Swimming depth and thermal history of individual Atlantic salmon (*Salmo salar* L.) in production cages under different ambient temperature conditions ☆

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ABSTRACT

Salmon production cages at sites with a pronounced thermal stratification give individual fish an opportunity to choose their thermal environment. The behavioural responses of individual salmon to such stratification, however, are poorly documented. Information about spatial distributions and temperature experience of individual Atlantic salmon (initial weight 1.5 kg) was gathered over a period of 4 months (mid-August to early-December) using data storage tags. Fish were stocked at normal or high densities in triplicate 2000 m^3 production cages at 5.6–14.5 (ND) or 15.7–32.1 (HD) kg m^{-3}, and valid data were collected for 12 ND and 11 HD salmon. There were large inter- and intra-individual variations in swimming depth, with indications that the salmon performed behavioural thermoregulation in an attempt to maintain body temperature within the range of 8–20 °C. Stocking density influenced the average swimming depth and body temperature, indicating competition for preferred thermal space in periods of unfavourably high temperature (towards 20 °C) in large parts of the cage volume. Analysis of temporal behavioural patterns demonstrated a higher variability during day than night and that 60 to 70% of the individuals displayed cyclic diel patterns in either swimming depth or body temperature in at least one out of three sub-periods. The results are discussed in relation to bio-energetic and thermal stress theory and possible consequences for growth variation in salmon cages. Generally, this study suggests that individual swimming depth and body temperature is in part a response to available temperature interacting with stocking density and time of day, while some individual variation cannot be ascribed to the measured variables.

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1. Introduction

Salmon production cages in Norway are often situated in fjords that offer sheltered and easily accessible sites. Water quality at these sites is often characterised by strong thermal and saline vertical stratification (Johansson et al., 2006, 2007; Oppedal et al., 2007). Behavioural studies of such caged Atlantic salmon (*Salmo salar* L.) at the group level using echo-sounders (Bjordal et al., 1993) strongly suggest that swimming depth and schooling density are modulated both by photo- and thermoregulatory behaviour (Fernö et al., 1995; Oppedal et al., 2001; Juell and Fosseidengen, 2004; Johansson et al., 2006; Johansson et al., 2007; Oppedal et al., 2007). The environmental preferences are traded off against motivational factors such as feed and perceived threats (Juell et al., 1994a; Fernö et al., 1995). Further, the space used by caged salmon groups is influenced by high stocking density (Johansson et al., 2006). Several studies suggest that

salmonids perform behavioural thermoregulation in sea-water (Sutterlin and Stevens, 1992; Reddin et al., 2004; Oppedal et al., 2001, 2007) and during migration to sea (Sauter et al., 2001). It seems likely that individuals may crowd for preferred thermal space in a stratified environment (Johansson et al., 2006), although dominance hierarchies are unlikely to develop under typical commercial densities of caged salmon (Juell, 1995). Rapidly fluctuating temperatures have been reported to be stressful to fish (Wedemeyer, 1973; Barton and Schreck, 1987), while similar fluctuating temperatures in other studies show a positive effect on growth (Brett, 1971; Spigarelli et al., 1983; Bevelhimer and Bennett, 2000). Even though bimodal swimming depth distributions have been observed at group level (Juell et al., 1994a; Oppedal et al., 2007), which indicate inter-individual variation in depth preferences, the variability in swimming depth of individual fish within these groups remains largely unknown (Juell and Westerberg, 1993; Bégout et al., 2000).

Only a few studies have related the individual behaviour of salmonids in cages to environmental variation. Sutterlin and Stevens (1992) reported that during early summer, within a temperature range of 3 to 18 °C, small groups of both rainbow trout (*Oncorhynchus mykiss*) and Arctic charr (*Salvelinus alpinus*) held in separate 8 m-deep cages showed a preference for temperatures around 13.5 °C. They also

observed 12 h cycles of 3–4 °C difference in preferred temperature in rainbow trout.

The principal aims of the study was to identify patterns in swimming depth (i) and resulting thermal history (ii) of individual salmon stocked at high or normal commercial densities in a thermally stratified cage environment. Subsequently, analyses were performed to determine whether such patterns were related to seasonal thermal stratification characteristics (iii), time of day (iv), stocking density (v) or individual characteristics (vi) such as fish size.

2. Materials and methods

2.1. Fish and study site

The study was performed at the Institute of Marine Research cage-environment laboratory at Solheim, Norway (60°N 4°E), a typical fjord site with a brackish layer at surface. Triplicate 15 m deep cages (2000 m^3) were stocked with Atlantic salmon (NLA strain) at normal (ND) (5.6 ± 0.3 kg m^{-3}) and high (HD) (15.7 ± 0.5 kg m^{-3}) densities on August 16th 2002 and grown until 14.5 ± 0.8 kg m^{-3} (ND) and 32.1 ± 1.1 kg m^{-3} (HD) by December 3rd the same year.

In each of the six cages, 8–10 individuals (1.42 ± 0.37 kg) were tagged with data storage tags (38.4 mm length $\times$ 12.5 mm diameter, 9.2 g weight in air and 5 g in water, DST-milli, StarOddi, Iceland). The tags were inserted into the body cavity through a 1.5 cm incision and closed with sutures while the fish were anaesthetised with Benzocain (Norsk Medisinaldepot, Bergen, Norway) at 0.15 ml l^{-1}. The fish were kept in a holding tank to recover from surgery, were then returned to their cage, and recordings started 3 weeks after surgery. The tags recorded swimming depth and body temperature once per hour and were inter-calibrated prior to the experiment at 3 m depth. Body length (cm) and weight (accuracy 5 g) was recorded at the start and the adipose fin was removed for later identification of the tagged fish at harvest. The initial average live body weights ($\pm$ SEM) of the two treatment groups were 1.28 ± 0.01 kg and 1.26 ± 0.02 kg, respectively. Thirty of the initial 58 tags were recovered, but 7 of these contained corrupted data. Useable data sets were obtained from 12 of the ND salmon (3, 4 and 5 from each of the 3 cages) and 11 HD salmon (3, 4 and 4 per cage) of average initial weight 1.50 ± 0.34 kg with individuals ranging from 0.77 to 2.2 kg. The missing tags consisted of 13 fish with tag loss while 15 were undiscovered at harvest or mortalities. Due to practical limitations of the harvesting procedure the tags were recovered at uneven time points from the slaughter-house, from December 2002 to July 2003, when the size and sex of the fish were recorded. Specific growth rate (SGR, % per day) was calculated from the formula: $\text{SGR} = (e^q - 1)100$, where $q = (\ln(W_2) - \ln(W_1))/(t_2 - t_1)$ and W_2 and W_1 are the average live body weights at times t_2 and t_1, respectively (Houde and Scheckter, 1981).

