A MULTIPLE APPROACH TO BEHAVIOUR STUDIES OF SALMON REARED IN MARINE NET PENS

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ABSTRACT

The behaviour of Atlantic salmon in culture was investigated by various techniques with the ultimate goal of characterizing the behaviour typical for a situation with rapid growth. Differences in behaviour between and within fish groups and the effect of environmental variation was especially studied. Seasonal and daily changes of the behaviour are also described.
INTRODUCTION

Farm animals should be kept under conditions that promote growth and prevent diseases. Growth rate may represent the best ultimate measure of successful rearing. More instantaneous estimates of the prosperity of the animals are, however, important when trying to optimize rearing conditions. Behavioural and physiological studies are essential in this connection.

Knowledge of the behaviour of fish under aquaculture conditions was of importance already two thousand years ago for e.g. choosing the optimal stocking densities of the Chinese carp species (Bardach et al. 1972). In modern times, surprisingly few behaviour studies on fish in aquaculture have, however, been made, although results from other experiments are often interpreted in terms of behaviour. The growth pattern of juvenile salmonids is thus often explained as an outcome of aggressive interactions between the fish (e.g. Refstie and Kittelsen 1976, Fagerlund et al. 1981).

Rearing salmonids in marine net pens is a growing industry. Under natural conditions, salmon seem to be organized in loose groups and typical schooling does not take place. When such a species is confined to small net cages in high densities, considerable modifications of the behaviour must take place.

Two behaviour studies on salmon and rainbow trout in net cages have been conducted (Sutterlin et al. 1979, Phillips 1985). These studies gave important information on e.g. the typical swimming speed, feeding and general behaviour. But the behaviour of salmon cannot be expected to be constant under all conditions. The influence of variations in environmental factors has not yet been studied. There is also little information on differences in behaviour between different populations and rearing units and between fish within a pen. Furthermore, little is known about daily rhythms in activity and seasonal differences.

The aim of the present study is to describe different aspects of the behaviour of salmon in marine net pens with the ultimate goal to characterize the behaviour typical for a situation with rapid growth. Special emphasis was put on changes in behaviour over time and variations between and within groups. The influence of environmental factors was also investigated. The effect of variations in light level was studied in particular by comparing shaded and unshaded pens. In addition to observations on behaviour, some data on heart rate and blood parameters are included to get an idea of the relationship between the behaviour and physiology of the fish.

MATERIALS AND METHODS

The study was made at Austevoll Marine Aquaculture Station. The fish were held under standard rearing conditions in net pens (12x12x6 m). They were fed dry pellets (Ewos Vekstra) by automatic feeders, in addition to hand feeding to satiation twice daily on week days. Weekly food consumption was recorded. Length and weight of a sample of the fish were measured every third month (see Huse et al. 1988). Treatment against parasitic copepods was made in accordance with normal rearing practise. The day before handling or de-lousing, the fish were not fed. During handling, the fish were anesthesized with benzocaine.

Data were mainly collected from two sources:

1. The behaviour of the fish in five pens was categorized according to visual observations from the surface. Data about the experiment are given in Table 1. Three pens were covered
with fine mesh polyethylene netting absorbing 40 or 70% of the light, except during periods with snowfall in December - March.

The pens were stocked with two culture populations with about the same biomass per pen (see Huse et al. 1988). The fish from the commercial hatchery "Fitjarlaks" were transferred to sea at one year of age in May 1986. The fish produced at Matre Aquaculture Station were transferred June 1986.

Table 1. Data about the experiment.

