Aquaculture 290 (2009) 296–303

Contents lists available at ScienceDirect

Aquaculture

journal homepage: www.elsevier.com/locate/aqua-online

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

David Johansson [a,*,1], Kari Ruohonen [b], Jon-Erik Juell [a], Frode Oppedal [a]

[a] Institute of Marine Research, NO-5984 Matredal, Norway
[b] Finnish Game and Fisheries Research Institute, Turku Game and Fisheries Research, Itäinen Pitkäkatu 3, FI-20520 Turku, Finland

ARTICLE INFO

Article history:
Received 28 September 2007
Received in revised form 27 January 2009
Accepted 13 February 2009

Keywords:
Fish behaviour
Telemetry
Vertical distribution
Thermal stratification
Thermoregulation

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.

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

☆ This work is published in memory of Jon-Erik Juell.

* Corresponding author. Tel.: +46 521 60 54 92.
E-mail address: david.johansson@o.lst.se (D. Johansson).
[1] Present address: County Administrative Board of Västra Götaland, SE-521 84 Vänersborg, Sweden.

0044-8486/$ – see front matter © 2009 Elsevier B.V. All rights reserved.
doi:10.1016/j.aquaculture.2009.02.022

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 × 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 (±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: $SGR = (e^{q-1})100$, 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 μE m^{-2} 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

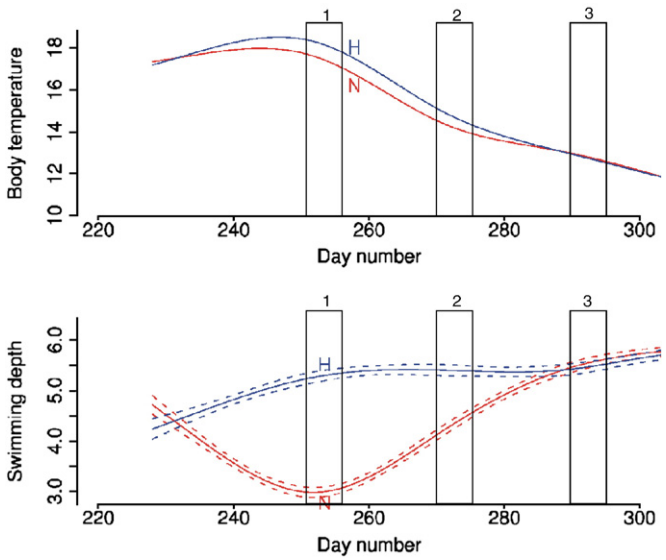

Fig. 1. The figure at top illustrates a linear regression model using restricted cubic splines analysing the interaction between body temperature (°C), treatment (H = high stocking density, N = normal stocking density) and time. The bottom figure illustrates the same analysis with swimming depth (m)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