The fish were fed to apparent satiation at 0900–1200 and 1400–1600 h each day, with satiation being evaluated on the basis of feeding responses and waste feed present under the fish observed using underwater cameras. Depth profiles of temperature, salinity and light intensity were measured with an YSI 6600 CTD (Yellow Springs Instruments, Ohio, U.S.A.) close to the farm using pre-programmed winches recording three profiles per hour. All data were condensed to hourly averages at 0.5 m intervals prior to analysis.

2.2. Data analysis

Environmental data for each observed swimming depth at specific times were extracted from the database, producing a separate environmental data set for each fish to validate the DST data set.

In order to separate the general effect of stocking density, a general linear model with restricted cubic splines based on the design package of the R language (Harrell, 2001) was used to analyse the interaction between either body temperature or swimming depth and stocking

density in time throughout the whole observation period. Splines are functions defined piecewise by polynomials and can be used as a modern alternative to polynomial functions to characterise nonlinear relationships in linear models (Venables and Ripley, 1999). Cubic spline uses cubic polynomial as the basis.

To present high resolution data, the period of data analysis was reduced. Thus, three four-day sub-periods (sp) with different and relatively stable thermal profiles were selected for further analysis of the individual data (8–12 September (sp1), 28 September to 2 October (sp2) and 18–22 October (sp3)).

Within each sub-period, external mean temperature over all depths, mean body temperature and SD for each individual were calculated. Cyclic rhythms in swimming depth and body temperature were analysed by spectral analysis (fast Fourier transform, spectrum function of the R language) for each individual within each sub-period. Spectral analysis can be used to estimate the spectral density function of a given time series (Chatfield, 1984) and to represent an observed time series as a superposition of sinusoidal waves of various frequencies allowing identification of the peak frequencies (Diggle, 1990). On the basis of this analysis, the behaviour of individuals was classified as diel (18–32 h), less than diel (<18 h) or none (>32 h). This helped to identify swimming patterns during different thermal conditions.

The mean body temperature and mean swimming depth were analysed for differences between day and night by ANOVA. Night was defined as the hours during which light intensity was below $0.1~\mu\text{E m}^{-2}\text{s}^{-1}$. Day was defined as the interval starting at the second hour after night (dawn) to the hour before dusk, i.e. 1 h between night and day was excluded in the morning and evening. Feeding periods were excluded from the defined day since feeding is known to alter the swimming depth of the fish (Bjordal et al., 1993; Juell et al., 1994b).

Inter-individual differences in body temperature variation were analysed in relation to cyclic rhythms, diel behaviour and swimming depth using the Fligner–Killeen test, which is one of the most robust tests against departures from normality among the several tests for heterogeneity of variance (Conover et al., 1981).

In order to reveal size dependent thermal preferences, the relationship between the initial body weight and mean body temperature of the fish was analysed using Pearson's product moment correlation for all three sub-periods. The same test was used to
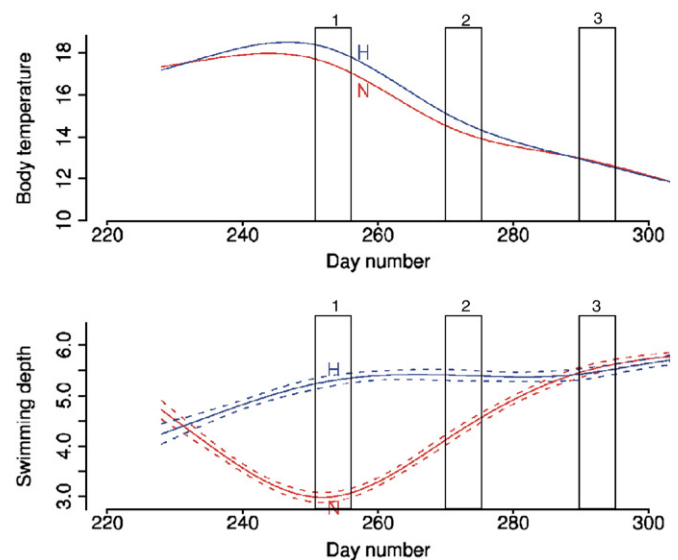

Fig. 1. The figure at top illustrates a linear regression model using restricted cubic splines analysing the interaction between body temperature (°C), treatment (H = high stocking density, N = normal stocking density) and time. The bottom figure illustrates the same analysis with swimming depth (m) as the dependent variable. The columns denote the time of the three different sub-periods.

analyse the correlation between the variation in body temperature (SD) for the whole period and specific growth rate over the whole period. The latter was only performed on the five fish at ND that were recovered at the end of the experiment. All statistical analyses were performed using R version 2.2.0 (R Development Core Team, 2005).

3. Results

3.1. Effect of stocking density and environment

Fish in the HD group had up to 0.8 °C higher mean body temperature than ND fish from day 240 to day 280 (Fig. 1) corresponding to the early autumn period when the highest sea temperatures were observed. The body temperatures between stocking densities differed at average body temperatures above 13.5 °C. This coincided with a clear difference in swimming depths as more fish of the HD group swam in the deeper warmer water than in the ND group (Figs. 1 and 2). The treatment effects declined with the general decrease in the water temperature with season, reversal of the inclination of the thermocline and the establishment of a thick,

uniform layer in the deeper parts of the cage. Towards winter, this layer held the warmest water available and was occupied by most fish.

