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THE ACTIVITY OF ALEVINS OF ATLANTIC SALMON AND RAINBOW TROUT, INCUBATED ON DIFFERENT SUBSTRATES

by

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ABSTRACT

Atlantic salmon (Salmo salar) and rainbow trout (S. gairdneri) eggs were incubated in plexi-glass aquariums. After hatching, alevins were kept in darkness, two groups of each species without substrate, two groups in gravel and two groups in Astroturf artificial substrate.

Every sixth day after hatching until the end of emergence, their activity was monitored with a video recording system in a five minutes period of darkness, followed by five minutes exposure to light. The use of ordinary 60 watts bulb lights and infrared light, made it possible to measure their swimming distances within a definite coordinate system in the aquariums, both in darkness and under illumination.

Alevins of both species showed a higher activity when incubated without substrate than those within the two substrates. The differences in activity were, however, least developed between the groups of rainbow trout.

Activity, caused by lack of ventro lateral support among the flat screen reared Atlantic salmon alevins, was most conspicuous between days 8 and 23. Illumination caused increasing activity until days 28 and 40 of rainbow trout and Atlantic salmon, respectively. The presentation of food stimulated the alevins to increase their activity.

INTRODUCTION

The salmonid alevins require minimal disturbances from hatching to first feeding. They should minimize their activity to permit maximal conversion of yolk into body tissue, and minimal wastage of this energy supply through locomotion (Thorpe 1981). These requirements are secured within the gravel redds of the rivers.

Any irregular surface which prevent rolling on the sides of their yolk sacs, removes the stimulus which releases further swimming, and thereby reduces locomotor activity in trout alevins (S. trutta) (Marr 1963). Marr (1966) showed that the largest Atlantic salmon alevins (Salmo salar) at first feeding were those reared on a corrugated surface in darkness. Artificial hatching plastic substrates have been tried with promising results in commercial hatcheries (Ingebrigtsen 1982).

Atlantic salmon (Hansen & Møller 1985) and sea trout alevins (Hansen 1985) incubated on Astroturf artificial substrate absorbed their yolk faster and more efficiently, had lower mortality both in the hatchery and during first feeding, and grew faster during first feeding, than alevins reared on flat screens. Similar effects were not found for rainbow trout alevins (S. gairdneri), reared on Astroturf artificial substrate (Nortvedt et al. 1985).

Marr (1965) found that locomotor activity of salmon embryoes was reduced by a decrease in light intensity. Woodhead (1957) observed that brown trout and rainbow trout alevins showed pulses of activity during an observation period of 15 minutes. It was also noted that the activity of these alevins increased with age. Such an ontogeny of behaviour reveals the responsiveness of the alevins to the environment or the stimulus situation. Similarly, there excists an ontogeny of coordinations (Baerends 1971).

The purposes of the present investigation were as listed below:

1. Make a qualitative description of the swimming behaviour befo-

re emergence of Atlantic salmon and rainbow trout alevins.

2. Evaluate the method which was choosen for quantification of this behaviour.
3. Investigate whether differences in growth and yolk absorption rate of alevins reared at different substrates are caused by relative differences in activity in a specific period of the alevins development.
4. Investigate whether illumination causes the same increase in activity as lack of ventro lateral support.
5. Observe whether the alevins showed an ontogeny of responsiveness to this stimulus.
6. Investigate if feeding has influence on their activity.
7. Compare the ontogeny of swimming behaviour of the two species.

Following abbreviations will be used in the present paper:

ATR = astroturf reared
FSR = flat screen reared
GR = gravel reared

MATERIALS AND METHODS

Eggs and aquariums

Atlantic salmon eggs, obtained from A/S Fiskekultur, Matredal, and rainbow trout eggs from Matre Aquaculture Station were incubated, hatched and fed in six plexi-glass aquariums (Fig. 1), the same way as described by Nortvedt (1986a). Each aquarium consisted of two observation chambers with Astroturf artificial substrate, gravel or no substrate.

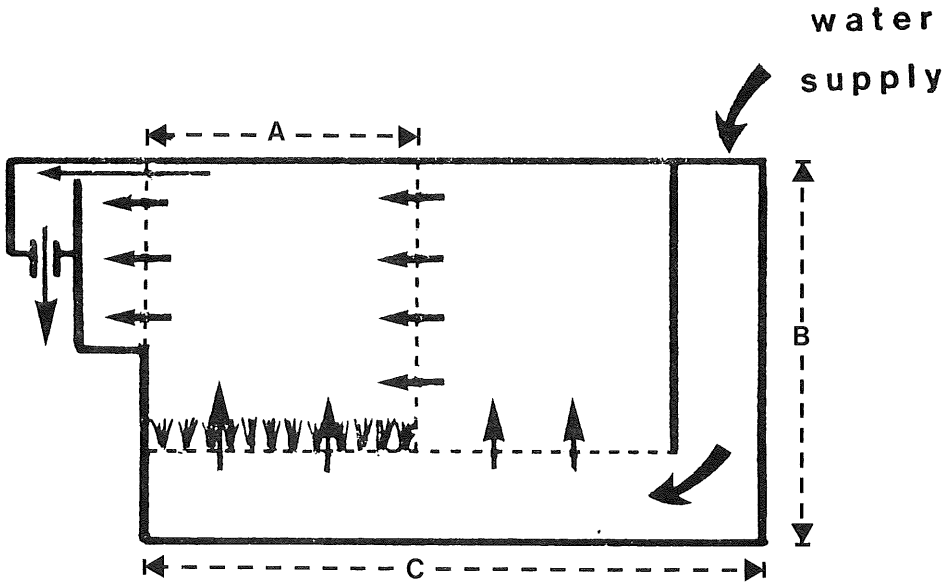

Fig.1: Aquarium with two observation chambers, one with Astroturf and one without substrate. The arrows indicate the water flow. A=17.5 cm, B=25.5 cm, C=41.0 cm.

The aquariums which were not under observation, were covered with a special adapted cap of canvas, coated inside with a black sheet of polyethylene, to prevent penetration of light. The aquariums were placed inside a tent of black double layer polyethylene, to shade them from daylight in the hatchery.

Each aquarium had its own separate water supply from a common reservoir, and the flow rate through each one was kept steadily at 1 l/min., controlled every third day.

Experimental design

Six groups of 25 alevins of each species were observed in the 12 observation chambers. The aquariums of the rainbow trout were numbered from 1 to 3, and those of the Atlantic salmon, from 4 to 6. Following combinations of the three types of substrate were used in the two observation chambers:

Aquarium no. 1 and no. 4: Astroturf (A)/without substrate(N)
Aquarium no. 2 and no. 5: Without substrate (N)/gravel(G)
Aquarium no. 3 and no. 6: Gravel(G)/Astroturf(A)

The present investigation of rainbow trout and Atlantic salmon, respectively, started the 0 and 2 day posthatching, and terminated the 39 and 68 day. The half the groups of alevins of Atlantic salmon (5N, 5G, 6A) and rainbow trout (2N, 2G, 3A) were fed dried capelin eggs (Mallotus villosus) every third day from day 30, until the end of the experiment.

The temperature was measured daily. It varied between 6,0 and 7,6°C, with a mean value of 6,8°C. The pH varied from 6,0 to 8,0, with a mean value of 6,5 through the experiment.

The observations

The swimming behaviour was observed every third day by the use of a video recording system, supplied with infrared light during darkness. The movements of the alevins within a coordinate system in each observation chamber, were quantified at least every sixth day. These quantitative observations were complemented with qualitative behaviour observations by eye.

The aquariums and video recording system were placed as seen in Fig. 2. The observer stayed inside the tent during recording.

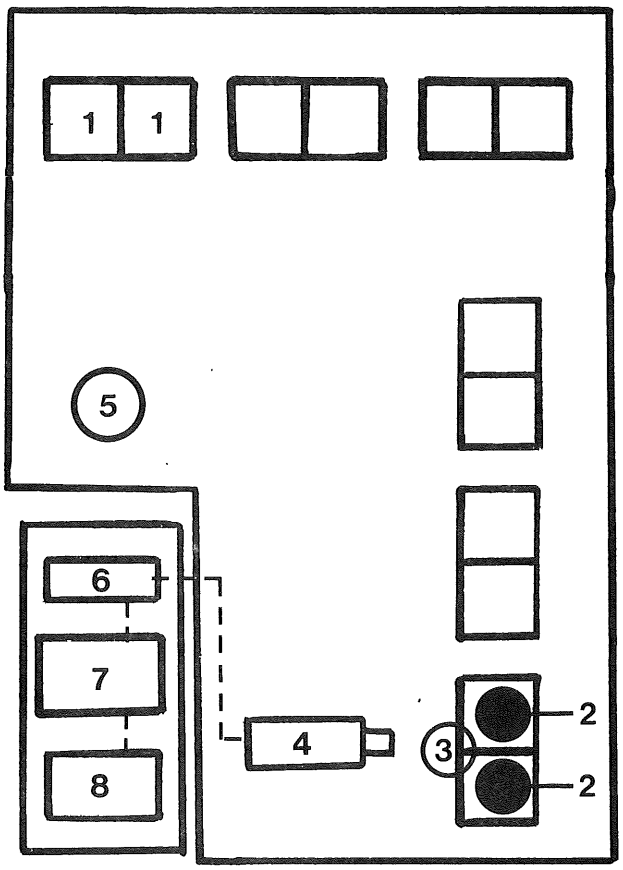

Fig. 2: Schematic view of the behaviour observation set-up. Dashed lines denote connections.

1) Observation chamber.
2) Infrared light (Badger, 500W/860nm).
3) Bulb light (Phillips, 60W).
4) Video camera (CCTV Corp., model GBC with ENK TV Zoomlens, 1:1, 8/12.5-75mm, macro).
5) Observer.
6) Time recorder (FOR.A, VTG - 22).
7) Video cassette recorder (Sony, SL - C9E).
8) Video monitor (Trinitron, PVM - 6030ME).

Following a standardized period of 10 minutes in darkness and silence after "ready for recording", the video recorder was started with a remote control (Sony RMT - 212). A recording sequence of 5 minutes in darkness under infrared illumination, was immediately followed by a similar period under ordinary bulb light illumination. Each infrared light (500W) was placed 10 cm above the water surface. Due to the flow rate, the temperature in the surface water did not rise during 5 minutes exposure to infrared light. The tilted bulb light (60W) was placed 10cm above and 10cm in front the center of the aquarium front wall. The two observation chambers of each aquarium were recorded simultaneously. The camera was placed approximately 70 cm in front of the aquarium recorded.

The three aquariums with Atlantic salmon alevins were recorded within the same 2-hour interval either during morning (0800 - 1000 h.) or evening (2000 - 2200 h.), whereas those of rainbow trout alevins were recorded during the next two hours. Evening or morning was not chosen systematically. Due to the summer time in Norway from the 31 of Mars 1985, the recording was consequently delayed one hour by the clock. The order of the aquariums recorded was reversed every second day of recording to avoid possible systematic disturbances or habituation.

Quantifying the activity

To quantify the activity of the alevins under the two different conditions of illumination, the behaviour of the alevins was subdivided into two categories of movement:

1) Moving along
   the bottom or at the substrate surface with short burst movements, but without leaving it.
2) Swimming freely in the water column or moving along more than half the bottom area in one run.

The first category was quantified by counting the total numbers of position changes of all the alevins within each half minute period of observation. These results were rearranged to fit average no. of position changes/alevin/minute (pc/a/m), scaled for mortality. A change of position of each alevin was defined as either turning 180 within a restricted area of 4 x 5 cm

in a x,z- coordinate system, drawn at the bottom or surface of the substrates, or moving from one such area to the next.

To quantify the second category of movement, the coordinate system was extended along the vertical y-axis. The x,y-coordinate system was drawn at the front of all the twelve observation chambers. All the movements in the xyz-space were projected into this x,y-plane.

Although the observation chambers were constructed with a total height of 19 cm, the water level restricted this height to 18 cm. Caused by some problems in observing and distinguishing the exact positions of the alevins near the surface, maximum y-value was set each time an alevin showed activity in this region between 17 and 18 cm above the bottom.