<table>
<thead>
<tr>
<th>Pen</th>
<th>Cover</th>
<th>Fish</th>
<th>Visual observation period</th>
</tr>
</thead>
<tbody>
<tr>
<td>9</td>
<td>-</td>
<td>Matre</td>
<td>4.2 - 25.9 1987</td>
</tr>
<tr>
<td>10</td>
<td>70%</td>
<td>&quot;</td>
<td>&quot;</td>
</tr>
<tr>
<td>11</td>
<td>40%</td>
<td>Fitjar</td>
<td>4.2 - 17.9 &quot;</td>
</tr>
<tr>
<td>12</td>
<td>70%</td>
<td>&quot;</td>
<td>4.2 - 24.9 &quot;</td>
</tr>
<tr>
<td>13</td>
<td>-</td>
<td>&quot;</td>
<td>4.2 - 25.9 &quot;</td>
</tr>
</tbody>
</table>

2. A detailed description of the behaviour of salmon in relation to environmental factors was also made. Two pens with Fitjar fish with and without shading were studied during a cycle of one year from October 1986 to September 1987 (Pens 12 and 13, see Table 1).

The environmental parameters were recorded by automatic sensors (Table 2). Most sensors were placed on an observation raft about 20 m from the pens. The sensors functioned as a rule satisfactory but repeated calibration was necessary. Data about current velocity and direction from an ultrasonic current meter were unfortunately not reliable but earlier recordings of the current in the area show that the velocity is generally below 5 cm/s.

The sensors were connected to a HP-1000 minicomputer with a HP 3497 front-end processor. Environmental data were usually sampled every 10 min. More information about the system is given in Bjordal et al. (1986).

Table 2. Sensors recording environmental variation.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Sensor Type</th>
<th>Placement below surface</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature</td>
<td>Thermistor</td>
<td>0, 2.5 and 5 m</td>
</tr>
<tr>
<td>Salinity</td>
<td>Inductive cell (Bergen Nautic)</td>
<td>2.5 m</td>
</tr>
<tr>
<td>pH</td>
<td>Endress &amp; Hausser</td>
<td>0.3 m</td>
</tr>
<tr>
<td>Oxygen</td>
<td>&quot;</td>
<td>2.0 m</td>
</tr>
<tr>
<td>Water level</td>
<td>Conductance pole (Endress and Hauser)</td>
<td>-</td>
</tr>
<tr>
<td>Light level</td>
<td>Photometric sensor (Photodyne)</td>
<td>-</td>
</tr>
<tr>
<td>Meteorological data</td>
<td>Aanderaa weather station</td>
<td>-</td>
</tr>
</tbody>
</table>
The behaviour of the fish was observed both visually from the surface and by underwater-TV. Group structure, swimming speed and direction and horizontal and vertical distribution were classified in different categories in all pens each week-day around noon, unless the water was too turbid (see Table 3). When there were several divisions of fish in a pen, the behaviour of the dominant part was recorded. Observations not falling into distinct categories were omitted.

Surface activity was recorded for five min in pens 12 and 13 each week day at noon. A leap was defined as a jump with most of the body above the water surface and a roll as marginally breaking the surface.

Table 3. Behaviour categories for penned salmon observed from surface. The abbreviations used in Table 4 are given within brackets.

<table>
<thead>
<tr>
<th>Behaviour/distribution</th>
<th>Category</th>
</tr>
</thead>
<tbody>
<tr>
<td>Group structure</td>
<td>Regular structure with the fish swimming in a school (S)</td>
</tr>
<tr>
<td></td>
<td>No schooling (NS)</td>
</tr>
<tr>
<td></td>
<td>Divisions of fish with different structure (D)</td>
</tr>
<tr>
<td>Swimming direction</td>
<td>Round the pen (R)</td>
</tr>
<tr>
<td></td>
<td>Irregular (I)</td>
</tr>
<tr>
<td></td>
<td>The fish are holding station against the current (C)</td>
</tr>
<tr>
<td>Swimming speed</td>
<td>Practically no swimming (NS)</td>
</tr>
<tr>
<td></td>
<td>Low swimming speed (L)</td>
</tr>
<tr>
<td></td>
<td>Moderate swimming speed (M)</td>
</tr>
<tr>
<td></td>
<td>High swimming speed (H)</td>
</tr>
<tr>
<td>Horizontal distribution</td>
<td>Ring formation with least fish in the middle of the pen (R)</td>
</tr>
<tr>
<td></td>
<td>Evenly dispersed (E)</td>
</tr>
<tr>
<td></td>
<td>Asymmetric distribution with fish clumped in the center or side of the pen (A)</td>
</tr>
<tr>
<td>Vertical distribution</td>
<td>High distribution with upper fish at 0-2 m depth (H)</td>
</tr>
<tr>
<td></td>
<td>Deep distribution with no fish 0-2 m depth (D)</td>
</tr>
<tr>
<td></td>
<td>Evenly dispersed (E)</td>
</tr>
</tbody>
</table>

