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**THE TIMING OF EMERGENCE 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, individual swimming height above the bottom were monitored with a video recording system. The use of infrared light made it possible to observe the positions in the water column in darkness.

Mean swimming height in a coordinate system and percentage occurrence in specific heights above the bottom were used as measures on emergence from the bottom.

Emergence was more conspicuous among the rainbow trout alevins (196 - 226 day degrees) than Atlantic salmon alevins (335 - 400 day degrees). After emergence, the rainbow trout alevins swam close to the water surface, and 50 % of them became photopositive on day 39 (269 day degrees). The Atlantic salmon stayed closer to the bottom after emergence, and they became heedless to light at this stage. This reflect different evolutionary strategies. Neither substrates nor feeding made influence on overall timing of emergence.

INTRODUCTION

The salmonids are physostomes (Jones and Marshall 1953). Towards the end of the larval stage this causes them to emerge from the bottom substrates to the water surface, to snap air and fill their swimbladders. This happens at a specific stage of development, but environmental factors can make inhibitory or accelerating influences on the emergence behaviour (Bams 1969).

The behaviour of salmonid alevins within natural and artificial gravel redds has been extensively studied by Stuart (1953), Woodhead (1957), Bams (1969), Dill and Northcote (1970a,b) and others.

Alevins of Oncorhynchus, Salmo and Salvelinus are initially negatively phototactic (Mason 1976). That means that they actively turn away from the light. This is in contrast to several marine larvae (Dannevig 1932, Soleim 1942), which are photopositive. However, also among freshwater species, some alevins become photopositive (Hoar et al. 1957). This change is sudden and saltatory (Balon 1979).

Different hypothesis, on the influence of light on the emergence behaviour of salmonids, has been put forward. These can be stated as follows:

H1: Light initiates the downward movement of salmonid alevins (Carey and Noakes 1981). Photoresponse shift precede the onset of alevin emergence (Carey 1985).

H2: Light is not the primary releasing factor of downward movement. Light does not initiate emergence.

In the present investigation, it was decided to compare the timing of emergence in Atlantic salmon (Salmo salar) and rainbow trout (S. gairdneri) alevins, and to test the above hypothesis on alevins of the two species. Inspired by a possible enhanced development among Astroturf reared alevins (Hansen 1985), the

purpose was also to observe whether the Astroturf reared alevins emerged earlier than the flat screen reared ones. The effect of feeding was also tested.

MATERIAL AND METHODS

Experimental conditions

Atlantic salmon eggs, obtained from A/S Fiskekultur, Matredal, and rainbow trout eggs from Matre Aquaculture Station the spring 1985, were incubated, hatched and fed in six plexi-glass aquariums (Fig.1), the same way as described by Nortvedt (1986a). Each aquarium had two observation chambers with Astroturf artificial substrate, gravel or no substrate, arranged in different substrate combinations. Six groups of 25 alevins of each species were observed in the 12 observation chambers. The temperature varied between 6.0 and 7.6 °C, with a mean value of 6.8 °C. The light intensity of the bulb light at the water surface was 9.4 W/m². Food was introduced on days 29 and 30 of Atlantic salmon and rainbow trout, respectively.