The recording sequences were later analysed by the use of a developed RPL procedure (software) (see Appendix D) on a Digital Professional 350 PC. The positions of each moving alevin were observed every third second during half a minute, and dictated into a microcassette recorder (Sony M-10). After observing all the moving alevins in this half minute sequence, the first alevin was followed in the next sequence. Each alevin was followed in this stepwise way until the record terminated. The data on the microcassettes could then be transfered to RS/1 tables on the Digital PC and analyzed by drawing a vector from point to point of each observation. In this way, the cumulative distances of each and all the alevins could be computed, and the relative difference in activity compared between the groups.

The swimming activity of each alevin per minute was calculated, based on data of total activity, numbers of alevins incubated and the mortality they suffered.

RESULTS

Survival

The survival of the alevins during the observation period can be seen in Tables 1a,b. The highest mortality was seen in the group of fed Atlantic salmon alevins, incubated without substrate. They showed a mortality of nearly 50 % during the investigation. This mortality was primarily due to the fact that they became cripples, which could not be observed immediately after hatching. None of the other groups showed a mortality higher than 12 %.

Table 1a: Survival of the rainbow trout alevins.

DATE	DAY no.	DAY DEGREES	1A	1U	2U	2G	3G	3A
22 MAR	0	0	25	25	25	25	25	25
21 APR	30	204	24	25	25	25	25	25
30 APR	39	269	24	25	25	22	22	25

Table 1b: Survival of the Atlantic salmon alevins.

DATE	DAY no.	DAY DEGREES	4A	4U	5U	5G	6G	6A
2 MAR	0	0	25	25	25	25	25	25
19 MAR	17		24	25	19	24	24	24
31 MAR	29		24	25	18	24	24	23
12 APR	41		24	25	16	24	24	23
30 APR	59	400	24	25	14	24	23	23
9 MAY	68	465	23	25	13	22	22	23

Qualitative observations of behaviour

The behaviour of both species was influenced by the substrates they were incubated in and the conditions of light and darkness. The alevins did, however, show an ontogeny of behaviour to these environmental conditions as they grew older.

Rainbow trout

The FSR alevins did not show large congregations in the corners of the observation chambers, but were mostly widespread at the bottom. They seldomly turned over to their sides, but showed a high frequency of remarkable jumping right up and down at their yolk sacs from day 6. The angle to the bottom was estimated to be 30°, and was rapidly decreasing. They were continuously working with their caudal and pectoral fins, to keep balance.

The ATR alevins did also show this jumping within the substrate, but the activity was lower. Six hours after hatching, 30% of the GR were still in the upper surface layer, but none were left the third day posthatching. The first alevin emerged to the gravel surface again at day 27, and 50% of the alevins had reached this position at day 33.

Until day 28, illumination increased the activity of the alevins. They left the bottom and the substrates at an early stage (Nortvedt 1986b), and the behaviour was similar for all the groups investigated at day 39.

At day 18, the FSR alevins showed aggressive pushing and hard thrusts against each other. From day 27, clear chasing of other alevins by swimming head down and pushing them away, was observed. The attacked alevins tried to maintain their positions for a while.

When food was first introduced, the activity increased among the alevins, and the most active ones swam to the surface, where they stayed for several minutes. They did, however, not snap the food particles the first days, but were observed to swim in re-

verse away from the food. After they were able to control buoyancy, they were also clever in maintaining position in the water column, by moving their right and left pectoral fins alternately. The first food particle was snapped at day 39. They showed no interest to the food if the particles sank to fast. None of the rainbow trout alevins were, however, observed to swallow any of these food particles.

Atlantic salmon

The first two days after hatching, the FSR alevins layed mostly on their sides, only moving their pectoral fins. They were widespread on the bottom, and showed no increase in activity during illumination. About 50% of the alevins incubated in gravel had disappeared from the surface layer, whereas all the ATR alevins stayed quiet between the bristles of the substrate.

Eight days posthatching, all the FSR alevins congregated in the corners and along the walls of the observation chambers most of the time. The darkest corner was chosen after several minutes of illumination. Each alevin tried to keep its head in the inmost part of the corner, and they showed increased tail beat frequency and violent wriggling of their bodies. The "best" position was achieved by the most active alevins. They lay on their yolk sacs with the body axis in an about 45 degrees angle to the bottom screen. Those observed freely on the bottom tipped over to their sides when they were not moving. This behaviour caused them to right themselves up and swim, but they tipped over again as soon as they stopped without support. This swimming was
performed by short bursts of movement along the bottom. If one of these alevins swam into a group of other alevins, this was a trigger to increased activity among the other ones as well. The activity pattern thus appeared as several pulses of movement. At day 14, they still tipped over, but were more clever in supporting themselves by bending the caudalfin over to one of their sides. The burst swimming lasted however longer, and so did the reestablishment period after exhaustion.

At day 20, the yolk sac was less plump and more protruded backwards. Now, they tipped seldom over, but when they did,

the burst movements could bring them across the bottom several times in few seconds, and suddenly up along the wall to the surface and down again. At day 31, the yolk sac was reduced to about half its original size, and the alevins did not tip over to their sides anymore. At this moment, they supported themselves by one of the pectorals. After som minutes, they changed the loading from one pectoral fin to the other. From day 34, the FSR alevins were widespread on the bottom, and no groups could be observed.

The ATR and GR alevins did not show any of the falling and righting responses described. At day 8, none of the GR alevins could be seen in the surface layer of this substrate. But several was seen within pockets in the gravel along the plexiglass walls. The other were hiding inside the gravel bed. They maintained their positions in the specific pockets for two weeks. At day 25, about 50% of the alevins had emerged to the gravel surface, where they mostly stayed quiet. If one of the alevins moved, however, it took some time before it found a new satisfactory position among the gravel.

Similarly, ATR alevins did very seldom change position the first three weeks of their life. They stayed widespread within this substrate, but sometimes two alevins lay side by side, although in opposite direction. At day 20, the first alevin was seen to place its head at the top of the bristles. At days 29 and 38, respectively, 20% and 50% of the alevins were situated at the surface of this artificial substrate.

Until day 40, the illumination increased the activity of the FSR alevins, as is later described under the quantitative observations. The swimming endurance became more complex, and several bursts to the surface were observed from day 20. After this day, it was a tendency to swim more freely above the bottom during illumination. The reactions to illumination of the GR and ATR alevins in the same period were to retract themselves, head down into the dark crevices of the gravel or between the bristles of the artificial Astroturf substrate. But also these alevins showed sudden bursts to the surface at days 29 or 35, respectively.

None of the alevins took food during darkness. The first food

particle was snapped at day 47, but it was spitted out. The alevins showed rather high activity during feeding (see quantitative measurements), and the behaviour during feeding was quite similar between the groups of Atlantic salmon alevins. Most of the alevins turned away and tried to hide from the food when it sank down as a swarm. At day 59, most of the alevins showed interess to the food when it was introduced as single particles. They did, however, not swallow the food particles until day 68. But they held it in the mouth, swam around with it, spitted it out and tried again on the same particle.

Position changes

Figs. 3a-c and 4a-c show the position changes of the alevin per minute (pc/a/m) through the entire experimental periods of both fed and unfed rainbow trout and Atlantic salmon, respectively.

Rainbow trout

The position changes of all the groups of ATR and GR alevins, were below 0.15 pc/a/m during darkness. During illumination, however, the alevins in these substrates showed an increase at day 33 which continued to rise until day 39, except for the unfed ones in Astroturf. They showed a maximum value the 42 day. The fed ones in gravel and Astroturf showed a maximum value of 1.25 and 0.7 pc/a/m, respectively. All the groups of the FSR alevins showed a maximum value 13 days posthatching. These values were 1.2 and 2.6 pc/a/m in darkness and under illumination, respectively.

Atlantic salmon

The positon changes of all the groups of ATR and GR alevins, were below 0.15 pc/a/m before day 42, whereafter they began to rise in darkness. The fed ones in both substrates rose to between 0.45 and 0.50 pc/a/m at day 68. Both the groups of the illuminated alevins showed a rather variable pattern from day 29, when they started to increase the number of position changes. The fed GR alevins showed a maximum value of 0.9 pc/a/m the 53 day, whereas those in Astroturf showed a maximum value

the same day of 0.55 pc/a/m. The FSR alevins in darkness showed a maximum value of 0.7 pc/a/m at day 17, and the increase in this activity did not start before day 14. The illuminated alevins showed an increase in activity from day 5, and it continued to rise, although very variable, to 1.6 pc/a/m the 38 day and 2.2 pc/a/m the 41 day of the unfed and fed ones, respectively. After these days, both the illuminated groups showed a sharp decline in this activity.

Swimming activity within each recording sequence

Figs. 5 to 7 show the development of swimming activity of unfed rainbow trout alevins through each recording sequence. Similar bargraphs are displayed for the Atlantic salmon alevins in Figs. 8 to 10. Bargraphs were not made those days when the alevins showed 100% activity during 30 seconds within the 10 minutes sequence.

Rainbow trout

When the ATR alevins became active, they showed an even total activity during the 5 minutes in darkness. On day 33, their highest activity during illumination was during their first 30 seconds of action. The FSR alevins showed an incoherent activity pattern some few hours after hatching. The activity distribution in both darkness and under illumination stabilized as the alevins got older. The activity when the light was turned on was generally high the first minute during the whole experimental period, except from days 18 to 23. The GR alevins showed pulses of activity under illumination. This activity was highest during the first 30 seconds.

Atlantic salmon

In the period between days 35 and 68, the swimming activity of the ATR alevins varied within each sequence. Their swimming activity during illumination was highest during the first minutes, but generally low. The FSR alevins in darkness showed continued activity only in short periods until day 53, when it became more widespread. The swimming activity during illumination was highest after some minutes of exposure the first 20 days

posthatching. Thereafter, this activity was mainly highest the first minutes after the light was turned on. The swimming activity of the GR alevins, was generally variable and incoherently distributed in darkness during the whole investigation period. Their swimming response to light did not start immediately after exposure. At day 59, they sank down to the bottom when the light turned on.

The total swimming distance within each observation chamber

Rainbow trout

After day 28, the activity of all the groups were lower during illumination than in darkness (Figs. 11a-f). The unfed ATR alevins started their swimming activity on day 23, and on day 33 the swimming distance during 5 minutes in darkness peaked with 3800 cm. The corresponding value for the fed ones were found on day 30, and amounted to 1200 cm. The activity of the FSR alevins started at day 0 during illumination, and at day 7 in darkness. Two peaks in swimming activity was found, the first on day 13, and the second towards the termination of the experimental period. The first peak value was highest among the illuminated alevins. The fed alevins showed a maximum in darkness at day 30 of 2300 cm, whereas the unfed ones showed a maximum at day 39 of nearly 6500 cm within 5 minutes. The activity of the unfed and fed GR alevins peaked on days 30 and 33, respectively. The highest total swimming activity for both groups were found on the last day of the experiment.

Atlantic salmon

After day 40, the activity of all the Atlantic salmon groups were always equal to or lower during illumination than in darkness (Figs. 12a-f). The activity of the unfed ATR alevins in darkness started on day 35, and peaked with 1050 cm per 5 minutes on day 53. The activity of the FSR alevins was low the second day posthatching. Thereafter it increased and reached a local maximum at day 12, except for the alevins in 4N during darkness. The unfed alevins showed a new and even higher maximum total swimming activity of 1800 cm per 5 minutes the 59 day,

whereafter it declined. The total swimming activity of the fed alevins continued to increase, and reached a value of 3400 cm per 5 minutes at the termination of the experiment. The swimming activity of the unfed GR alevins started in darkness at day 38. It reached a maximum value of 2300 cm per 5 minutes the 59 day, whereafter it decreased. The fed alevins increased their activity at the commencement of first feeding during illumination, and reached a maximum of about 350 cm per 5 minutes the 35 day. After a decline in total swimming activity, it reached about the same activity level from day 50 and onwards. The alevins in darkness did not start their swimming activity before day 43, whereafter it continued to rise to 1000 cm per 5 minutes the last day of observation.

The total number of active alevins observed within each observation chamber

When many alevins performed several bursts of activity during a sequence, these numbers were exceeding the actual numbers of alevins in each observation chamber.

Rainbow trout

In all the rainbow trout groups the number of active alevins increased from day 30 (Fig. 13a-c). The highest numbers here were observed among the illuminated alevins. The FSR alevins showed a global maximum for all the groups at day 13. The highest observed value during illumination that day was 26 alevins observed per minute.