A light-sensitive UTV-camera (Osprey OE 1321, 0.005 lux) was mounted to a pan-and-tilt unit in a way that allowed pens 12 and 13 to be observed by rotating the unit. The camera was used to record the swimming speed of the fish. The duration of 10 complete tail-beats for 10 fish swimming close to the net wall was recorded in each pen each week-day at noon. In addition, the fish were video-taped for at least one minute per pen each day at noon for later analysis of group structure and occurrence of other behaviour patterns. A colour camera (Osprey OE 1336, 35 lux) was moved to different positions in pens 12 and 13 to study e.g. feeding behaviour.

The heart rate of eight fish in pens 12 and 13 was recorded by acoustic tags operated into
the body cavity with electrodes attached to the pericardium. The weight of the fish was 1-2 kg. Tagged fish that were caught later were in good condition and had a normal growth rate. The tags lasted up to 2.5 months. Heartbeats triggered the tag to emit high frequency sound which was received by a hydrophone (Holand 1975). Manual recordings of heartbeat frequency were made several times daily on week days. An automatic system giving mean heart rate every minute (Floen et al. 1988) was used for some fish.

Blood samples for analyses of cortisol, leucocrit and hematocrit were taken 20 times throughout the year from a sample of five fish in each of the pen 12 and 13. The fish were caught with a dip net with a maximum time of six minutes between the initiation of the operation and taking the blood sample from the last fish. Plasma cortisol was determined with radioimmunoassay using human antiserum with a limit of detection of 1.4 µg/100 ml cortisol. Values below 1.4 were taken as 0.7.

RESULTS

Environmental factors

The environmental conditions were closely followed during a cycle of one year. The temperature at 2.5 m depth is given in Figure 1. There were minima in January and the beginning of April and a maximum in July - August. The oxygen content ranged between 7.2 and 12.2 mg/l and showed a maximum in March - April. The pH and salinity of the water were relatively constant with ranges between 8.1 and 8.7 and 26 and 34 % respectively. Maximum tidal variation was 2 m.

![Figure 1](image)

*Figure 1.* The temperature at 2.5 m depth during a cycle of one year. The curve is based on daily mean values from 11:30 a.m. to 0.30 p.m.

The light level increased in April and decreased in September (Figure 2). There were also marked variations between days.
The integrated daily light level in lux during a cycle of one year. Missing values are caused by faults in the sensor or logging device.

The behaviour of the fish

Group structure

Table 4 presents the mean percentage of the different categories of behaviour from the visual observations during the whole observation period. The Fitjar salmon was generally swimming in a kind of school with a fairly regular group structure although there could be divisions of the fish behaving differently. The Matre fish were usually oriented more randomly with more irregular swimming. The difference in group structure between Fitjar and Matre fish was significant for all pen combinations (p<0.001, chi-square test). No difference was found between pens with different shading within the same population.

In a school, the relative position and swimming speed of individual fish was not constant, but there was a general swimming direction and velocity. The relative position of fish swimming at different distances from the center of the pen was relatively constant and the swimming speed of fish at the periphery was thus several times higher than at the center.

When there were divisions of fish in a pen, one group could form a school and another group have a more unordered structure. The latter usually consisted of smaller fish close to the surface.

The observations reported up till now refer to the group structure during day-time. At dusk, the school was disintegrating within few minutes with a loss of ordered structure and a marked decrease in swimming speed. Physical contacts between the fish and between fish and the net wall were then observed. The change in group structure was closely related to
the light level during four days in March, the change in the pen without shading took place at 7.32 - 7.45 p.m. at a mean light level of 0.32 lux (0.24 - 0.36).