The three selected sub-periods to be analysed in detail represented distinctive seasonally different thermal gradients typical for early (sp1), transition (sp2) and late autumn (sp3) at the site (Fig. 2). In sp1 high sea temperatures (up to 20 °C) were observed in most of the water column, with a variable, narrow and cooler surface layer (down to 13 °C) and a mean water temperature of 18.5 °C. In sp2 the temperature range was larger (10–19 °C), including a warm water layer at 2 to 6 m depth with a steep thermocline above and below and a mean water temperature of 13.3 °C. In sp3 a cold surface layer (down to 8 °C) was observed with a variable and narrow thermocline around 1 m, a total vertical temperature range of 8–14 °C and a mean temperature of 12.6 °C. The salinity profile was comparable between all sub-periods with lower values and large variation (the halocline) in shallow waters while more stable deeper down (Fig. 3). In sp1 and sp3, the halocline extended down to a depth of 3 m, with salinity increasing from 15–21 at the surface to approximately 30 ppt below the halocline. In sp2 the brackish water extended to around 6 m depth with values from 12 at surface to 30 ppt below the halocline.
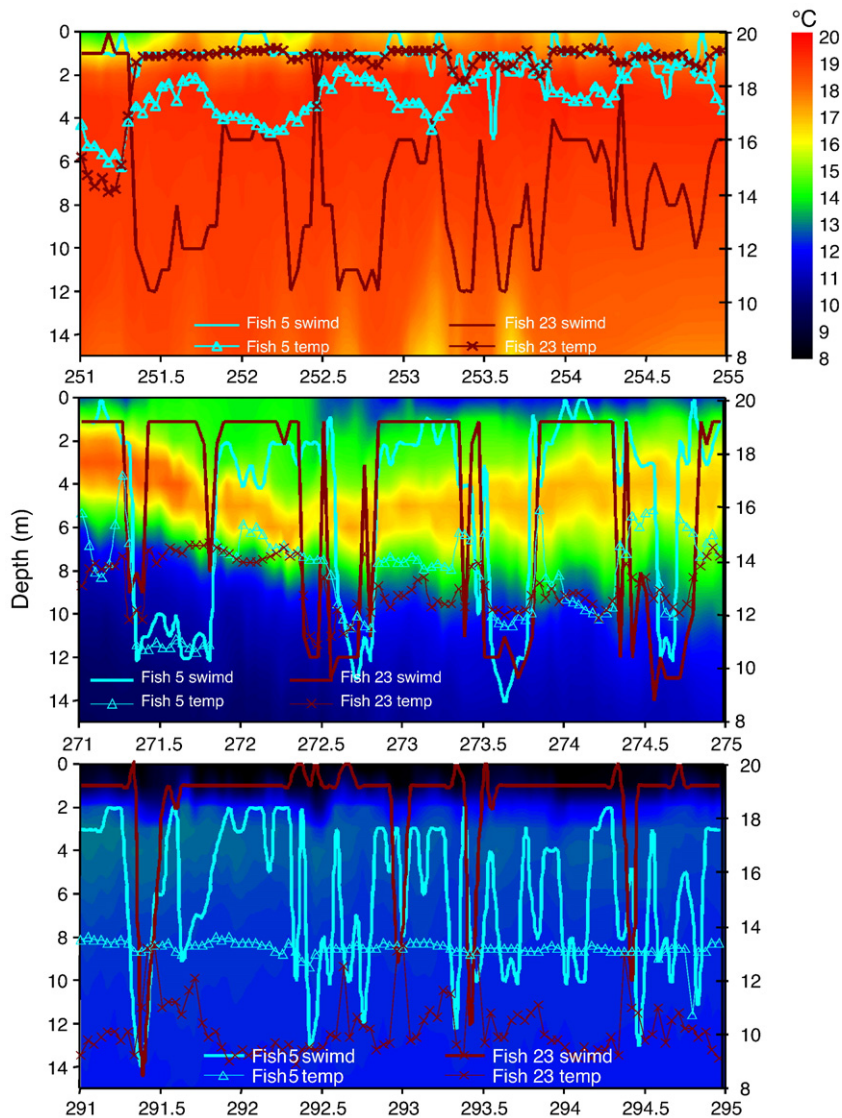

Fig. 2. Environmental water temperature (colour scale, °C), body temperature (temp) and swimming depth (swimd) of two individual fish within sub-period 1, 2 and 3 at top, middle and bottom respectively. The left vertical axis represents the depth from 0–15 m and the right vertical axis body temperature (°C). The horizontal axis represents the day number of the year (integer represents midnight and .5 denotes midday). The swimming depth (solid line) and body temperature (fish#5 = triangle; fish#23 = x) of two fish with different diel behaviours are illustrated with turquoise and dark red lines, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
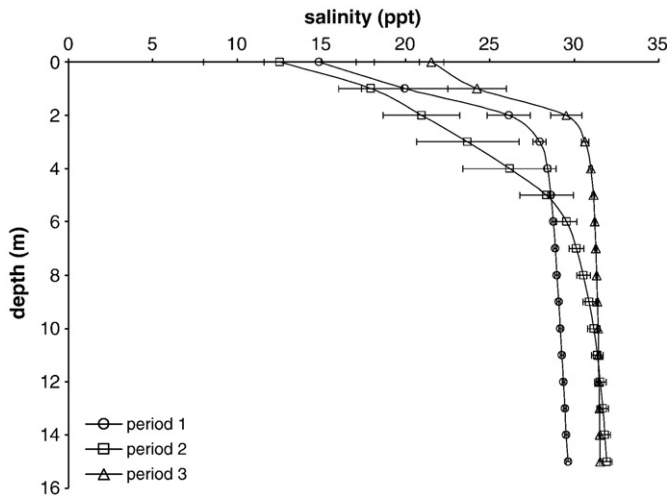
Fig. 3. Salinity presented as mean $\pm$ SD for each depth interval during each sub-period. The vertical axis represents depth (m) and the horizontal axis salinity (ppt).

3.2. Seasonal and diel patterns of swimming depth and body temperature

In sp1 the mean swimming depth was more shallow ($F = 35.6$, $P < 0.001$) and less variable ($P < 0.01$) at night compared to day (Fig. 4).
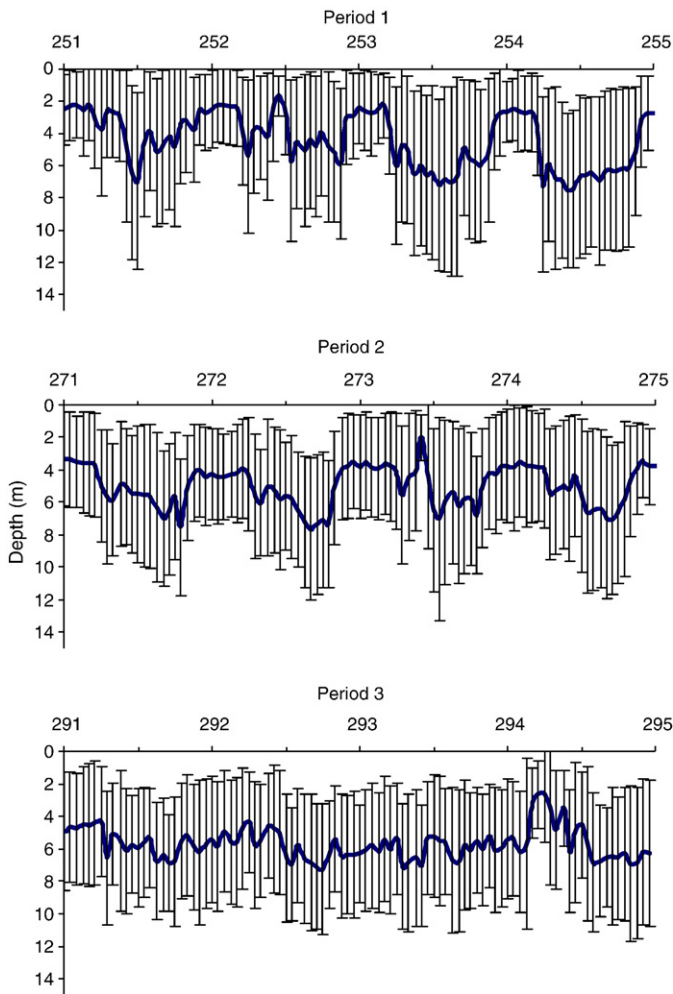