Atlantic salmon

In all the Atlantic salmon groups in darkness, the numbers of fed alevins observed per minute were increasing towards the last day of observation (Fig. 14a-c). The unfed alevins in darkness showed maximum values at day 59, whereafter the numbers decreased. The numbers of active ATR and GR alevins, were highest at day 53 during illumination, whereafter fewer alevins were active per minute. The FSR alevins in 4N were observed about 14 times per minute at day 14. This was the global maximum value observed of Atlantic salmon alevins. The fed and unfed FSR

groups were seldom observed during illumination after day 38. Both groups showed, however, a new increase in actively swimming alevins in darkness from day 53.

Swimming distance per minute of the average alevin

The swimming distances of the rainbow trout and Atlantic salmon alevin per minute are summarized in Tabs. 2a,b. SI-units (m/sec.) would yield very small and meaningless values here.

Table 2a: The swimming activity (cm/minute/alevin) of rainbow trout, incubated in different substrates under illumination or in darkness.

DATE	DAY no.	DAY DEGREES	1A DARK	1A LIGHT	1U DARK	1U LIGHT	2U DARK	2U LIGHT
22 MAR	0	2	0.0	0.0	0.1	0.4	0.0	0.0
25 MAR	3	21	0.0	0.0	0.0	1.7	0.1	1.9
28 MAR	6	40	0.0	0.0	1.6	10.5	0.5	8.1
4 APR	13	85	0.0	0.0	2.8	14.7	9.5	18.7
9 APR	18	120	0.0	0.0	1.3	8.4	0.8	9.0
14 APR	23	154	6.3	0.0	0.1	2.5	0.3	3.5
19 APR	28	183	0.0	0.0	0.1	2.4	0.0	1.1
21 APR	30	204	0.0	0.0	8.8	5.5	18.9	2.2
24 APR	33	226	31.3	7.7	23.6	16.5	17.4	12.1
30 APR	39	269			51.7	21.9		

Table 2a continues...

DATE	DAY no.	DAY DEGREES	2G DARK	2G LIGHT	3G DARK	3G LIGHT	3A DARK	3A LIGHT
22 MAR	0	2	0.0	0.0	0.0	0.0	0.0	0.0
25 MAR	3	21	0.0	0.0	0.0	0.0	0.0	0.0
28 MAR	6	40	0.0	0.0	0.0	0.0	0.0	0.0
4 APR	13	85	0.0	0.0	0.0	0.0	0.0	0.0
9 APR	18	120	0.0	0.0	0.0	0.0	0.0	0.0
14 APR	23	154	0.0	0.0	0.0	0.0	0.0	0.0
19 APR	28	183	0.0	0.0	0.0	0.0	0.0	0.0
21 APR	30	204	0.0	0.0	5.3	2.7	9.6	4.5
24 APR	33	226	8.4	1.9	9.1	4.0	9.2	2.7

Table 2b: The swimming activity (cm/minute/alevin) of Atlantic salmon, incubated in different substrates under illumination or in darkness.

DATE	DAY no.	DAY DEGREES	4A DARK	4A LIGHT	4U DARK	4U LIGHT	5U DARK	5U LIGHT
4 MAR	2	14	0.0	0.0	0.4	0.0	0.4	0.0
10 MAR	8	55	0.0	0.0	2.8	5.1	1.5	4.7
16 MAR	14	93	0.0	0.0	11.3	9.3	0.0	5.4
22 MAR	20	131	0.0	0.0	3.9	3.3	1.4	4.3
31 MAR	29	190	0.0	0.0	0.9	4.7	0.0	5.0
6 APR	35	230	1.0	0.0	0.2	0.9	0.0	1.8
9 APR	38	251	0.0	0.0	0.0	1.1	0.0	2.7
14 APR	43	285	1.2	0.0	0.0	0.1	4.7	0.1
21 APR	50	335	0.7	0.0	1.5	0.8	1.3	0.5
24 APR	53	357	8.8	1.2	10.1	0.6	6.5	0.2
30 APR	59	400	6.1	0.0	14.8	1.5	27.9	0.5
9 MAY	68	465	1.9	0.4	10.4	1.5	53.3	0.3

Table 2b continues...

DATE	DAY no.	DAY DEGREES	5G DARK	5G LIGHT	6G DARK	6G LIGHT	6A DARK	6A LIGHT
4 MAR	2	14	0.0	0.0	0.0	0.0	0.0	0.0
10 MAR	8	55	0.0	0.0	0.0	0.0	0.0	0.0
16 MAR	14	93	0.0	0.0	0.0	0.0	0.0	0.0
22 MAR	20	131	0.0	0.1	0.0	0.0	0.0	0.0
31 MAR	29	190	0.1	1.0	0.0	0.0	0.0	0.0
6 APR	35	230	0.0	2.9	0.0	0.3	0.0	0.0
9 APR	38	251	0.1	2.0	1.4	0.1	1.4	0.4
14 APR	43	285	0.3	0.2	0.4	0.4	1.5	0.2
21 APR	50	335	4.0	2.3	0.6	0.4	4.2	0.5
24 APR	53	357	5.6	2.1	5.9	3.7	5.6	6.5
30 APR	59	400	5.8	2.8	20.2	1.0	12.0	2.1
9 MAY	68	465	9.0	2.9	1.4	0.0	18.2	4.7

DISCUSSION

The qualitative description of alevins activity revealed which characteristics of the behaviour were most conspicous in periods of the alevins life. Such temporal studies also gave me the possibility to describe the ontogeny of their activity characteristics. The different activity patterns were, however, occuring at different intensities and strength, due to the stimulus situation and the alevins handling of the situation at their specific stages of development. In harmony with the purposes of the present investigation, I therefore found it necessary to quantify the movements of the alevins.

To analyse these movements, I had to split up the activity patterns in appropriate behaviour units. This is why partly temporally overlapping, but different parameters were used to quantify the activity. To do so, several wellknown fish movement methods were evaluated.

Those methods can be devided into categories of electromecanic, photoelectric, photographic and video technics, which will briefly be discussed here. The electromechanical methods have among others been utilized by Ali (1964), Kramer & Ali (1965), Richardson & Mc Cleave (1974) and Varanelli & Mc Cleave (1974). They are based on the principle that the movements of the water, caused by the activity of the fish, are sensed by a suspended mechanical device. The drift of these solids cause completing of an electric current , which are integrated. Similarly, pairs of electrodes have also been used (Swift, 1964). These methods can be applied with several fishes in an aquarium, but will then only roughly estimate the activity patterns, and not actually the levels of different types of activity.

The photoelectrical methods, as demonstrated by Gibson (1970) Kleerekoper (1977), Kleerekoper et al (1970), Sato & Terao (1983) and Steele (1984) give the possibility of recording the movements of the fish in a two-dimensionale coordinate system or a photoelectric "gate". Photoelectrical cells are placed in a square matrix. Interruption of a light beam by the fish, increases the resistance or triggers a switching circuit, and thereby decides the position of the fish. Several positions are registered

by a computer. These methods can be applied with infrared light beams, and can be expanded to three dimensions, but only with one fish at the time. Thereby, no interactions between individuals nor correlations between specific behavioural patterns can be investigated by these methods.

Pitcher (1975) has reviewed the photographical shadow and stereoscopic methods. The author concludes that the use of mirrors affects the fishes' behaviour, and these methods are sensitive to light. However, Pitcher advices a periscopic technic, which combines a perisopic image via mirrors with a direct view on one photograph. The vertical separation of the two views, applied on a videotape, seems to be a promising method of observing fish in three dimensions. It would, however, not work in my experimental design, without large economical costs, due to the long installation and calibration procedure for each unit recorded.

The employment of video in recording the behaviour of fishes has become usual the last years. Both Rosenthal et al. (1984) and Webb (1980) applied this method in two-dimension studies of swimming activities. Their single picture analyses, however, seem to be some very time consuming analysis. I therefore used a method quite similar to the strategy chose by Buchanan et al. (1982). They also projected the actual moving path into a plane perpendicular to the viewer (camera). They further extended their calculations to include the third dimension by making certain assumptions about the swimming distribution within the aquarium. These assumptions of randomly swimming in the horizontal direction and normally distributed swimming rates could, however, not be applied in the present investigation.

Making observations in three dimensions is of course the best approach to uncover the behaviour of fishes. Huse and Skiftesvik (1985) applied an elegant computer aided technic to register three dimensional movement together with the logging of certain behavioural characteristics. Both the camera lens and the horizontally and vertically movements of the camera were controlled by a joystick. When the camera were moved or focused, this was registered by a computer, which logged position data at certain intervals. This method can, however, not

be applied to more than one individual at the time. It is furthermore sensitive to light, due to the focusing in depth of field. Moreover, Salmonid alevins are probably moving to fast to be detected by this method.

Two video cameras, perpendicular to each other, could be used to obtaien the coordinates (x,y,z) in three dimensions, as described by Dunbrack & Dill (1984). They observed, however, only three positions of a single fish's movement at the time. This method is, when applied in the same manner as mine, very time consuming. But it offers better possibilites to researchers in observing the orientation component of activity and the exact swimming routes, provided that the records can be coordinated. Simenstad et al. (1981) report that video systems are available, which can record two signals simultaneously on a split-image format on the tape.

A very promising technic seems to be that described by Potel and Wassersug (1981). Their Galatea system uses a computer grahics display, a computer driven projection cathode ray tube and a digitizing pen, which make it possible to "record the x,y-position of hundreds of points in an hour". In this system two-dimension images can infer three-dimension movements by the help of a calibration object with six or more known non-copolar reference points. A video version of this system is, however, expensive (US $ 10.000 in 1981).

The method applied in the present investigation was a compromise between the purpose of the investigation and the equipment available. The projection of movements onto one plane will not measure the true path of swimming. In addition, observing the positions every third second, will only give the average route swimmed by the alevins. This technic make hard demands on the concentration of the observer, and a higher observation frequency is not recommended, unless slow motion is analysed. Preliminary observations of the behaviour of the alevins showed that they most frequently made swimming movements in the longitudinal direction of the aquarium, that is perpendicular to the observer, that they started their development of emergence up along the walls of the observation chamber, and that they later made long unidirection movements in the water column. Although

some sudden bursts to the surface were not measured by this technic, these observations support the validity of the method as a measurment of relative differences in activity between the groups. However, some variations in the measurements should be expected.

The advantages of observing positions in a coordinate system, are due to the exact vector calculations one can integrate in a computerbased programme. The software procedure developed, can quickly be extended to include calculations of movements in the third dimension. Similarly angle orientation could be computed. Scratching these coordinate systems on the walls of the observaton chambers instead of at the monitor, makes it possible to freely place the video camera in nonfixed positions relative to the aquariums. It is further recommended for future detail studies of the behaviour of salmonidae alevins, that one observes the early activity of the alevins at the bottom from above. Later, when the alevins show the tendency of emergence, observation through the walls will give the best images of activity. Although observations of activity at the bottom through the plexiglass walls were assumed to be satisfying during the present investigation, the saltatory activity behaviour of the rainbow trout alevins within the Astroturf artificial substrate, was probably somewhat underestimated.

The most remarkable results from the present investigation is the conspicuous difference in activity during darkness, observed between the groups of the substrate and FSR alevins. Before days 30 and 35, respectively, the rainbow trout and Atlantic salmon alevins were almost completely inactive in the substrates, although the rainbow trout alevins showed some early jumps and restlessness. In the rivers, this similar period before emergence to the gravel surface of the redds is dependent on temperature, as observed on trout (S. trutta) by Stuart (1953). He found that development could be retarded or accelerated at any stage from fertilization to first feeding. Consequently, the interval days from hatching to emergence to the gravel surface varied from 29 to 63 days, due to the varying temperatures during the different winters of observation.

The alevins are protected from both predators and physical

stress within their gravel beds in the rivers. But this strategy is evidently inborn and still appearing among these cultured species. In the present investigation, they searched down from the gravel surface in darkness during their first days of development. This fact suggests that a positive geotaxi is the proximal factor, which releases this behaviour. Similarly, it seems to be a negative geotaxi which leads them to the surface again at a later stage. The alevins observed within the gravel pockets or the Astroturf substrate were always seen to rest at their yolk sacs. This observation emphasizes the importance of gravity as a stimulus to the alevins. Light wil also affect this emergence behaviour, but its function seems to be more as a modifier, in that the alevins retract their bodies down in the substrate during illumination. This will protect them from predators. Thigmotaxi could also explain their tendency to appear within crevices.

