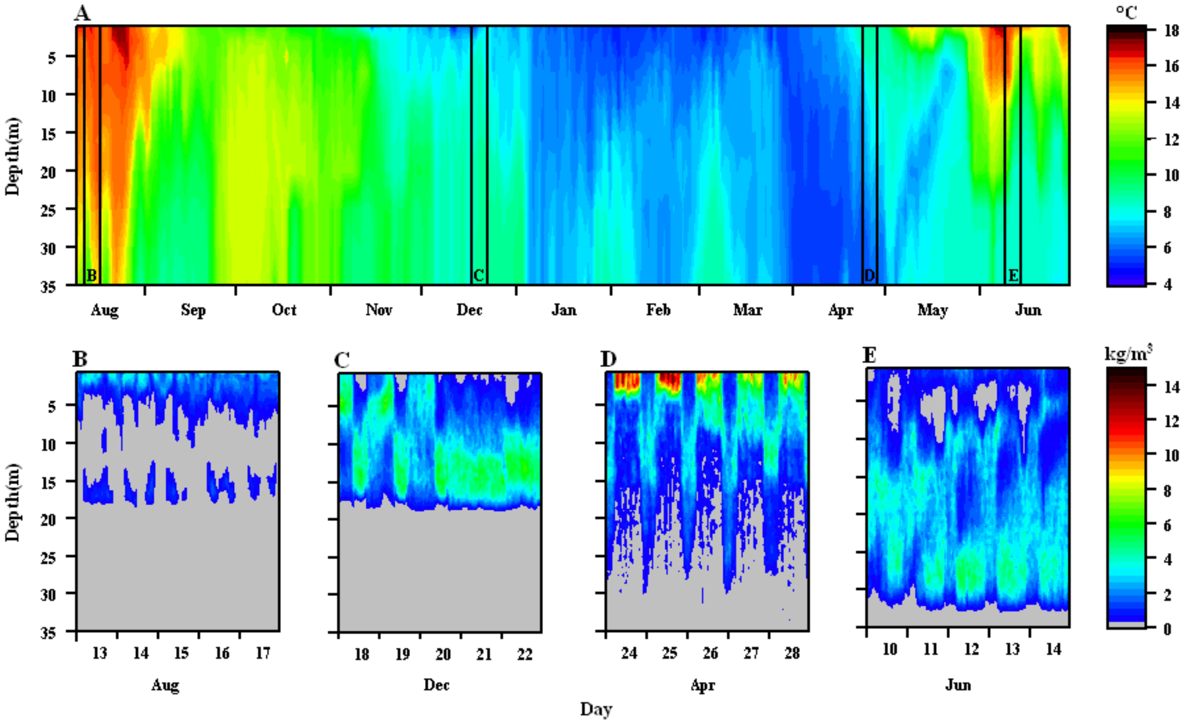

A
Dep th(m)
5
10
15
20
25
30
35
B
C
D
E
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
°C
18
16
14
12
10
8
6
4
B
C
D
E
13
14
15
16
17
Aug
18
19
20
21
22
Dec
24
25
26
27
28
Apr
10
11
12
13
14
Jun
Day
kg/m^3
14
12
10
8
6
4
2
0

Figure 3.