Fig. 4. Mean $\pm$ SD swimming depth of all individuals (pooled data) in the 3 different sub-periods (Periods 1, 2 and 3). The vertical axis represents depth (m) and the horizontal axis day number of year (integer represents midnight and .5 denotes midday).

This resulted in a lower ($F = 4.36$, $P < 0.05$) and less variable ($P < 0.01$) body temperature at night compared to day. The pattern was reflected in the time-series analysis, where most individuals displayed cyclic rhythms in either swimming depth or body temperature, while 40% displayed pronounced rhythms in both (Table 1). There was, however, no correlation between the variation in swimming depth and the variation in body temperature during this period ($r = -0.05$, $P = 0.82$).

In sp2 similar pattern as in sp1 was observed with fish swimming closer to surface at night and deeper down at day ($F = 13.15$, $P = <0.01$) resulting in the opposite diel change in temperature to sp1; higher mean body temperatures at night compared to day ($F = 4.94$, $P = <0.05$). There was a trend to less variation in body temperature at night compared to day ($P = 0.06$), while there was an overall greater variation in both swimming depth and body temperature in sp2 compared with sp1 coinciding with a wider range of temperatures available (Table 2). Time-series analysis displayed diel patterns in swimming depth and temperature but less compared to sp1. Only 17% of individuals displayed cycles of both, while 43% displayed a swimming depth rhythm and 35% displayed a rhythm in body temperature (Table 1). The fish that shifted depths exhibited the greatest differences in body temperature interpreted from the positive correlation between the variation in swimming depth and the variation in body temperature ($r = 0.56$, $P = 0.005$).

In sp3 there were no differences between night and day in either mean swimming depth ($F = 0.37$, $P = 0.55$), variation in swimming depth ($P = 0.76$), mean body temperature ($F = 1.85$, $P = 0.18$) or variations in body temperature ($P = 0.44$). This coincided with a narrow range of sea temperatures available. Still, 65% of the individuals displayed a diel cycle in swimming depth, 35% a cyclic pattern in body temperature and 30% in both swimming depth and body temperature (Table 1). Additionally, the absolute change in both swimming depth and body temperature was lower than during the previous periods. During sp3 no correlation between the variation in swimming depth and body temperature was evident ($r = 0.09$, $P = 0.67$).

There were no differences between individuals with or without a diel temperature rhythm and variation in body temperature (sp1:

Table 1
Presence of diel rhythms in swimming depth or body temperature defined as Diel (18–32 h), Less diel (<18 h) and None (>32 h) for the individual fish (Fish id.) in normal (N) and high (H) stocking density treatment during three sub-periods.

Fish id.	Treatment	Sub-period 1		Sub-period 2		Sub-period 3	
		Depth rhythm	Temp. rhythm	Depth rhythm	Temp. rhythm	Depth rhythm	Temp. rhythm
1	N	Diel	Diel	None	Diel	Diel	Less diel
2	N	Less diel	Diel	Less diel	None	Less diel	Less diel
3	N	Diel	Diel	None	None	Diel	Diel
4	N	Diel	Diel	None	None	None	Less diel
5	N	Diel	Diel	Diel	Diel	Diel	Diel
6	N	Diel	Diel	Diel	Diel	Less diel	None
7	N	Less diel	None	Less diel	Diel	Diel	Diel
8	N	Diel	Diel	Diel	Less diel	Diel	Less diel
9	N	Less diel	Diel	Less diel	None	Diel	Less diel
10	N	Less diel	None	Less diel	None	Diel	Diel
11	N	Less diel	Less diel	None	Diel	None	Diel
12	N	None	Less diel	Diel	Less diel	Diel	Less diel
13	H	Diel	Diel	Diel	Less diel	Diel	Diel
14	H	None	Less diel	Diel	None	Diel	Diel
15	H	Diel	Less diel	Diel	Less diel	Diel	Diel
16	H	Less diel	Less diel	Less diel	None	Diel	None
17	H	Diel	Less diel	None	Diel	Diel	Less diel
18	H	Diel	Diel	Diel	Diel	Diel	None
19	H	Less diel	Diel	None	Less diel	Diel	Less diel
20	H	Diel	Diel	Less diel	Less diel	Less diel	Less diel
21	H	Less diel	Less diel	None	None	None	Less diel
22	H	Less diel	Diel	Diel	Diel	Less diel	None
23	H	Diel	None	Diel	None	Less diel	None

The data is based on time series analysis of hourly registrations of swimming depth and body temperature in each individual.

Table 2
Mean body temperature $\pm$ SD (°C) and mean swimming depth $\pm$ SD (m) for each individual (Fish id.) during three sub-periods within normal (N) and high (H) stocking density treatment.