Although the rainbow trout alevins left the gravel surface at a lower age than did the Atlantic salmon alevins, they appeared later at the gravel surface again. One should, however, expect the reverse situation, because the rainbow trout alevins showed an accelerated development in several ways, compared to the Atlantic salmon, especially in that they emerged from the substrates and became photopositive at an earlier stage (Nortvedt 1986b). The appearance at the gravel surface again could, however, be explained by the greater size of the Atlantic salmon alevins at the same age. The gravel pockets or crevices in these artificial gravel beds could no longer keep them after day 25. This is in agreement with the observations of Stuart (1953). He found that the rate of progress through the gravel could be related to the rate of modification of body shape. This theory is supported by the observation that 50% of the Atlantic salmon alevins did not appear at the surface of the Astroturf artificial substrate before day 38.

In conclusion, the alevins prefer to stay within their substrates during their first period of development. When offering them an environment quite different from the substrates, as the flat screens of the hatching trays, it is natural to ask whether this will make influence on their behaviour. Marr (1963) observed that trout alevins had no static stability in the ver-

tical plane. This caused them to roll over on to the sides of their yolk sacs whenever they stopped swimming. Dill (1977), Hansen (1984) and Stuart (1953) observed the same congregation in the corners of Atlantic salmon and rainbow trout, Atlantic salmon, and trout, respectively, as in the present investigation. Dill observed this behaviour particularly among rainbow trout alevins during illumination, and explained this crowding into the corners as "a result of reduced righting behaviour because of upright support provided by the aquarium walls and conspecifics". I support this hypothesis, but my observations during darkness are contradictioning his findings, in that this phenomenon mainly appeared among the Atlantic salmon alevins in the present investigation, and in fact mostly during illumination among the rainbow trout alevins. Dill's observations of several orientation characteristics therefore seem to me to be a result of illumination. His aggregations of individuals in corners, where only 10 alevins were studied in each aquarium, are moreover sparse.

Based on behaviour and growth studies, Nortvedt et al. (1985) concluded that no positive effect could be achieved by incubating rainbow trout in Astroturf artificial substrate. It is therefore apparently surprising that the results of the present investigation include relatively many position changes/alevin/minute, high total swimming activity and many alevins observed per minute of both species in darkness, with peak values from day 12 to day 17.

The FSR rainbow trout alevins did, however, show peak values of all these characteristics at day 13, and showed a more narrow temporal range than did the Atlantic salmon alevins. This should be seen in association with their limited tendency of falling and righting. The observations that the rainbow trout alevins made a smaller angle of their body axis to the bottom screen and that they showed a greater ability to rest on their yolk sacs than did the Atlantic salmon alevins, explain why they very seldom were observed to aggregate in the corners. They also left the bottom screen at an earlier stage when they made swimming movements.

It is therefore concluded that the rainbow trout alevins

developed a better swimming ability at an early stage than Atlantic salmon alevins. The support of substrates is therefore not necessary to the rainbow trout alevins. The early emergence of rainbow trout (Nortvedt 1986b) further makes this a plausible conclusion.

I assume that these swimming properties are caused by a relatively small yolk sac without appendage, and thereby a decreased drag force (Bainbridge, 1961), a better coordination of the fin movements at this stage and a relatively greater amount of red muscles of the rainbow trout alevins. Tsukamoto and Kajihara (1984) found that the relatively large yolk sac of ayu larvae (Plecoglossus altivelis) was no hydrodynamic embarassment to the larvae, because their swimming ability decreased as the yolk sac decreased. But after my opinion, this observation could be due to energy deficit at the end of the yolk sac period. Dabrowski (1986) stated that the cost to overcome the enhanced effect of viscosity and intramuscular resistance is serious to the alevins. Although electromyography shows that both red and white muscles are recruited for sustained swimming, it is shown that the threshold swimming speed of rainbow trout for recruitment of white fibres is 3 - 3.6 body lengths/sec. (Hudson in: Johnston & Moon 1980). Development of red muscle fibres is therefore important to the alevins as soon as they start free-swimming. Such fibres were recognized in alevins of free-swimming rainbow trout of about 500 day-degrees' age from fertilization by Nag & Nursall (1972). They stated that "the earlier appearance of white fibres is related to the early development of short, strong bursts of muscular activity". Such behaviour was observed during the falling and righting period of the present investigation. The literature tells nothing about the appearance of red muscles in Atlantic salmon alevins. This fact calls for further research in the future, together with morphometrical measurements and fin coordination capabilities, related to behaviour.

The difference in absolute values seen of the total swimming distance parameter between the species, emphasizes the importance of splitting the behaviour into subunits. The groups which showed a low total swimming distance and few alevins observed swimming per minute did, however, increase their position changes in about the same interval. These observations reveal that

activity consists of complex behaviour patterns. Different levels and types of activity within similar environments were probably due to the difference in restlessness, and thereby the trigging level of some individuals in each observation chamber. Besides, a higher percentage of cripples among some of the flat screen reared Atlantic salmon alevins, probably affected the activity level. There were always some alevins who dominated in an activity sequence, but it was impossible to observe whether the same individuals dominated each day of observation.

Although there were some variation in activity among the flat screen reared Atlantic salmon alevins, they showed a difference in activity from those incubated in the substrates. This phenomenon was observed between days 8 and 35, but was particularly conspicuous in the period between days 8 and 23 (55 and 152 day degress). Consequently, this is the period where the substrates are most important as support to the Atlantic salmon alevins during artificial rearing.

The moderate activity of both species in all the observation chambers in the following period is probably reflecting their apperance at the surface of the substrates, and the better ability of the Atlantic salmon alevins to support themselves. During this period, the rainbow trout alevins showed agonistic behaviour, but this involved only small bursts of activity, due to the fact that they tried to maintain specific positions all over the bottom. Such territoriality among older individuals is wellknown (Fernø & Holm 1986, Holm & Fernøe 1986, Kalleberg 1958, Norman 1985). My obserservations of early social behaviour are in disagreement with the conclusions of others (Cole & Noakes 1980, Dill 1977, Huntingford 1986, Noakes 1978), who stated that rainbow trout alevins did not begin agonistic behaviour before after emergence. I observed agonistic behaviour of these alevins from day 18 (120 day degrees), whereas 50% emergence appeared at day 30 (204 day degress) posthatching (Nortvedt, 1986b).

The earlier agonistic behaviour observed in the present investigation could be caused by the higher fish density (0.14 alevins/cm), compared to Dill (0.03 alevins/cm) and Cole & Noakes (0.01 alevins/cm). The fact that high fish densities

increase the frequency of agonstic interactions, is indeed showed by Cole & Noakes (op.cit.). In the real rearing situation at Matre Aquaculture Station, 2 litres (9.000) or 1.5 litres (12.000) Atlantic salmon or rainbow trout eggs, respectively, are incubated in a tray of 40x40 cm. These densities give a rather high potential of agonistic behaviour before transfer to first feeding.

During the present investigation, I did not observe yolk sac constrictions, as described by Hansen and Møller (1985). But elongation of the Atlantic salmon's yolk sac was noted. Hansen and Møller (op.cit.), however, did their investigations on far higher alevin densities, however. I therefore conclude that the rearing density of alevins is a proximal factor, with a great potential to cause increased activity among the bottom adapted Atlantic salmon alevins. Further research within this field should closer investigate this phenomenon, and reveal wether the different commercial available substrates have different carrying capacities.

The decrease in position changes/alevin/minute and increase in total swimming activity, which followed the intermediary low activity period, were due to the development of emergence (Nortvedt 1986b). The rainbow trout showed a remarkable low increase in numbers of actually observed alevins per minute, compared to the high level this parameter showed at day 13. But the total swimming distance was still increasing. In fact, during development of emergence, each rainbow trout alevin swam for a longer period and were seldom observed near the bottom. This increasing continuity are also reflected in the bargraphs (see Figs. 5 to 10). At day 39, the emergence of rainbow trout alevins was completed, and the behaviour was identical among these groups. Due to the large data material, swimming activity of only one representative group of rainbow trout was consequently measured.

The increase in swimming activity from day 50 of the Atlantic salmon alevins were also due to their development of emergence, although less conspicuous than that observed among the rainbow trout alevins. After completeness of emergence, the alevins were observed to control buoyancy. It is therefore concluded that

this second activity period was not actually a stressing period of high metabolic costs, as is in agreement with Nortvedt (1986a). This fact confirms the conclusion that the most unfavourable period to the flat screen reared Atlantic salmon alevins was between days 8 and 23, posthatching. Further detail studies should be concentrated within this interval at the present temperature.

It is evident that light affects the behaviour of both Atlantic salmon and rainbow trout alevins. The development of photopositivity is dealt with in another paper (Nortvedt 1986b), but it is well worth noting that prior to emergence, the alevins were photonegative.

According to Ali (1961) the visible spectrum of Atlantic salmon yearlings ranges from 364 to 690 nm. The behaviour of Atlantic salmon alevins during darkness was investigated in a preliminary study with a Badger 500 w/720 nm infrared searchlight. The alevins responded by increased activity to this illumination after day 30, and subsequent measurements by a monochromator and an oscilloscope confirmed that this filter let through som white light. The late response to this illumination could be due to the low intensity of this light, and that the vision was not sufficiently developed before this age. According to Rahmann & Jeserich (1978), myelination of the visual neuronal fibres of rainbow trout alevins begins 26 days (208 day degrees) posthatching, and induces the end of the synaptogenesis period, thereby improving the vision.

In the present investigation, the 860 nm infrared light filter was assumed to prevent penetration of white light. But a similar measurement showed that also this filter let through som white light, though at an even lower intensity than the previous one. Woodhead (1957) found that the duration of activity of brown trout, rainbow trout and Atlantic salmon alevins were directly proportional to the log of the light intensity, over a limited range. The low light intensity during the present investigation was assumed to be sufficiently low too prevent such activity, and in fact, no response to this "infrared" illumination could be observed among the alevins.

During the first day of observation of both species, hardly ar reaction to illumination could be observed, although some changes of position were noted. This is probably explained by the development of their visual system. The retina of an Atlantic salmon alevin is not completely developed, but reaches proper proportions in the fry (Ali 1963). "The main phase of synaptogenesis of rainbow trout begins about one week after hatching, and continues up to the age of one month, when the larvae start swimming freely" (Rahmann & Jeserich 1978).

The general trend from the second day of observation was an increased activity level during illumination of the FSR alevins of both species. GR Atlantic salmon alevins also showed an early increase in activity during illumination from day 29, which was probably due to their early occurrance at the gravel surface. These activity levels were higher than those during darkness until days 28 or 40 of the rainbow trout or Atlantic salmon alevins, respectively. These observations revealed that illumination of the intensity presented, acted as an additional stressor to the falling and righting stress the flat screen reared alevins experienced.

However, was this stress as serious as the stress due to lack of support and shelter? According to Figs 11b & 12b, this physical factor affected the behaviour of the two species differently. Illumination was not observed to increase the activity of the Atlantic salmon alevins furthermore during their most critical period. This was probably because of their already high stress level, and it showed that the twice stressing conditions not necessarily doubled their activity stress. However, when the falling and righting stress decreased, an enlarged activity stress, due to illumination, was experienced by the flat screen reared Atlantic salmon alevins from day 20 to day 30.

The flat screen reared rainbow trout alevins, however, showed increased swimming activity due to illumination during the entire period from day 3 to 23. The maximum swimming activity at day 13 of these alevins during darkness was doubled during illumination. The rainbow trout alevins showed a conspicuous transference from photonegativity to photopositivity after emergence. It is therefore speculated if the exposure of these alevins at

this early stage, when their internal mechanisms were not prepared to this change in illumination, resulted in a higher swimming activity than did the Atlantic salmon alevins. The results from the exposure of both species, however, emphasizes the importance of covering these alevins from illumination in the hatcheries, until emergence.

After days 28 or 40 of rainbow trout or Atlantic salmon, respectively, the activity during darkness increased more rapidly than under illumination. This was caused by the development of emergence of the two species in darkness (Nortvedt 1986b).