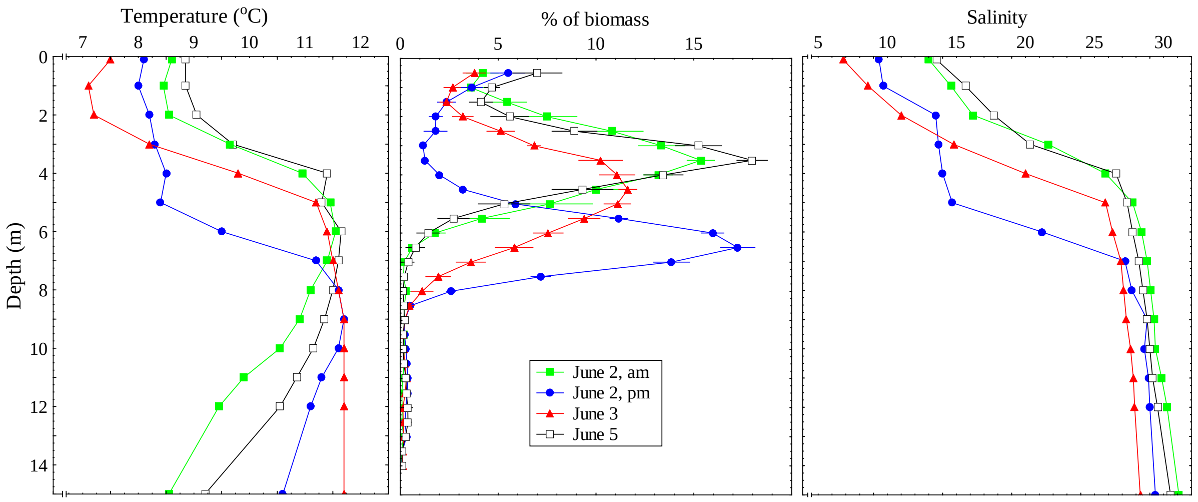
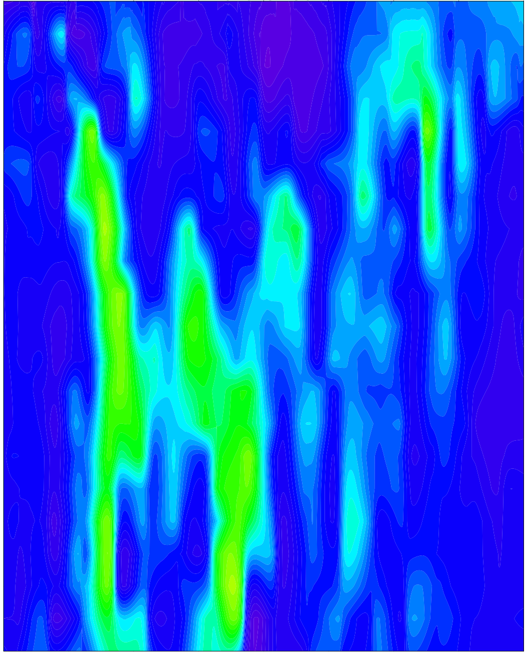

Temperature (oC)
7
8
9
10
11
12
% of biomass
0
5
10
15
Salinity
5
10
15
20
25
30
Depth (m)
0
2
4
6
8
10
12
14
June 2, am
June 2, pm
June 3
June 5

Figure 4.

Reference



Cage centre

DO (%)