Fish id.	Treatment	Sub-period 1		Sub-period 2		Sub-period 3	
		Temperature	Depth	Temperature	Depth	Temperature	Depth
1	N	18.6 ± 0.9	1.8 ± 0.8	14.4 ± 0.5	1.9 ± 1.3	13.2 ± 0.4	8.1 ± 3.7
2	N	18.3 ± 1.0	1.5 ± 1.1	14.6 ± 0.5	2.3 ± 1.3	13.1 ± 0.7	4.5 ± 2.7
3	N	17.0 ± 1.1	0.6 ± 0.5	12.8 ± 0.9	2.2 ± 3.6	11.6 ± 1.3	3.7 ± 3.8
4	N	18.6 ± 0.5	6.1 ± 5.2	15.2 ± 0.7	3.4 ± 1.4	12.9 ± 0.2	6.2 ± 2.6
5	N	17.7 ± 1.0	1.1 ± 0.7	13.5 ± 1.6	4.8 ± 4.5	13.2 ± 0.3	6.0 ± 3.4
6	N	17.9 ± 0.9	7.5 ± 6.1	12.6 ± 1.1	9.4 ± 2.5	13.1 ± 0.6	8.0 ± 3.3
7	N	18.2 ± 0.5	1.7 ± 1.8	12.7 ± 1.3	8.1 ± 3.9	13.2 ± 0.2	10.5 ± 3.1
8	N	18.6 ± 0.8	3.9 ± 4.0	13.3 ± 1.3	6.9 ± 4.2	13.2 ± 0.1	7.7 ± 2.3
9	N	17.7 ± 1.0	1.1 ± 0.6	14.9 ± 0.9	2.6 ± 1.6	13.4 ± 0.2	5.8 ± 2.6
10	N	18.2 ± 1.0	4.7 ± 5.2	14.3 ± 0.0	3.4 ± 2.4	12.9 ± 0.7	5.8 ± 3.7
11	N	19.1 ± 0.3	4.4 ± 3.4	14.5 ± 1.0	4.0 ± 2.6	13.2 ± 0.3	3.9 ± 2.0
12	N	18.4 ± 0.9	3.3 ± 3.8	14.3 ± 1.1	5.0 ± 3.3	13.3 ± 0.2	5.9 ± 3.0
13	H	18.0 ± 0.9	5.4 ± 5.5	13.7 ± 0.8	3.5 ± 3.9	11.2 ± 1.3	2.3 ± 2.7
14	H	19.3 ± 0.2	3.5 ± 0.9	15.3 ± 1.0	3.6 ± 1.2	13.0 ± 1.0	3.6 ± 1.0
15	H	19.0 ± 0.3	5.3 ± 3.5	15.4 ± 1.1	4.3 ± 2.2	12.8 ± 0.7	6.4 ± 4.2
16	H	18.9 ± 0.4	7.7 ± 4.4	11.7 ± 1.3	11.8 ± 2.5	13.2 ± 0.1	9.3 ± 3.0
17	H	19.0 ± 0.2	8.1 ± 3.7	15.0 ± 1.2	6.4 ± 2.6	13.2 ± 0.2	8.7 ± 4.0
18	H	18.5 ± 1.2	2.2 ± 1.2	14.4 ± 1.8	6.1 ± 4.2	13.3 ± 0.2	7.0 ± 3.5
19	H	19.2 ± 0.2	8.4 ± 2.1	15.0 ± 1.0	5.9 ± 1.7	13.4 ± 0.1	5.6 ± 1.1
20	H	18.7 ± 1.0	2.8 ± 2.4	14.8 ± 1.9	5.3 ± 3.9	12.4 ± 1.3	4.2 ± 3.7
21	H	19.0 ± 0.2	9.0 ± 1.4	14.3 ± 1.6	7.4 ± 2.4	13.1 ± 0.4	7.6 ± 3.3
22	H	18.1 ± 1.1	3.3 ± 4.1	14.3 ± 1.2	3.3 ± 3.2	12.9 ± 0.5	3.0 ± 2.4
23	H	18.7 ± 1.2	7.3 ± 3.3	13.1 ± 1.0	4.6 ± 5.0	10.3 ± 1.1	1.7 ± 2.5

$P = 0.28$, sp2: $P = 0.84$ and sp3: $P = 0.44$). The large inter-individual variation in swimming depth and body temperature during all periods is shown in Table 2 and Fig. 5.

To summarize, in many fish a diel rhythm in swimming depth with the fish ascending towards the surface during the night and dispersing to use more of the available water volume in the daytime was observed (Fig. 4). This diel pattern was most pronounced in sp1 and sp2.

3.3. Individual fish behaviour — thermoregulation?

Large individual variation was one of the major findings. This is illustrated by superimposing the swimming depth and resulting body temperature of two individuals on the thermal environment (Fig. 2). Fish#5 was the only fish that showed a consistent diel rhythm in both body temperature and swimming depth during all sub-periods, while fish#23 showed inconsistency through variable diel cycles in swimming depth between sub-periods and no diel cycle in body temperature (Table 1).

In sp1, fish#5 swam shallow and up to the surface in several observations at night resulting in a diel rhythm in both swimming depth and body temperature. Fish#23 swam in the deeper part of the cage with large variation and a diel rhythm in swimming depth. But, as this fish swam in the homogeneous warm water it showed no diel rhythm in body temperature. The mean body temperatures of fish#5 and fish#23 were 17.7 and 18.7 °C respectively (Table 2), while mean external temperature outside the cages during sp1 was 18.5 °C. In sp2, both fish displayed a diel rhythm in swimming depth, but resulting in a significant diel rhythm in body temperature of Fish#5 only. Generally, the two fish used a larger depth interval than during sp1 and migrated through the peak temperature but seemed to avoid it with few observations recorded at this depth. The mean body temperatures of the fish in sp2 were 13.5 °C in fish#5 and 13.1 °C in fish#23 while external temperature was 13.3 °C. In sp3 only fish#5 displayed a diel rhythm in swimming depth and resulting body temperature. The mean body temperatures were 13.2 °C in fish#5 and 10.3 °C in fish#23, while external temperature was 12.6 °C.

In total, fish#5 avoided the large water volumes of relatively high temperatures in sp1 and experienced a lower body temperature compared to the external average. In the latter sub-periods fish #5

avoided the coldest volumes (and warmest in sp2) resulting in an experience of a higher body temperatures than the external average. The swimming depth pattern of fish #23 resulted in the opposite temperature experiences compared to the available.

3.4. Size, growth rate and variation in body temperature

No correlations were evident between body weight at the start of the experiment and body temperatures during the three periods (sp1: $t = 0.06$ $P = 0.80$, sp2: $t = -0.07$ $P = 0.75$ and sp3: $t = -0.06$ $P = 0.78$).

Five of the six fish that were recovered just after the end of the experiment were from the ND group. These fish had specific growth rates ranging from 0.58–1.16% bw day^{-1} during the experimental period. There was a significant negative correlation between growth rate (SGR) and variation in temperature (SD) ($r = -0.89$, $P < 0.05$). However, due to the low number of fish these data only exemplify the range of variation in the growth of caged fish.