The generally high swimming activity for several minutes during a recording sequence under illumination, was temporarily displaced and concentrated to the first 30 seconds of record, as the alevins developed. This result was caused by the strategy of sinking down when the lights were turned on. This behaviour could be a strategy of predator avoidance in the rivers before emergence is developed. According to Thorpe (1981), "the principal advantages of larval development within the gravel bed appear to be the protection from predators, and the minimizing of locomotor activity".

One should feed the alevins at a frequency of about 5-10 times per hour, under normal rearing conditions (Refstie 1979). The feeding during the present investigation was consequently not like a realistic rearing situation. But it probably showed the very true response of the alevins to this stimulus, as can be observed in commercial hatcheries before the alevins habituate to the presentation of food.

The presentation of food stimulated the alevins to increase their activity, but the temporal reaction patterns in darkness or under illumination were different for the two species. The fed rainbow trout alevins showed increased swimming activity in both darkness and under illumination at the commencement of feeding, but this activity declined the following days, compared to the unfed alevins. The exception of this observation among the gravel incubated alevins was probably caused by their late emergence. This reaction to food showed that they were able to

detect the food particles in darkness, probably by their lateral line system. But they were never observed to snap the food during darkness.

The first increase in activity during feeding could be due to an excitement response, whereas the second decline probably was an expression of their confusion to the dense swarm of food particles (Milinski 1984). An alternative hypothesis is that the food particles sank to fast, which led to a decrease in food motivation. Such decrease caused a decline in swimming activity among carps (Cyprinus carpio) (Siegmund & Schulz 1983). The observations that they tried to hide themselves or swim in reverse from the dense swarm, that they increased their frequency of position changes during illumination and that they showed interest to the food particles when these were presented singly, all support the former hypothesis. The later decrease in position changes among both fed and unfed alevins was because of their development of emergence (Nortvedt 1986b). The still increased swimming activity of the unfed alevins was caused by their searching behaviour in the upper surface layer. It is concluded that the size of these food particles was not preferable to the rainbow trout alevins, because they were never observed to swallow this food.

The only exception from increased swimming activity in both darkness and under illumination of fed Atlantic salmon alevins, was that of the FSR alevins under illumination. But they showed an increase in position changes. All the groups of unfed alevins showed decreased swimming activity after day 59. These observations reveal the feeding success of the fed Atlantic salmon alevins, whereas the unfed groups probably had passed their most active searching period at the termination of the present investigation.

Although the Atlantic salmon alevins were confused by the particle swarm too, they probably handled this problem better than the rainbow trout alevins because they snapped the food particles after upward burst swimming from bottom or near bottom position. At this depth, the swarm of food particles had broken up. Moreover, they were able to ingest this particle size. If the food reached the bottom, however, they lost the interest

to it. This behaviour can also be observed with smolts (Stefansson, pers. comm.). No difference in feeding success was observed between alevins incubated in different environments. The low activity among alevins within the substrates, resulting in high efficiency before first feeding (Hansen 1984), reflected by no means a decreased feeding activity, as made caution against by a general statement of Blaxter (1969).

The ultimate factors of behaviour are those concerning the function of the behaviour. However, " for an understanding of the causal mechanism, a functional classification does not help, because evolution has developed a variety of solutions for analogous functional problems" (Baerends 1971). The proximal factors of behaviour in the present investigation were those acting as releasing stimuli, namely gravity, light, feeding and probably also density. They caused the activity patterns observed.

The consequences of this behaviour, with respect to growth and mortality, are very well documented by Hansen (1984,1985), Hansen and Møller (1985) and Marr (1965a,b). Could the reduced groth and low yolk conversion efficiency secondarily make influence on the behaviour at later stages of development? Taranger et al. (1985) showed that protein synthesis, RNA and DNA content, and the RNA/DNA ratio were higher in favour of Astroturf reared alevins, compared to flat screen reared ones. According to Packard and Wainwright (1973), total DNA quantities within the brain can be used as an indicator of its total cell numbers, and total RNA as a measure of their activity. They found that when resorption of yolk stopped and the alevins did not feed, brain growth (both wet weight and DNA) also stopped, and that the RNA content of the brain in "nonfeeders" dropped down sharply.

Given great differences in brains, I assume that this will make influence on the behavioural repertoire of the Atlantic salmon fries at later stages of development. This is confirmed by the decreased swimming activity of unfed Atlantic salmon alevins after day 59, whereas this was not demonstrated among rainbow trout alevins, because the observations were terminated at an earlier stage of their development. According to Taranger (op.cit.) and Hansen and Torrissen (1985), Astroturf incubation

favours growth of the fries during feeding. In conclusion, the behaviour repertoire will be less varied. This could also happen alevins in the rivers under unfavourable conditions. In this way, they would become easy targets to an experienced predator.

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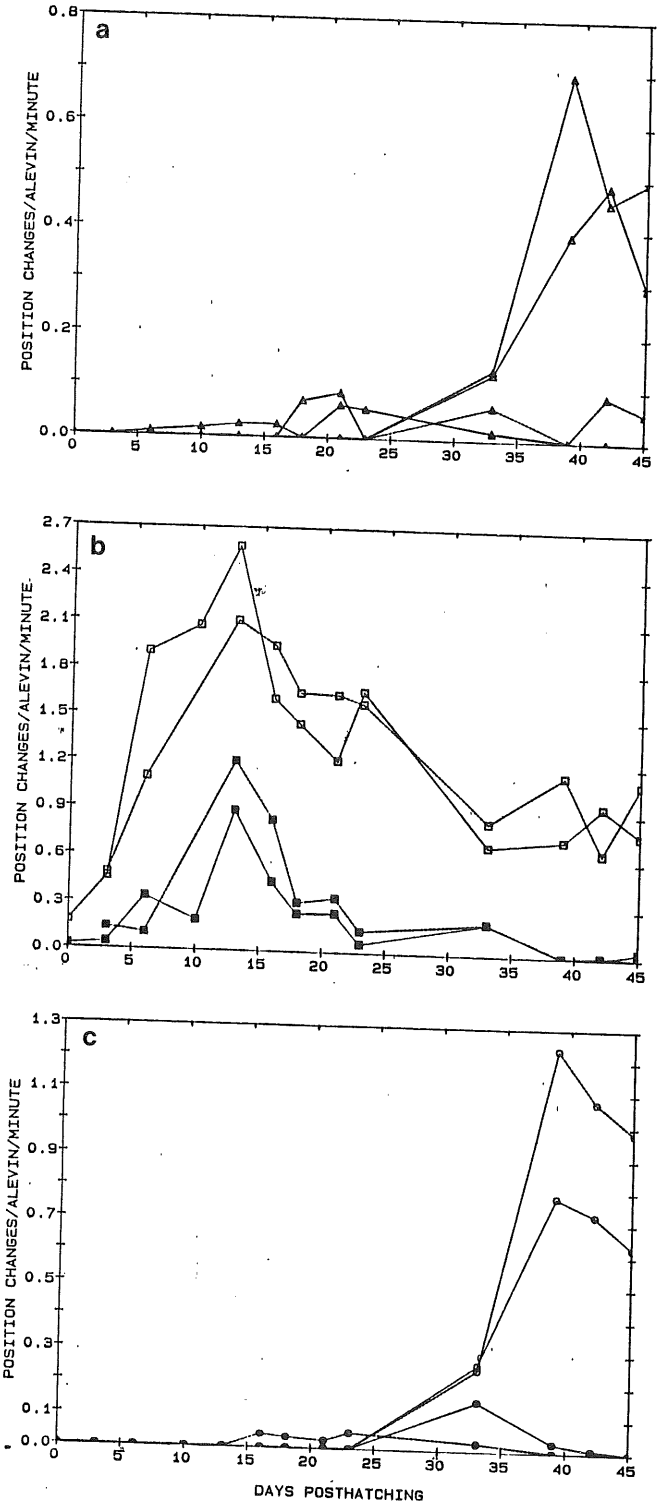

Fig. 3a-c: Position changes of the rainbow trout alevin per minute, plotted against days posthatching. Closed symbols denote activity during darkness. Open symbols denote illumination. Dashed line, fed. Single line, unfed. Note different scale of axis.
a) ▲,△ = ATR
b) ■,□ = FSR
c) ●,○ = GR

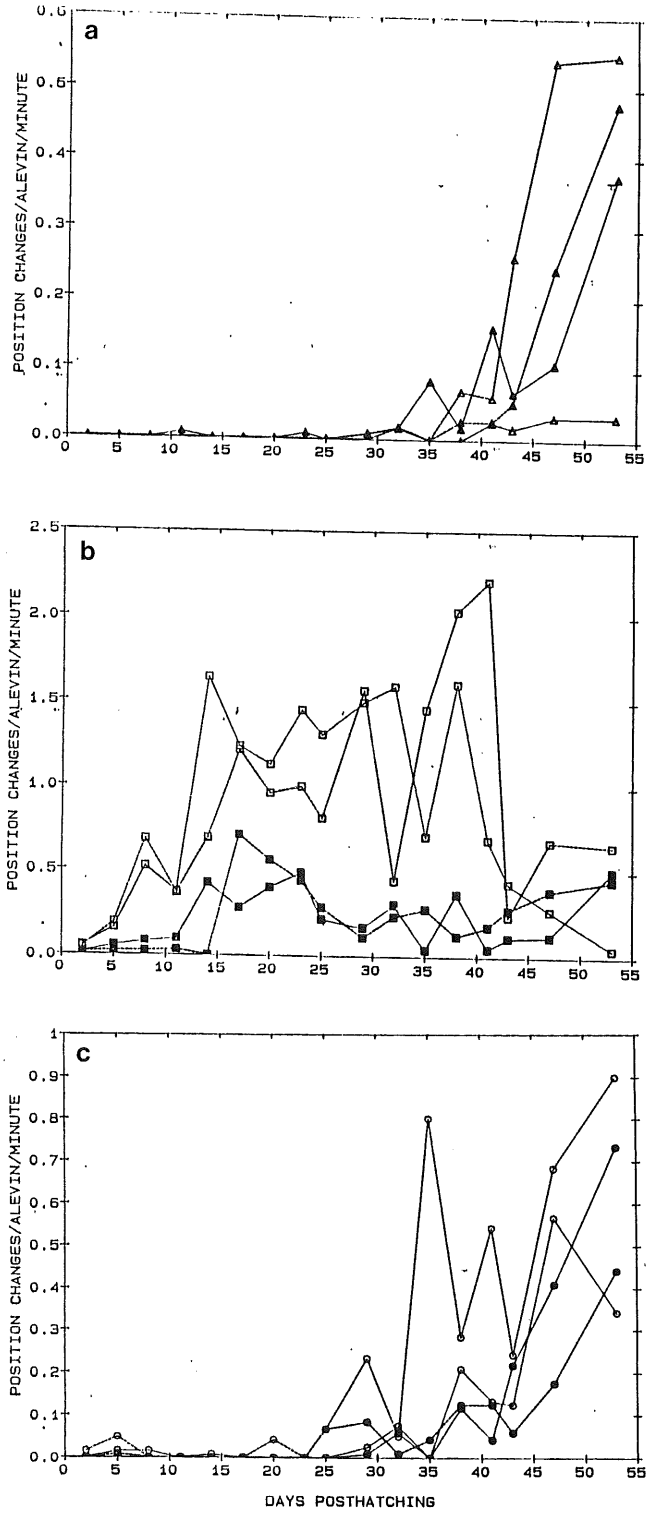

Fig. 4a-c: Position changes of the Atlantic salmon alevin per minute, plotted against days posthatching. See also Fig. 3.