Figure 5

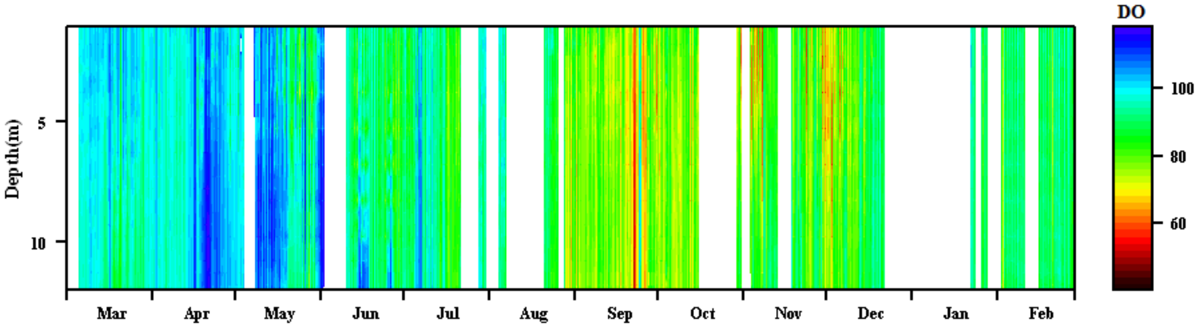
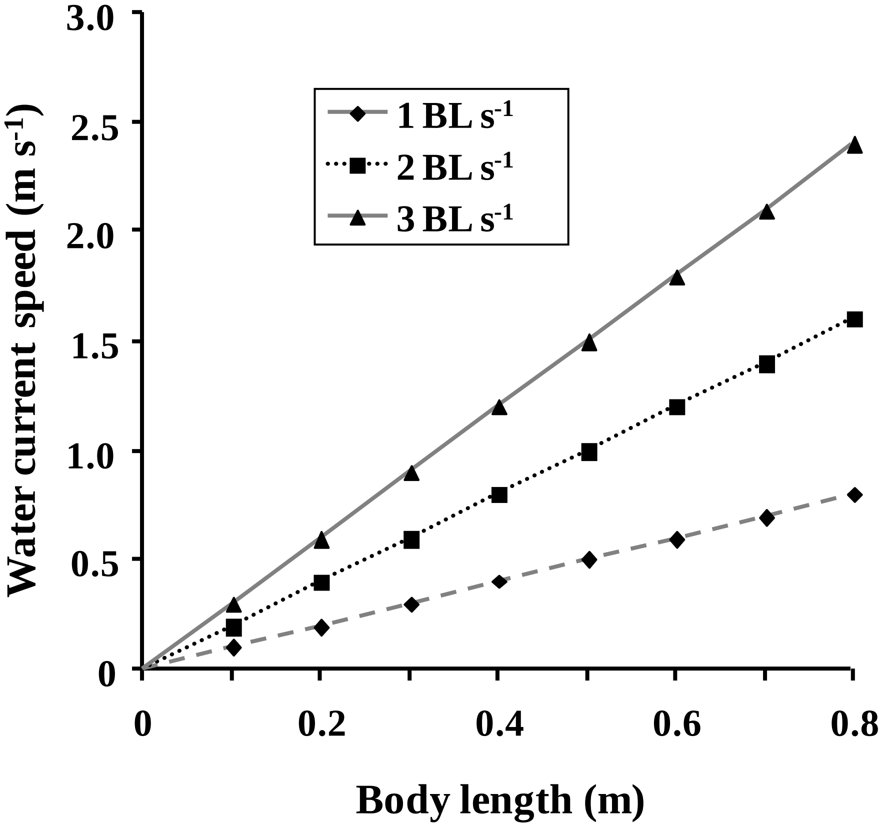

DO
100
80
60
Depth(m)
5
10
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb

Figure 6.



3.0
2.5
2.0
1.5
1.0
0.5
0
Water current speed (m s-1)
1 BL s-1
2 BL s-1
3 BL s-1
0
0.2
0.4
0.6
0.8
Body length (m)

Figure 7.

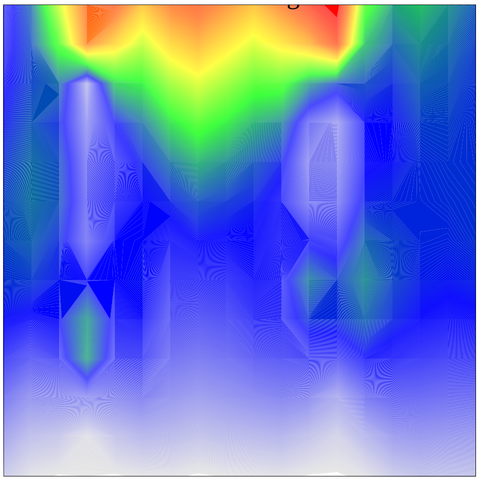


Figure 8.