4. Discussion

4.1. Environment and restrictions

This study confirms that salmon in production cages in Norwegian waters may be exposed to a considerable thermal stratification, especially in cages situated in fjords (Johansson et al., 2006, 2007; Oppedal et al., 2007). There are a number of unmeasured or unobserved variables that may have affected fish behaviour, including oxygen levels, motivational state and social interactions. There is evidence that salinity does not influence non-migratory salmon over the ranges observed (Bakke et al., 1991; Johansson et al., 2006). Therefore neither the variables that were not measured nor salinity and possible behavioural influences are discussed in detail here.

4.2. Diel variation

The behavioural data from early and mid autumn clearly demonstrated a diel rhythm in swimming depth, with more stable positioning closer to the surface at night compared with daytime. This concurs with studies for wild Atlantic salmon (*S. salar* L.), pink salmon (*Oncorhynchus gorbuscha*), coho salmon (*Oncorhynchus*
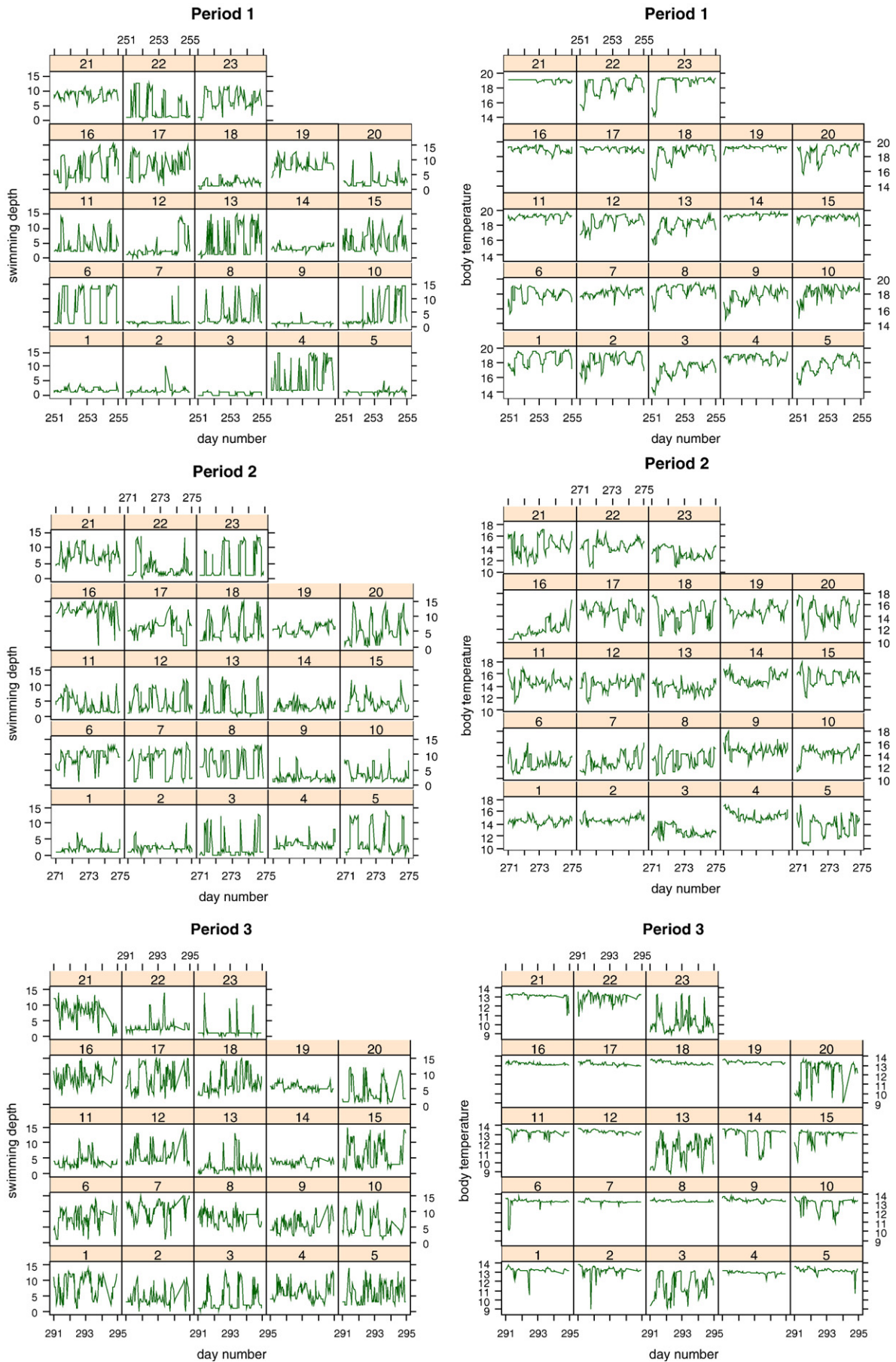
Fig. 5. Swimming depth and body temperature of all individual fish (1–23) during the three sub-periods (Periods 1, 2 and 3). The vertical axis represents swimming depth (m) in the figures on the left side and body temperature (°C) in the figures on the right side. Horizontal axis represents day number of the year with integer representing midnight.

kisutch) and steelhead trout (*O. mykiss*) (Walker et al., 2000; Reddin et al., 2004). Diel rhythms in the swimming depth of Atlantic salmon farmed in cages have been linked to diel variations in light intensity, feed attraction, perceived predation risk combined with temperature conditions (Juell et al., 1994a; Fernö et al., 1995; Oppedal et al., 2001; Juell and Fosseidengen, 2004; Johansson et al., 2006; Oppedal et al., 2007). Furthermore, the ascent to the surface at night has been hypothesised as a photo-regulatory behaviour aimed at maintaining schooling as the light fades at dusk (Juell et al., 2003; Juell and Fosseidengen, 2004). Thus, the observed diel cycle may reflect an avoidance of high light intensities and perceived predation risk during daytime, a preference for sufficient light for schooling during dusk and low surface predation risk at night.

The greater variation in swimming depth at daytime of the individuals may also be an effect of the same trade-off between attraction to feed and avoidance of high light intensities and perceived predation risk. However, even when feeding periods were excluded from the analysis, there was still a larger variation during the day. It is 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. Taken together, the daytime variation may reflect a general increase in swimming activity with more trade-offs between different needs during day than night. The similarity between day and night in the third period was likely due to a larger part of the cage volume being thermally uniform and within the preferred thermal range and stronger avoidance of lower surface temperatures.