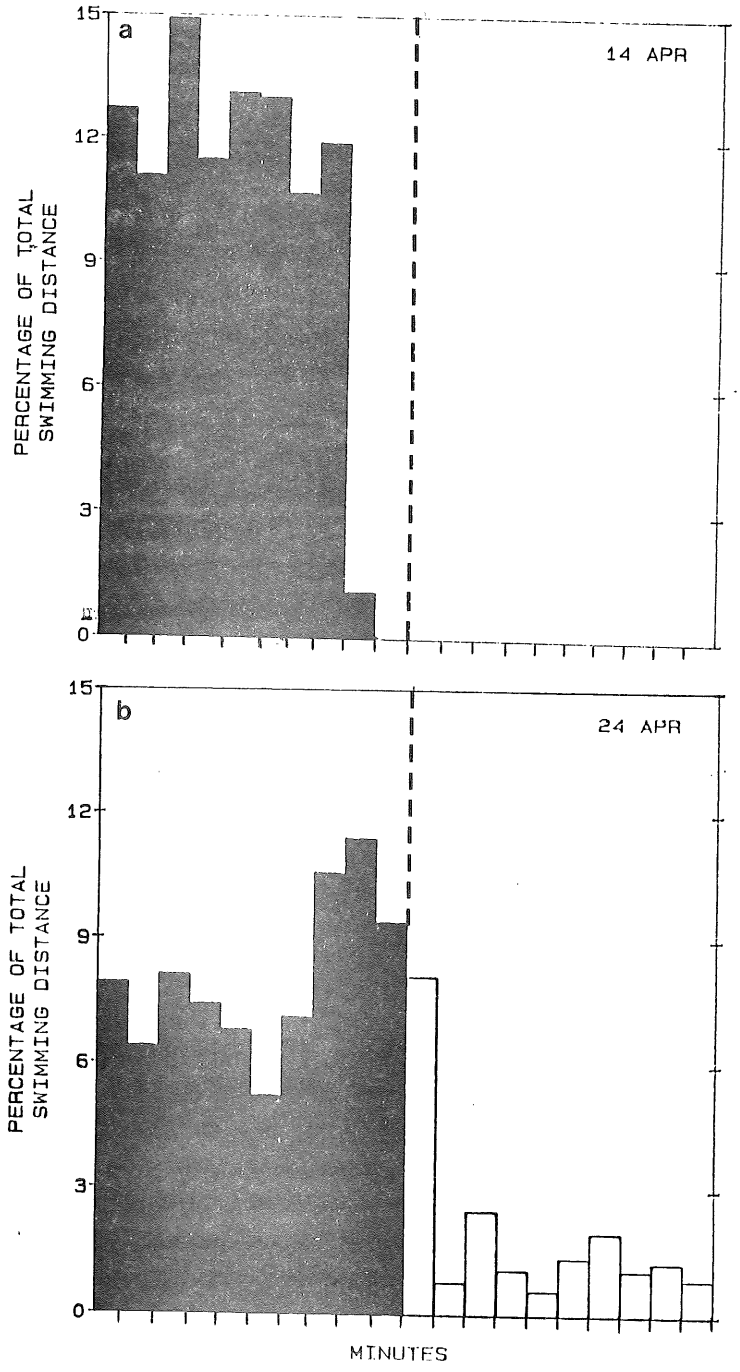

Fig. 5a-b: Total swimming activity through each recording sequence of unfed ATR rainbow trout alevins, expressed as percentage activity within each 30 seconds interval. Black and white bars illustrate activity in darkness and under illumination, respectively. Each bar group represents 30 secs. Vertical dashed line shows the time when the light was turned on. Note different scale on axis.

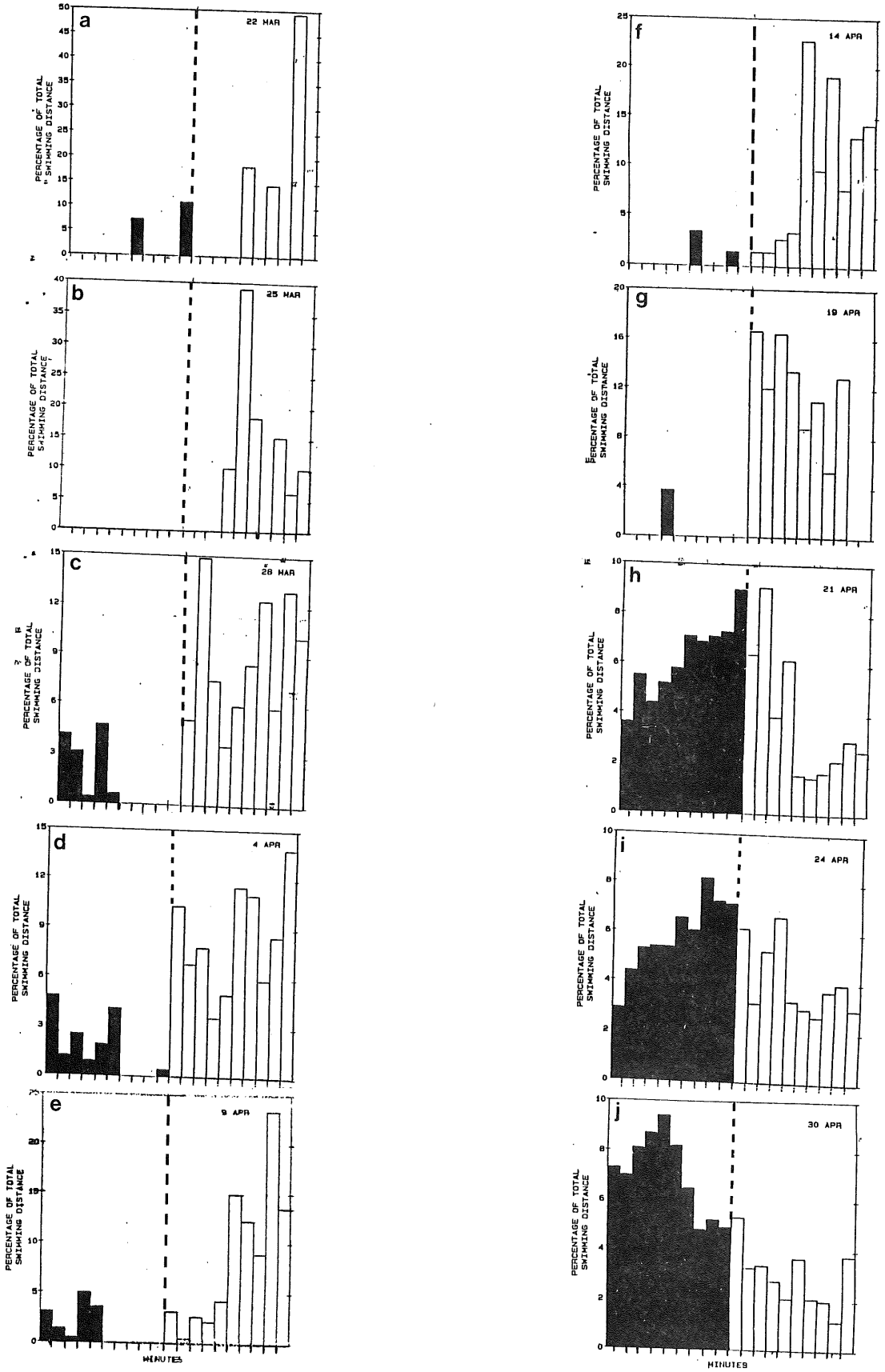

Fig. 6a-j: Total swimming activity through each recording sequence of unfed FSR rainbow trout alevins. See also Fig. 5.

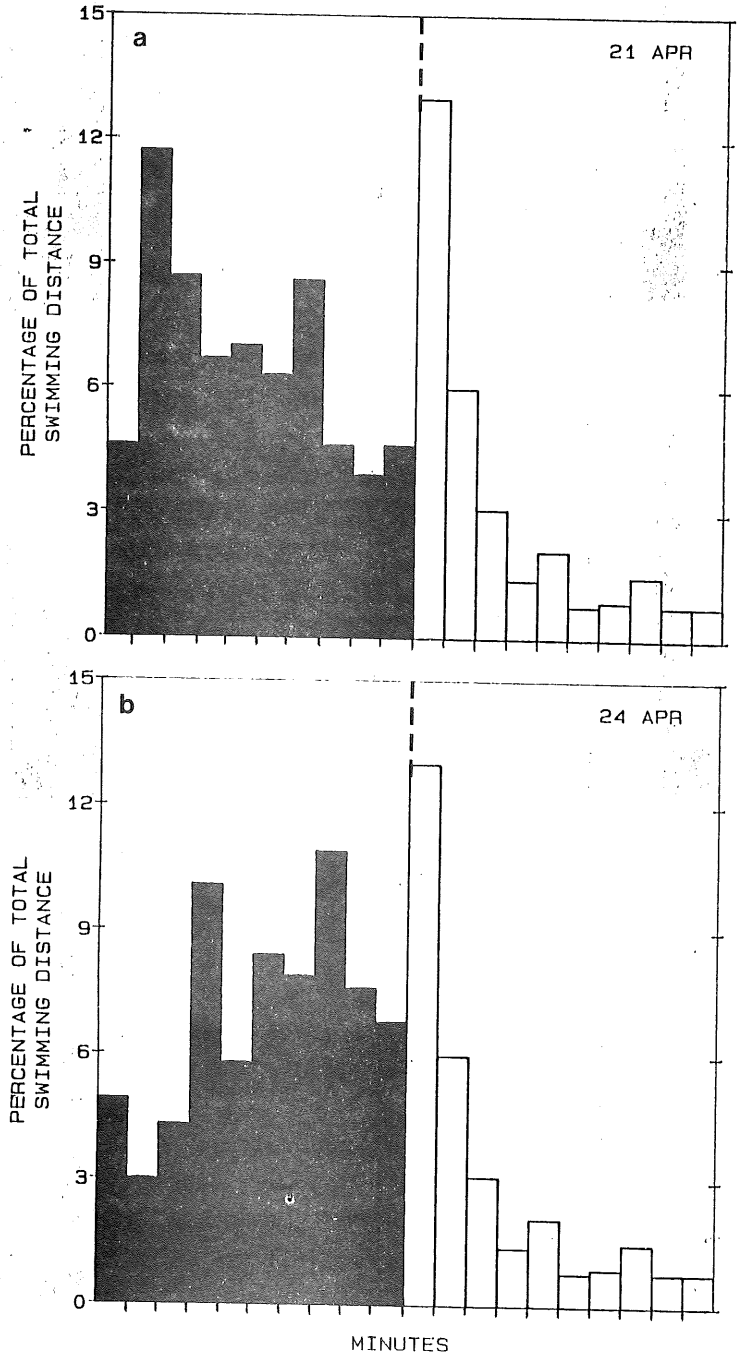

Fig. 7a-b: Total swimming activity through each recording sequence of unfed GR rainbow trout alevins. See also Fig. 5.

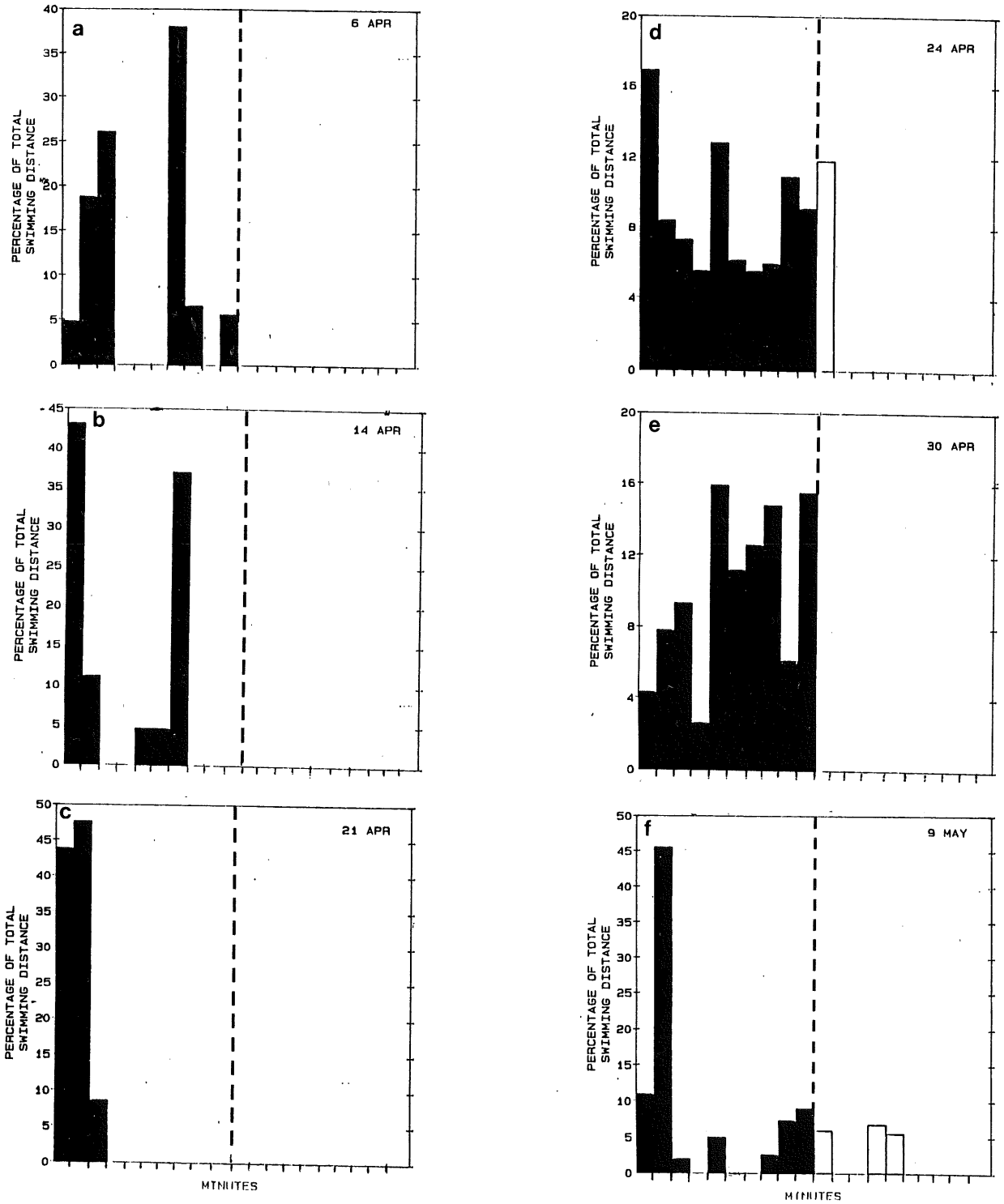

Fig. 8a-f: Total swimming activity through each recording sequence of unfed ATR Atlantic salmon alevins. See also Fig. 5.