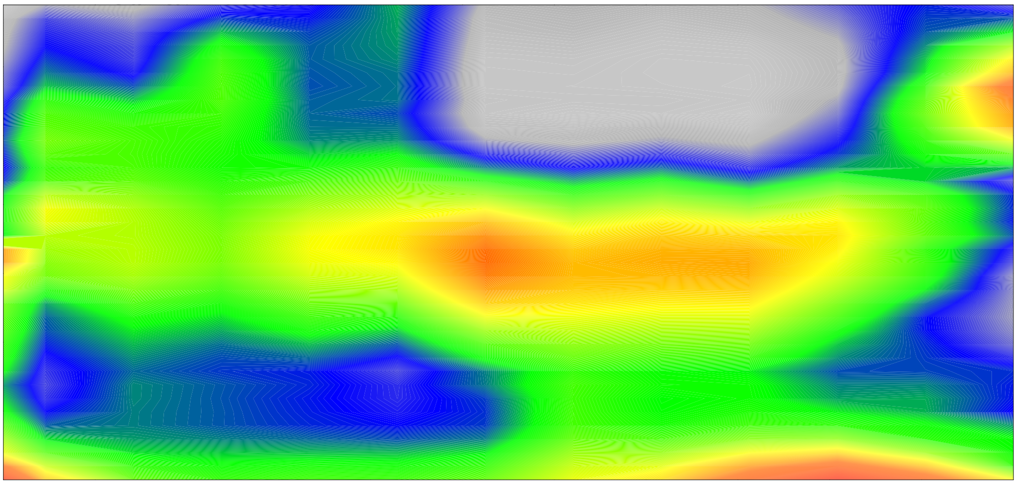


Figure 9.

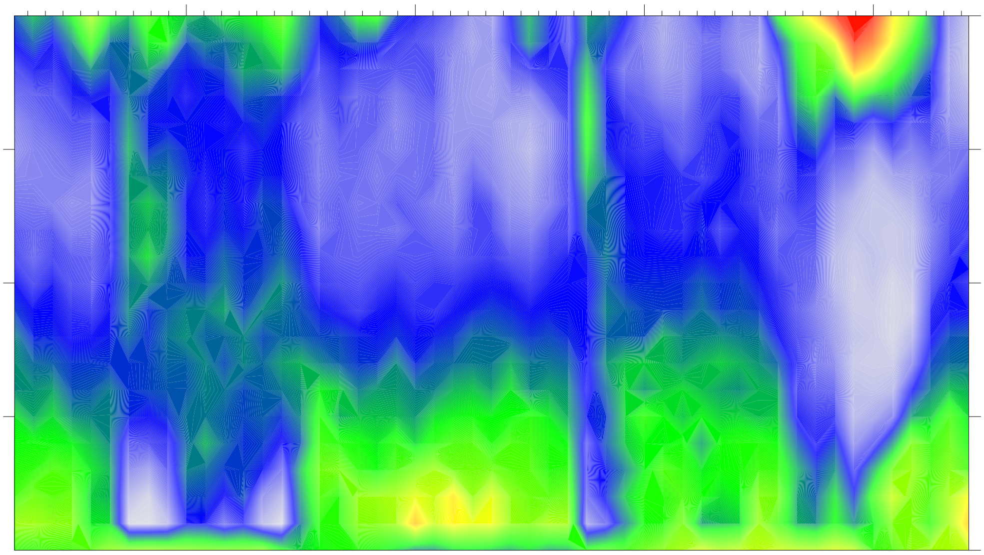
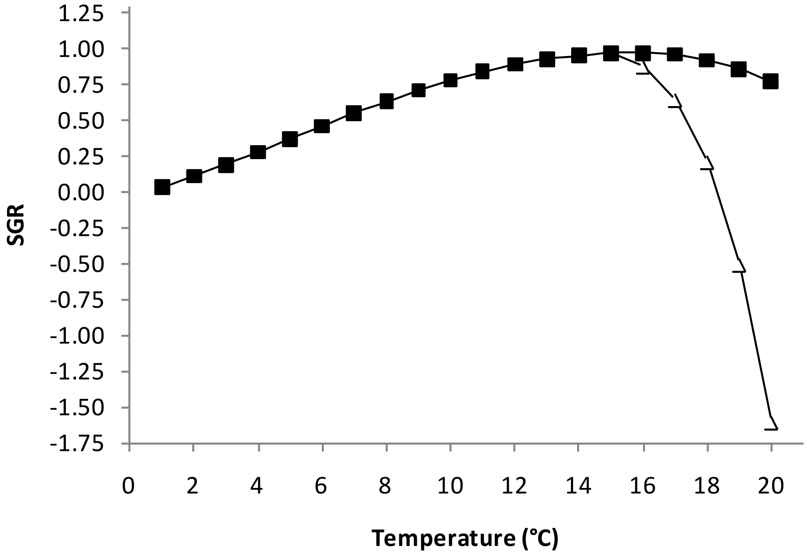


Figure 10.


1.25
1.00
0.75
0.50
0.25
0.00
-0.25
-0.50
-0.75
-1.00
-1.25
-1.50
-1.75
SGR
0
2
4
6
8
10
12
14
16
18
20
Temperature (°C)