4.3. Behavioural thermoregulation

Through behavioural thermoregulation, fish can optimise their physiological processes (Neill, 1979; Jobling, 1994). Active thermo-regulation was strongly indicated by the difference in body tempera-ture between stocking densities and by the spatial and temporal differences in thermal space use in all sub-periods. At night during early autumn, many individuals crowded at the surface and avoided the warmer water below, while during mid autumn they avoided the colder water at the surface (see Fig. 4). Also, active avoidance of the cold surface water (around 8 °C), both at day and night in late autumn, was seen by all individuals having a higher body temperature than the surface layer (>10 °C, Table 2). The results suggest that salmon thermo-regulated actively during periods but that this was tempora-rily traded off against e.g. light intensity, feed attraction, and perceived predation risk during daytime in some periods.

4.4. Thermal preference

Identifying a single optimal temperature in a production cage may be difficult for fish due to a constantly changing environment and the complex interactions between individuals. The observations revealed a large diversity in body temperatures. Even though thermal preference has often been thought of as one optimal temperature from a growth perspective, the observed diversity in body tempera-tures suggests that it might be more appropriate to consider the thermal preference as a temperature range rather than a fixed temperature. Magnuson (1991) concluded that the thermal niche could best be described as a range of preferred temperatures from 4 °C to 10 °C for a cold-water fish. Jobling (1981) summarized the literature and suggested a thermal preference range of 12–15 °C and an optimal growth temperature range of 14–18 °C for Atlantic salmon, while Johansson et al. (2006) suggested a thermal preference range of 16–17.5 °C for caged adult salmon at group level. Austreng et al. (1987) concluded that the growth rate of adult Atlantic salmon increases at least up to 14 °C and most salmonids are reported to have an optimal

growth rate between 12 and 17 °C (Jobling, 1994). This suggests that most of the body temperatures observed in this study were inside the thermal preference range and that the observed variation in body temperature may be caused by other abiotic and biotic factors.

4.5. Thermal stress vs. bio-energetic optimalisation

The hypothesis concerning thermal energetic optimalisation (Brett, 1971; Biette and Geen 1980), assumes that fish have the capacity to acclimate to or tolerate thermal changes, which to some extent contradicts the theory of thermal stress that suggests large variations in body temperatures reduce growth (Wedemeyer, 1973; Barton and Schreck, 1987; Bevelhimer and Bennett, 2000). Although the different thermal histories do not necessarily reflect different levels of success in behavioural thermoregulation, it is interesting to consider the results in the context of thermal stress. Thermal stress due to exposure to sub-lethal temperatures outside the thermal tolerance range or costs related to temperature acclimation within this range is likely to have had some effect on the fish observed in this study. For example, in early autumn the sea temperature was above the previously reported maximum growth temperature for Atlantic salmon. The higher mean body temperatures of individuals in the high density compared with the normal density group suggests that increased competition for preferred thermal space may have resulted in more of the high density fish having to acclimate to sub-optimal temperatures. The growth rates of the five individuals in ND also suggest that a large variation in body temperature reduces growth, possibly due to energetic costs related to thermal stress (Wedemeyer, 1973). However since this analysis only included five individuals it should not be treated as more than an indication.

4.6. Individual variation

Individual differences in thermal behaviour were demonstrated by detailed studies of two individuals. During the warmest period fish#5 had a lower body temperature than fish#23, while during the colder subsequent periods fish#5 had a higher body temperature, which could suggest that fish#5 was more successful in regulating its temperature closer to the optimal temperature for growth than fish#23 or that it was more highly motivated for another reason. It has been suggested that individual variation depends on factors such as sex, size, level of hunger, food availability, predation pressure, parasitism or competition from conspecifics (Woiwode and Adelman, 1992; Magurran, 1993; Jobling, 1994; Juell et al., 1994a). No relation-ship was observed between different preferred temperatures and start weight. However, since growth-rate data in this trial was limited for practical reasons, we cannot exclude the possibility of undetected growth or size related variation. A previous study of swimming depth and feeding indicated that there was a strong correlation between hunger level and surface attraction (Juell et al., 1994a). However, parts of that study used restricted feeding while the amount of feed in this experiment was unrestricted, giving individual fish the possibility of obtaining food at all depths in the cage. This may have led to less conform behaviours and the adoption of different feeding strategies reflected in the individual's swimming depth. In addition, the temporal feeding rhythms of individuals in a group may also be unsynchronized leading to inter-individual variation in hunger level and cyclic patterns of swimming depth (Juell, 1995). Folkedal (2006) found a positive correlation between eye cataracts and surface attraction, which suggests health status as one possible cause of individual variation. Taken together, the large intra- and inter-individual variation in swimming behaviour suggests the existence of an unsynchronized variability in the motivational status of individual fish, or that other significant environmental variables were not recorded or analysed.

5. Conclusion

In conclusion, the swimming depth and body temperature of one individual is most likely a result of multiple trade-offs between environmental preferences, motivational and social factors (Sutterlin and Stevens, 1992; Claireaux et al., 2000). This study suggests that in commercially stocked cages, fish avoiding high and low temperatures are also affected by stocking density. As a result, no one strategy is necessarily optimal, expected or even possible, either for all or individual fish at all times.

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References

Austreng, E., Storebakken, T., Åsgård, T., 1987. Growth rate estimates for cultured Atlantic salmon and rainbow trout. Aquaculture 60, 157–160.

Bakke, H., Bjerknes, V., Øvreeide, A., 1991. Effect of rapid changes in salinity on the osmoregulation of postsmolt Atlantic salmon (*Salmo salar*). Aquaculture 96, 375–382.

Barton, B.A., Schreck, C.B., 1987. Metabolic cost of acute physical stress in juvenile steelhead. Trans. Am. Fish. Soc. 116, 257–263.

Bégout Anras, M.L., Kadri, S., Juell, J.E., Hansen, T., 2000. Measuring individual and group swimming behaviour under production densities: test of a 3D multiple fish acoustic positioning system in a sea cage. In: Moore, A., Russell, I. (Eds.), Advances in Fish Telemetry. CEFAS, Lowestoft Publication, pp. 75–78.

Bevelhimer, M., Bennett, W., 2000. Assessing cumulative thermal stress in fish during chronic intermittent exposure to high temperatures. Environ. Sci. Policy 3, 211–216.