Table 4. Percentage of occurrence of different categories of behaviour. See Table 3 for explanation

<table>
<thead>
<tr>
<th>Pen</th>
<th>S</th>
<th>NS</th>
<th>D</th>
<th>R</th>
<th>I</th>
<th>NS</th>
<th>L</th>
<th>M</th>
<th>R</th>
<th>E</th>
<th>A</th>
<th>H</th>
<th>D</th>
<th>E</th>
</tr>
</thead>
<tbody>
<tr>
<td>9</td>
<td>9.0</td>
<td>54.9</td>
<td>36.1</td>
<td>24.6</td>
<td>75.4</td>
<td>4.6</td>
<td>90.2</td>
<td>5.3</td>
<td>25.3</td>
<td>67.4</td>
<td>7.4</td>
<td>80.3</td>
<td>8.0</td>
<td>11.7</td>
</tr>
<tr>
<td>10</td>
<td>8.1</td>
<td>55.7</td>
<td>36.3</td>
<td>25.4</td>
<td>74.8</td>
<td>3.1</td>
<td>96.1</td>
<td>10.9</td>
<td>20.0</td>
<td>76.8</td>
<td>3.2</td>
<td>84.7</td>
<td>6.9</td>
<td>8.4</td>
</tr>
<tr>
<td>11</td>
<td>72.2</td>
<td>0.0</td>
<td>27.8</td>
<td>100.0</td>
<td>0.0</td>
<td>2.1</td>
<td>6.3</td>
<td>91.6</td>
<td>100.0</td>
<td>0.0</td>
<td>0.0</td>
<td>18.5</td>
<td>73.9</td>
<td>7.7</td>
</tr>
<tr>
<td>12</td>
<td>70.0</td>
<td>0.0</td>
<td>30.0</td>
<td>100.0</td>
<td>0.0</td>
<td>2.0</td>
<td>13.1</td>
<td>84.9</td>
<td>98.5</td>
<td>1.5</td>
<td>0.0</td>
<td>19.7</td>
<td>70.5</td>
<td>9.9</td>
</tr>
<tr>
<td>13</td>
<td>71.9</td>
<td>0.0</td>
<td>28.1</td>
<td>99.0</td>
<td>1.0</td>
<td>1.0</td>
<td>9.2</td>
<td>89.8</td>
<td>98.5</td>
<td>1.5</td>
<td>0.0</td>
<td>12.0</td>
<td>82.0</td>
<td>6.0</td>
</tr>
</tbody>
</table>

Swimming speed and direction

The categories "High swimming speed" and "Fish holding station against the current" were not observed in this experiment. Fitjar fish were usually swimming with moderate speed round the pen (Table 4). The swimming direction was consistently counter-clockwise. Matre fish were more often swimming slowly with an irregular swimming direction. The populations differed significantly with regard to both swimming velocity and direction (p<0.001, chi-square test). Shading had no effect on the visual categories.

The swimming speed in pen 13 recorded as tail-beat frequency is given in Figure 3. The daily mean frequency for 10 fish varied between 71 and 136 complete tail-beats per min. The range of individual fish was 58 - 167. A small but significant difference was found between pen 12 and 13 with 2 % higher frequency in the pen without shading (p< 0.001, Wilcoxon matched-pairs signed-ranks test). The swimming speed in the two pens was closely correlated (r_s = 0.78, p < 0.001).

The tail-beat frequency decreased in both pens during the growth seasons in autumn and spring/summer but remained more constant during winter. De-lousing seemed to decrease activity. The swimming speed during the seven observation days after de-lousing was 4 -29 % lower than the speed the seven days before delousing, with a significant difference in five out of eight cases in pens 12 and 13 (p< 0.05, Mann-Whitney U test).