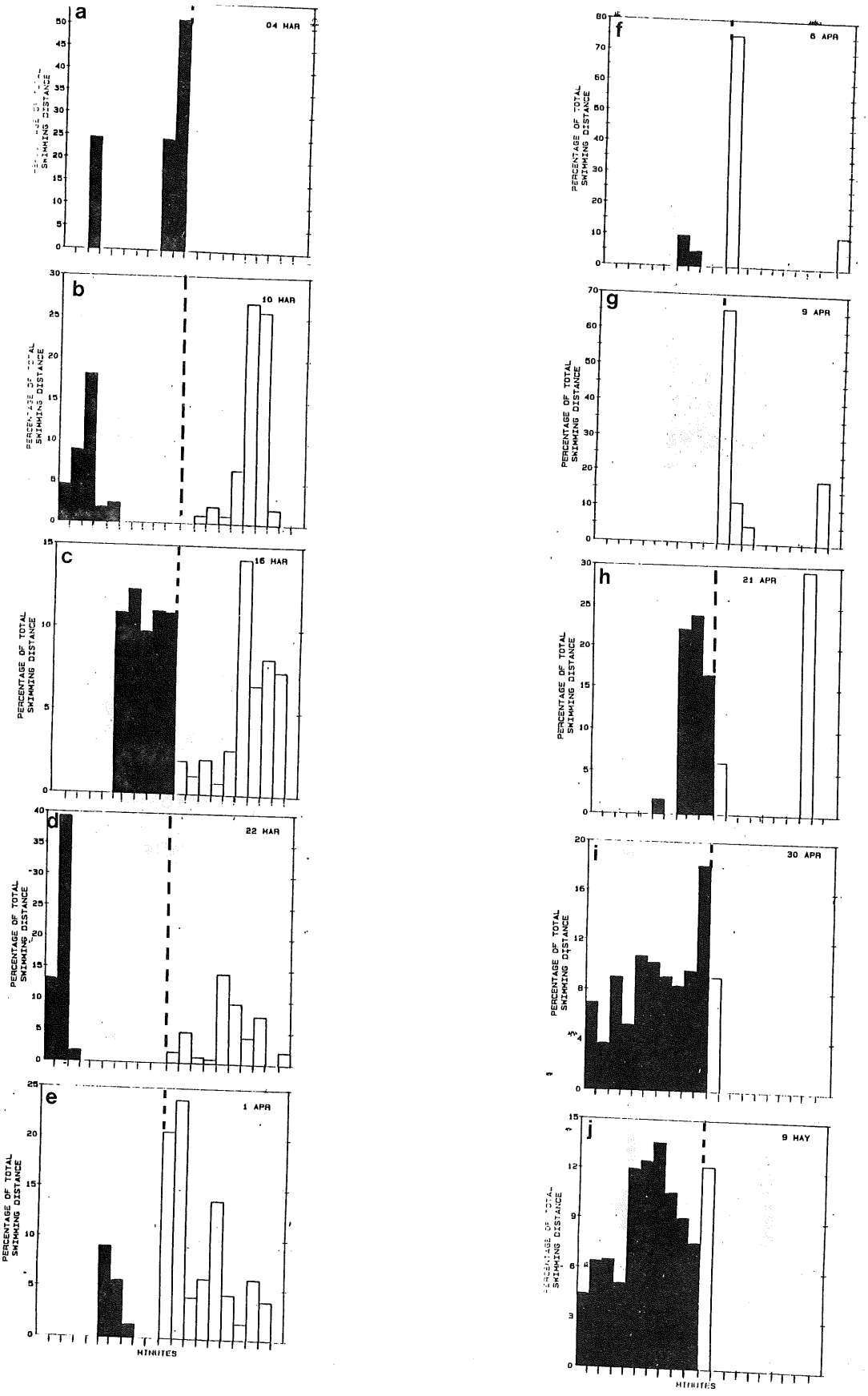

Fig. 9a-j: Total swimming activity through each recording sequence of unfed FSR Atlantic salmon alevins. See also Fig. 5.

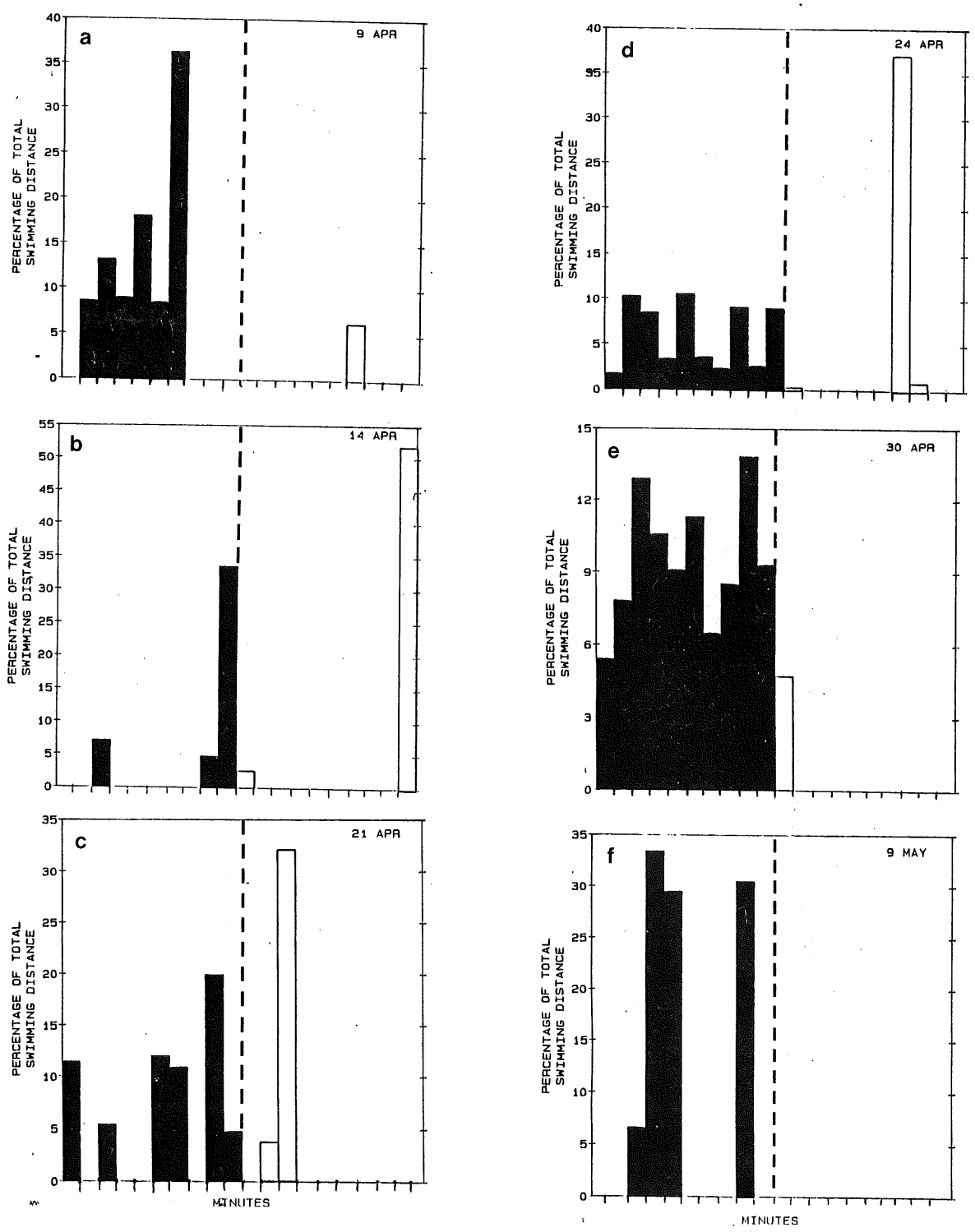

Fig. 10a-f: Total swimming activity through each recording sequence of unfed GR Atlantic salmon alevins. See also Fig. 5.

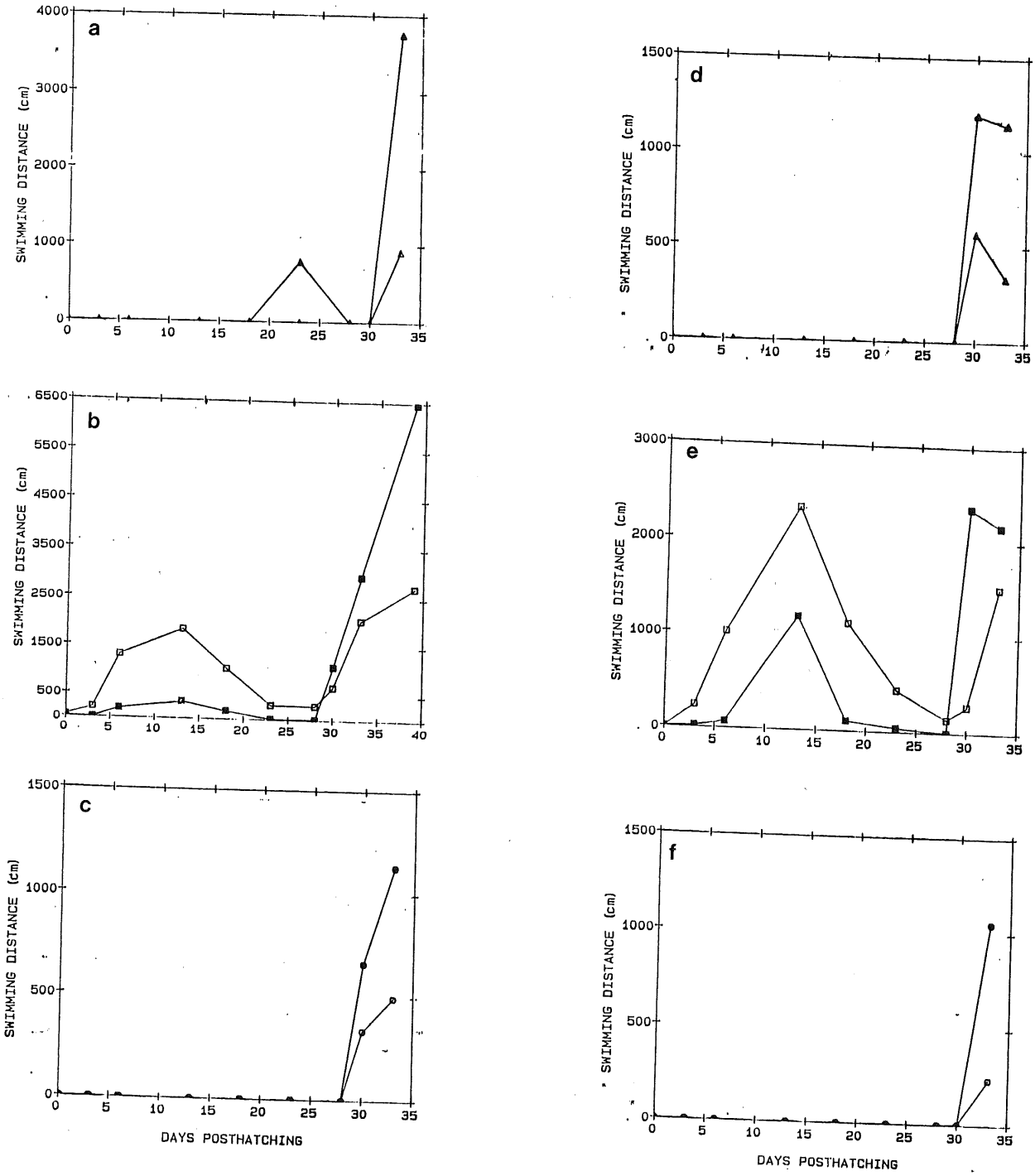

Fig. 11a-f: Total swimming distance of all the rainbow trout alevins in each observation chamber, plotted against days posthatching.
a-c: unfed alevins.
d-f: fed alevins (from day 30).
See also Fig. 3.