Biette, R.M., Geen, G.H., 1980. Growth of underyearling sockeye salmon (*Oncorhynchus nerka*) under constant and cyclic temperatures in relation to live zooplankton ration size. Can. J. Fish. Aquat. Sci. 37, 203–210.

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

Brett, J.R., 1971. Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). Am. Zool. 11, 99–113.

Chatfield, C., 1984. The Analysis of Time Series: An Introduction, 3rd edn. Chapman and Hall, New York. 286 pp.

Claireaux, G., Webber, D.M., Lagardère, J.-P., Kerr, S.R., 2000. Influence of water temperature and oxygenation on the aerobic metabolic scope of Atlantic cod (*Gadus morhua*). J. Sea Res. 44, 257–265.

Conover, W.J., Johnson, M.E., Johnson, M.M., 1981. A comparative study of tests for homogeneity of variances, with applications to the outer continental shelf bidding data. Technometrics 23, 351–361.

Diggle, P.J., 1990. Time Series: A Biostatistical Introduction. Oxford University Press, Oxford. 257 pp.

Fernö, A., Huse, I., Juell, J.E., Bjordal, Å., 1995. Vertical distribution of Atlantic salmon (*Salmo salar* L.) in net pens: trade-off between surface light avoidance and food attraction. Aquaculture 132, 285–296.

Folkedal, O., 2006. Effects of group size and light regime on swimming depth and social interactions of individual Atlantic salmon (*Salmo salar* L.) in a sea cage. Masters Thesis, University of Bergen, Norway.

Harrell Jr., F.E., 2001. Regression Modelling Strategies: With Applications to Linear Models, Logistic Regression, and Survival Analysis. Springer-Verlag, New York. 568 pp.

Houde, E.D., Scheckter, R.C., 1981. Growth rates, rations and cohort consumptions of marine fish larvae in relation to prey concentration. Rapp. P.-V. Re`un. — Cons. Int. Exp. Mer 178, 441–453.

Jobling, M., 1981. Temperature tolerance and the final preferendum — rapid methods for the assessment of optimum growth temperatures. J. Fish Biol. 19, 439–455.

Jobling, M., 1994. Fish Bioenergetics. Chapman & Hall, London. 309 pp.

Johansson, D., Ruohonen, K., Kiessling, A., Oppedal, F., Stiansen, J-E., Kelly, M., Juell, J-E., 2006. Effect of environmental factors on swimming depth preferences of Atlantic salmon (*Salmo salar* L.) and temporal and spatial variations in oxygen levels in sea-cages at a fjord site. Aquaculture 254, 594–605.

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

Juell, J.-E., 1995. The behaviour of Atlantic salmon in relation to efficient cage-rearing. Rev. Fish Biol. Fish. 5, 320–335.

Juell, J.E., Westerberg, H., 1993. An ultrasonic telemetric system for automatic positioning of individual fish used to track Atlantic salmon (*Salmo salar* L.) in a sea cage. Aquac. Eng. 12, 1–18.

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

Juell, J.E., Fernö, A., Furevik, D., Huse, I., 1994a. Influence of hunger level and food availability on the spatial distribution of Atlantic salmon, *Salmo salar* L., in sea cages. Aquac. Fish Manage. 25, 439–451.

Juell, J-E., Bjordal, Å., Fernö, A., Huse, I., 1994b. Effect of feeding intensity on food intake and growth of Atlantic salmon, *Salmo salar* L., in sea cages. Aquac. Fish Manage. 25, 453–464.

Juell, J.E., Oppedal, F., Boxaspen, K., Taranger, G.L., 2003. Submerged light increases swimming depth and reduces fish density of Atlantic salmon *Salmo salar* L. in production cages. Aquac. Res. 34, 469–477.

Magnuson, J.J., 1991. Fish and fish ecology. Ecol. App. 1, 13–26.

Magurran, A.E., 1993. Individual differences and alternative behaviour. In: Pitcher, T.J. (Ed.), Behaviour of Teleost Fishes. Chapman and Hall, London, pp. 441–477.

Neill, W.H., 1979. Mechanisms of fish distribution in heterothermal environments. Am. Zool. 19, 305–317.

Oppedal, F., Juell, J.E., Taranger, G.L., Hansen, T., 2001. Artificial light and season affect vertical distribution and swimming behaviour of post-smolt Atlantic salmon in sea cages. J. Fish Biol. 58, 1570–1584.

Oppedal, F., Juell, J.E., Johansson, D., 2007. Thermo and photoregulatory-behaviour influence swimming depth and schooling density of caged Atlantic salmon. Aquaculture 265, 70–81.

R Development Core Team, 2005. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reddin, D.G., Friedland, K.D., Downton, P., Dempson, J.B., Mullind, C.C., 2004. Thermal habitat experienced by Atlantic salmon (*Salmo salar* L.) kelts in coastal Newfoundland waters. Fish. Oceanogr. 13, 24–35.

Sauter, T.S., Crawshaw, L.I., Maule, A.G., 2001. Behavioural thermoregulation by juvenile spring and fall Chinook salmon, (*Oncorhynchus tshawytscha*), during smoltification. Environ. Biol. Fisches 61, 295–304.

Spigarelli, S.A., Thommes, M.M., Prepejchal, W., Goldstein, R.M., 1983. Selected temperatures and thermal experience of brown trout in a steep thermal gradient in nature. Environ. Biol. Fishes 8, 137–149.

Sutterlin, A.M., Stevens, E.D., 1992. Thermal behaviour of rainbow trout and Arctic char in cages moored in stratified water. Aquaculture 102, 65–75.

Venables, W.N., Ripley, B.D., 1999. Modern Applied Statistics with S-PLUS, 3rd edn. Springer-Verlag, New York. 113 pp.

Walker, R.V., Myers, K.W., David, N.D., Aydin, K.Y., Friedland, K.D., Carlson, H.R., Boehlert, G.W., Urawa, S., Ueno, Y., Anma, G., 2000. Diurnal variation in thermal environment experienced by salmonids in the North Pacific as indicated by data storage tags. Fish. Oceanogr. 9, 171–186.

Wedemeyer, G., 1973. Some physiological aspects of sublethal heat stress in the juvenile steelhead trout (*Salmo gairdneri*) and coho salmon (*Oncorhynchus kisutch*). J. Fish. Res. Board Can. 30, 831–834.

Woiwode, J.G., Adelman, I.R., 1992. Effects of starvation, oscillating temperatures, and photoperiod on the critical thermal maxima of hybrid striped × white bass. J. Therm. Biol. 17, 271–275.