Horizontal and vertical distribution

Fitjar fish most often had a ring-formed distribution with highest concentrations of fish 1 -2 m from the periphery (Table 4). The Matre fish were more often evenly dispersed or showed an asymmetric distribution (p< 0.001, chi-square test). No effect was found by shading.
Figure 3. The tail-beat frequency in pen 13 without shading. Each point represents the mean of 10 fish swimming close to the net wall. The curve is fitted by polynomial fitting of order 3.

The vertical distribution also differed between the populations (Table 4). The Fitjar fish went deeper in the pen than the Matre fish ($p < 0.001$). No significant effect of shading on the vertical distribution was detected from the surface observations. Camera observations showed, however, that the fish in the unshaded pen 13 often swam deeper in the pen than the fish in the shaded pen 12.

Changes over time of the visual categories

The most clear change over time was that the behaviour of Matre fish became more similar to Fitjar fish over time. In February, Matre fish were never observed to have an ordered group structure but in September they were mostly structured. A marked change took place in July. In June, most fish in pens 9 and 10 were structured during 5.6 and 17.7% of the observations respectively, but this increased to 50% in both pens in July ($p < 0.05$ for pen 9, chi-square test). Corresponding changes to a ring-formed horizontal distribution and a swimming direction round the pen also took place in July. The swimming speed remained, however, low. The change to a more structured state in the Matre fish seemed to be initiated at the end of May. In both pens, a subgroup of fish swimming regularly counter-clockwise along the net wall could then be distinguished.

The group structure in one pen with Matre fish not included in the experiment differed from all other pens. During the first months in sea water, the fish were unstructured. This was followed by a period with the upper part of the fish in the pen swimming clockwise and the lower part counter-clockwise. After about one year in the sea, all fish eventually swam counter-clockwise.

Also in the pens with Fitjar fish, there were periods with different 'visions of fish in a
pen. From May to August, there was one group of unstructured smaller fish near the surface in pens 11, 12 and 13.

De-lousing seemed to influence the fish although this was difficult to quantify because of poor observation conditions during the period of de-lousing in summer. Fitjar fish often moved closer to the surface for some days after de-lousing and Matre fish often showed improved group structure for some time. All fish swam slower after de-lousing.

Surface activity

The recorded number of leaps per 5 min in pens 12 and 13 varied between 0 and 227. The mean leaping activity was 14% higher in the unshaded than shaded pen (p< 0.001, Wilcoxon matched-pairs signed-ranks test) and the leaping activity in the two pens were closely correlated (rs = 0.85, p< 0.001). There was a marked seasonal rhythm with low leaping activity in winter (see Furevik et al. 1988).

The rolling frequency per 5 min varied between 0 and 132. No difference was found between the shaded and unshaded pen and the rolling activity in the two pens was positively correlated (rs = 0.36, p< 0.001). The rolling activity showed great variations between days but no clear seasonal rhythm. More information on surfacing behaviour is given by Furevik et al. (1988).

Appetite and feeding behavior

There was a seasonal rhythm in food consumption (Figure 4). The increase in appetite in May - June coincided with an increase in temperature.

Fig. 4 shows strong variations in appetite with six periods with low food intake in all pens. Five of these minima coincided with de-lousing, grading or fish measurements and the minimum in April in addition with a temperature minimum (see Fig. 1). The minimum around 15 January could be explained by low temperature (see Fig 1) in combination with fish measurements the week before.

![Figure 4](image-url)
A marked change in appetite over time was observed when comparing the Fitjar and Matre pens (see Fig. 4). Fitjar fish had generally higher food intake from the start of the experiment to June, but from July the appetite of Matre fish was at least as high.

When feeding started, the fish swam rapidly towards the feeder at the center of the pen. All fish in a pen did not, however, react in the same way towards the food. Analyses of video-tapes clearly demonstrated that a part of the fish often continued to swim around close to the bottom of the pen during feeding.

An individual fish taking a pellet typically made a burst and attacked the pellet from below. The intensity of the response could differ considerably and by the end of the feeding session, the fish took the pellet without a burst. Spitting out pellets was also observed (for more information on feeding behaviour see Juell 1988).