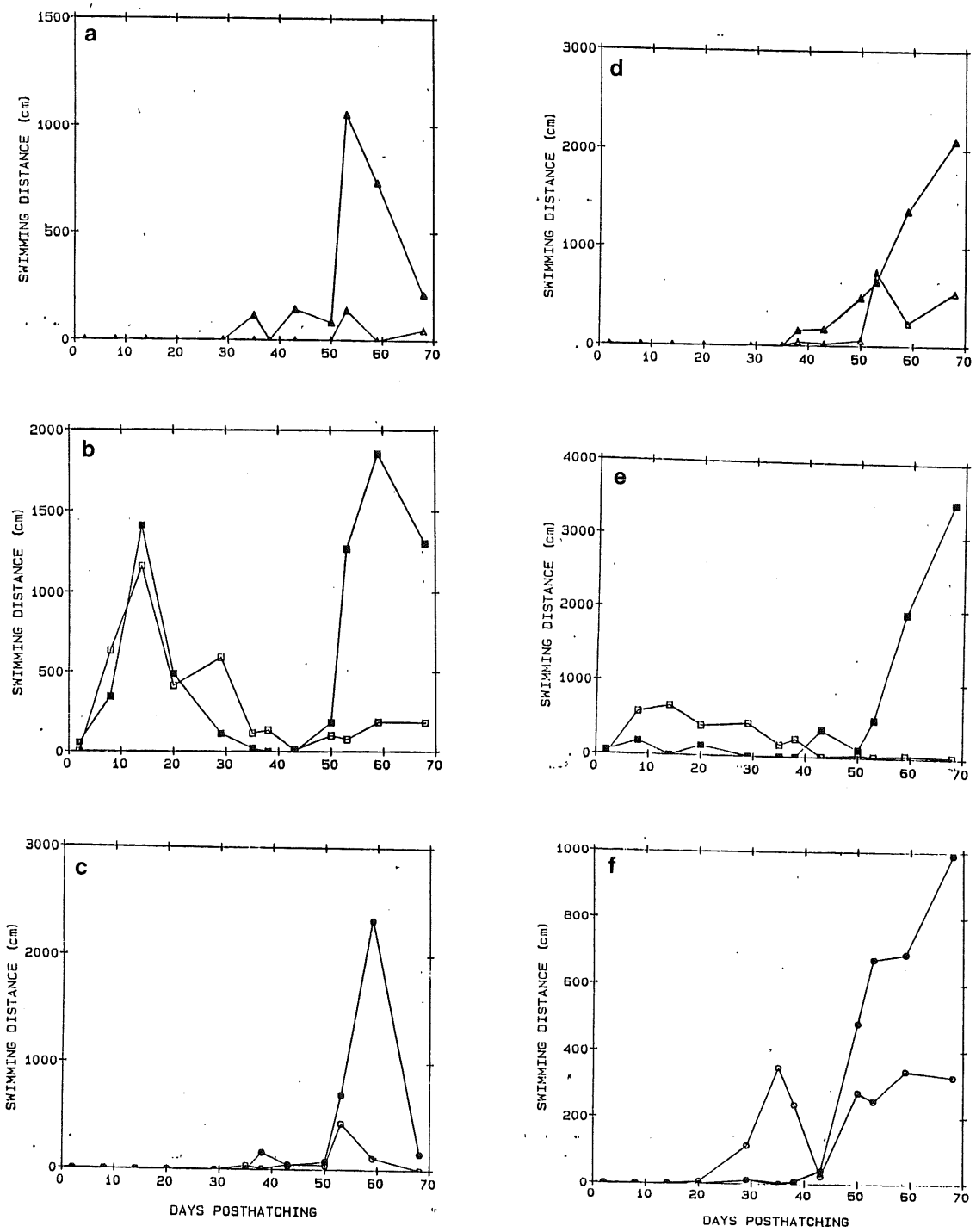

Fig. 12a-f: Total swimming distance of all the Atlantic salmon alevins in each observation chamber, plotted against days posthatching.
a-c: unfed alevins.
d-f: fed alevins (from day 30).
See also Fig. 3.

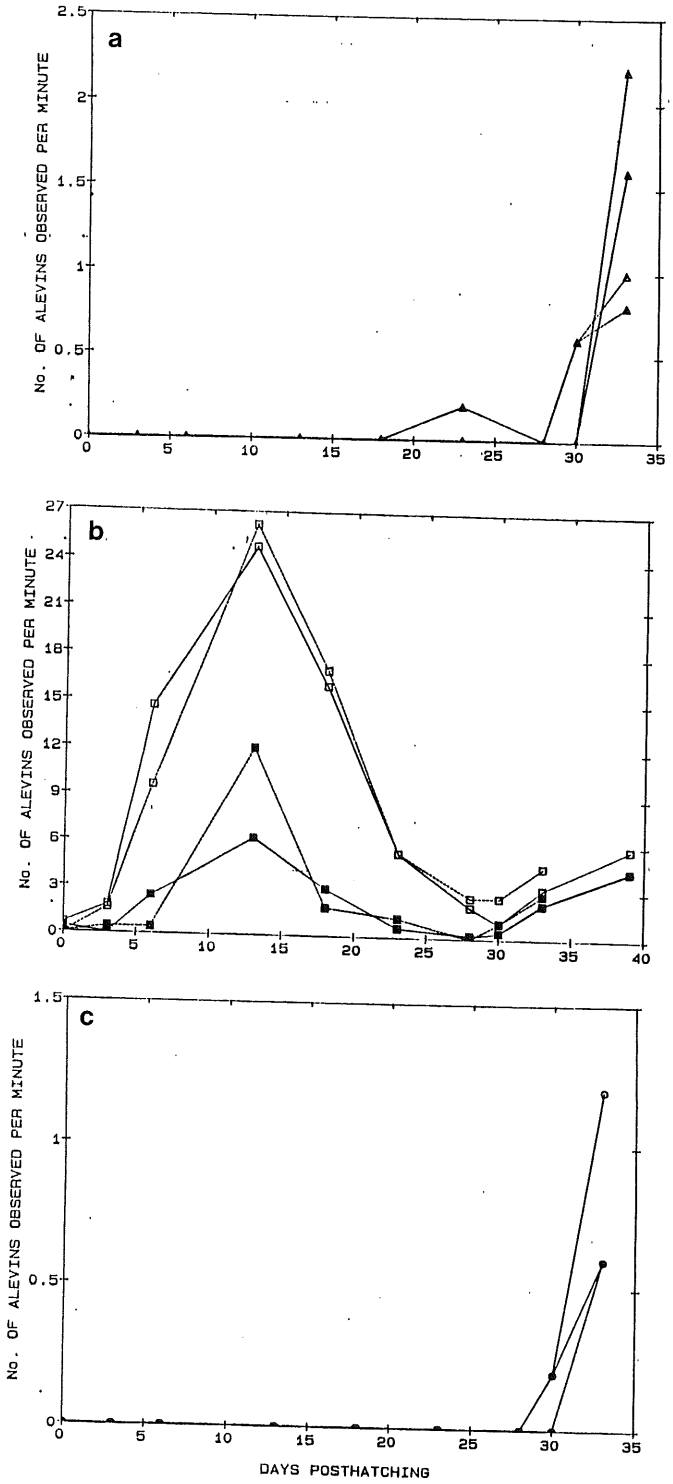

Fig. 13a-c: Number of rainbow trout alevins observed swimming per minute, plotted against days posthatching. These numbers are average values from their respective five minutes sequences. See also Fig. 3.

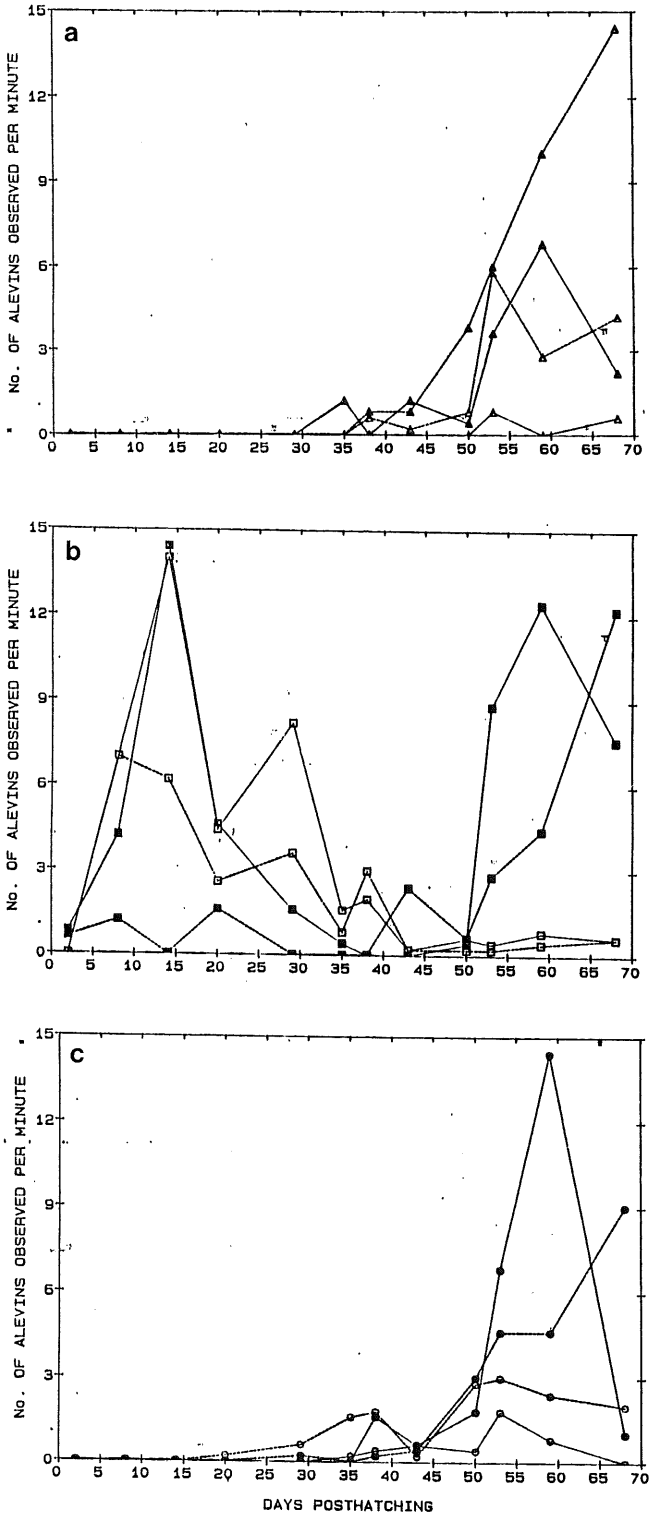

Fig. 14a-c. Number of Atlantic salmon alevins observed swimming per minute, plotted against days posthatching. These numbers are average values from their respective five minutes sequences. See also Fig. 3.