Other behaviour patterns

The fish did seldom anything but swim, leap, roll or feed. Fright reactions were occasionally observed. More details about the response to stressors are given by Bjordal et al. (1988).

The relationship between behaviour patterns

The correlation between the different behaviour patterns was investigated in the unshaded pen 13. There was no significant correlation either between tail-beat and leap ($r_s = -0.05$), tail-beat and roll ($r_s = -0.07$) or leap and roll ($r_s = 0.10$).

Influence of variations in environmental factors on the behaviour

The correlation between different environmental factors and the behaviour of the fish was investigated in the unshaded pen 13 during December-April, a period without disturbances such as de-lousing. The correlations were based on daily mean values of the environmental parameters from 1130 a.m. to 0300 p.m. With regard to temperature, only data from 2.5 m depth were used.

The only significant correlations found were a strong positive correlation between water temperature and leaping ($r_s = 0.64, \ p< 0.001$) and a negative correlation between light level and tail-beat frequency ($r_s = -0.28, \ p< 0.01$).

Heart rate

There was a great variation in heart rate both between and within individual fish (Figure 5). A seasonal rhythm with higher heart rate in summer is indicated. A daily rhythm with a peak around noon and reduced heart rate at night was also found (Figure 6).

Blood samples

The cortisol level showed similar tendencies in the shaded and unshaded pen (Figure 7). The basic level was below 1 µg/100 ml, but there were peaks with higher values in October-November, April and August-September. The leucocrit values also showed a peak in the autumn (Figure 8). The haematocrit values varied between 26.9 and 58.0 %.
Figure 5. The heart rate of eight fish in different seasons. One daily recording between 9 a.m. and 3 p.m. is used for each fish. The day of tagging and days with disturbances are omitted.

Figure 6. The daily rhythm in heart rate shown by automatic recordings of one fish in May 1987. The mean at day (10 a.m. - 2 p.m.) was significantly higher than the mean at night (0 a.m. - 2 a.m., p < 0.001, Mann-Whitney U test). The curves are fitted by polynomial fitting of order 2.
Figure 7. The cortisol level during a cycle of one year in pens 12 and 13.

Figure 8. The leucocrit values during a cycle of one year in pens 12 and 13.
DISCUSSION

The most common situation for salmon in marine net cages during day-time is that the fish are swimming round the pen with a relatively ordered group structure (see also Sutterlin et al. 1979). Leaping and rolling are often observed but other behaviour patterns, e.g. fright reactions (see Bjordal et al. 1988), seldom occur. The group structure disintegrates during feeding and at night.

This study is particularly concerned with variations of the behaviour of salmon in net pens. These variations are related to differences between groups, changes over time and influences by environmental factors.

In contrast to regular swimming, schooling and a ring-formed distribution was a situation with no school structure, an even horizontal dispersion and low swimming speed. Intermediate situations between these states classified as structured and unstructured respectively were also observed.

Salmon from Fitjar and Matre showed markedly different behaviour, with Fitjar fish being more structured. The unstructured behaviour of the Matre fish is not limited to the two pens in this study but has been observed in many pens at the station. This difference in swimming behaviour between these culture populations could have a genetic base (see also Sutterlin et al. 1979). An influence by environmental differences during early stages can, however, not be dismissed. An interesting possibility is that the unstructured behaviour of Matre fish in marine net pens is caused by the rearing practice of mixing parr groups with consistently opposite circular current direction in the tanks during the whole parr stage (Ole Torrisen, Matre Aquaculture Station, personal communication). The current direction of Fitjar fish varies during the parr stage (Arve Møkster, Fitjarlaks, personal communication). This explanation is supported by the change to a more structured behaviour of Matre fish over time in the seawater phase.

In marked contrast to the difference between populations was the close similarity between pens from the same population. The swimming and leaping activity in the two pens 12 and 13 was strongly positively correlated, and surface observations showed that changes in the behaviour often took place at about the same time in pens from the same population. Reactions to the recorded environmental variation could not explain this, as the behaviour of the fish was seldom correlated with the environmental parameters. Unrecorded environmental variation, e.g. abundance of zooplankton, in addition to a similar rhythm in rearing procedures may explain the similarity.

Differences between fish within a pen were, however, observed. In one pen with Matre fish, one group of the fish were swimming clockwise and another group counter-clockwise. Small fish showed an abberant unstructured behaviour swimming close to the surface. The feeding activity could also differ between the fish within a pen with one division of the fish swimming close to the bottom of the pen during feeding time. These observations stress that the fish in a pen should not be regarded as one unit. Differences exist between individuals and groups in the same way as under natural conditions (Magurran 1986). Such differences may be of great importance for e.g. the optimal feeding regime.

The behaviour of the fish in a pen could also change over time. Some changes could have to do with the growth of the fish with the resulting increase in density. The change in Matre fish to a more ordered group structure and the decrease in tail-beat frequency in Fitjar fish over time may be examples of that. One division of the fish in a pen often seemed to influence the rest of the fish to adopt their behaviour. The change of Matre fish from an unstructured to structured state was e.g. initiated by a part of the fish swimming along the net wall. Such gradual changes in a pen may be seen as adaptive decisions of individual fish joining the
group with greater benefits and less costs, e.g. with regard to feeding. This is, however, as yet poorly understood.

Other changes may be caused by seasonal variations, e.g. the decrease in leaping behaviour in winter (see Furevik et al. 1988). Diurnal variations were also found with a disintegration of the group structure at dusk and decreased swimming and reduced heart rate at night.

With the exception of a strong positive correlation between temperature and leaping and a negative correlation between light level and tail-beat frequency, the environmental parameters were not correlated with the behaviour. The last correlation may in addition be better explained by a decrease in tail-beat frequency during the growth season in spring than by a causal relationship. The behaviour was, however, influenced by other changes in the external environment. Treatment against ectoparasites led to a certain decrease in swimming speed. Leaping was also decreased by de-lousing (see Furevik et al. 1988). Shading led to a certain decrease in leaping and swimming. The effects were, however, small and shading did not influence growth (Huse et al. 1988).

In this study, some physiological parameters were also recorded. The cortisol level was generally low. Peak values in connection with the seasonal increase and decrease in day length and light level were, however, found. Interestingly enough, the peak in the spring came later and the peak in the autumn earlier in the shaded than unshaded pen. Such a relationship between a change in light level and cortisol level has to our knowledge not been reported earlier in fish, although it is known that the cortisol value can be influenced by the background light level (Baker and Rance 1978) and the time of day (Pickering and Pottinger 1983). The small peak in October-November could have some connection with the initiation of sexual maturation (Pickering and Christie 1981). The heart rate was recorded in some fish in this study and was generally between 30 and 60 beats/min. It would have been useful to use the heart rate as a measure of metabolism, but results from other salmonids indicate that the correlation is weak, as cardiac output is largely determined by variations in stroke volume (Priede and Tytler 1977). A marked increase of the heart rate is, however, found in salmon after exposure to stress and in connection with feeding (Bjordal et al. 1988).

It may then be concluded that although there is a kind of typical behaviour of salmon in marine net pens, marked variations exist between fish groups and different environmental situations. The question then arises of whether these variations have any consequences for the prosperity and growth rate of the fish.

Flitjar salmon had a more ordered group structure than Matre salmon and had a considerably larger size when slaughtered in spite of a similar growth rate during the experiment (Huse et al. 1988). Moreover, the appetite of Matre fish relative to Flitjar fish increased markedly in connection with a change to a more ordered group structure. These observations indicate that there is a connection between an ordered group structure and a favourable state with rapid growth. If the group structure in the seawater phase is influenced by the current conditions during the parr stage, this finding could have important implications for the rearing practice in the freshwater stage. The relatively rapid swimming often characterizing salmon with an ordered group structure does not seem to influence growth rate negatively (Braaten 1976, Totland et al. 1987).

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