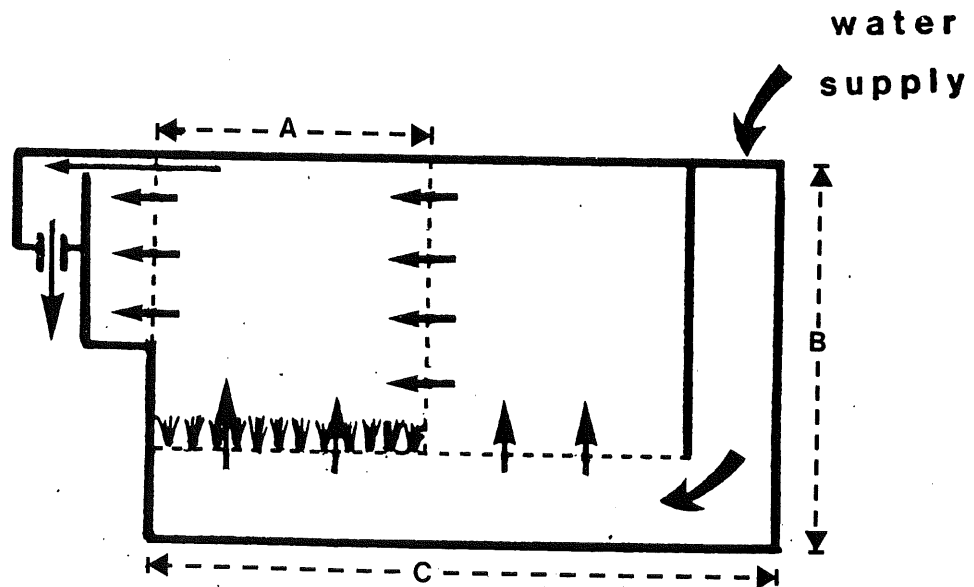


Fig. 1: Aquarium with two observation chambers, one with Astroturf and one without substrate. The arrows indicate the water flow. A = 17.5 cm, B = 25.5. cm, C = 41.0 cm.

Observations and analysis

Responses to illumination and emergence to the substrate surface were observed by eye, with particular attention to when the alevins eventually became photopositive. Emergence from the substrates to the water surface and vertical movements in the water column were recorded with a video camera. A recording sequence of 5 minutes in darkness was followed by 5 minutes during illumination, as described by Nortvedt (1986b) (Fig. 2). Observations on the rainbow trout and Atlantic salmon alevins were made every third day, and recording at least every sixth day from hatching to days 45 and 68, respectively. Only one representative group of rainbow trout was recorded on day 39.

The water column was subdivided into eight horizontal stacked zones, scratched on the front walls of the observation chambers. When analysing the recordings, the swimming heights of each alevin were noted every third second, during the two five minutes sequences. For each recording, maximum and mean swimming heights, and percentage occurrence in the horizontal zones were calculated, to achieve a measure on the timing of emergence.

The timing of 50% emergence to the water surface was defined as the date when more than 50% of the observations, during the 10 minutes of recording, were made in the upper half volume of the water column.

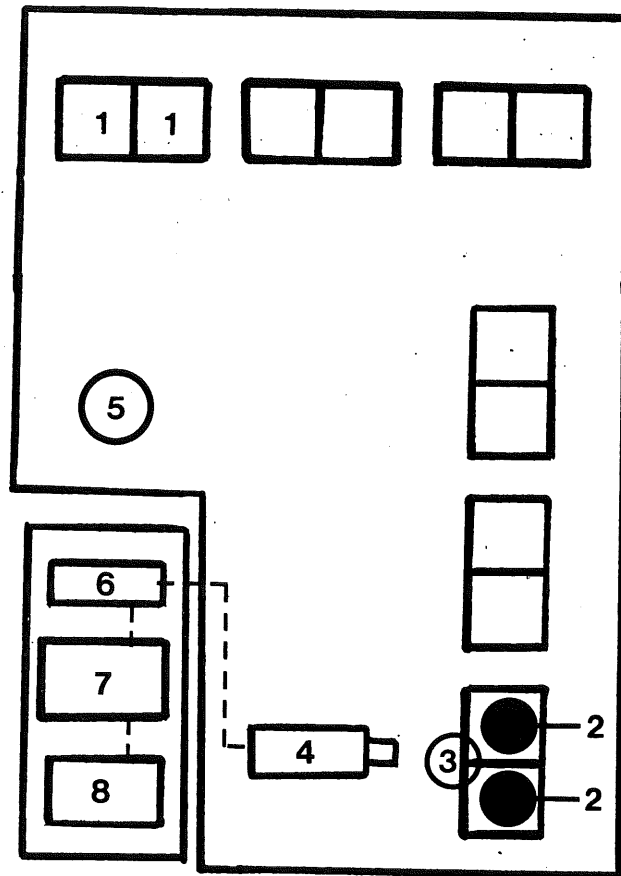


Fig. 2: Schematic view of the behaviour observation set-up.

Dashed line 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 - 6030 ME).

Rainbow trout photoresponse experiment

Rainbow trout eggs, in pooled groups from a number of females at Matre Aquaculture Station, were incubated in three separate hatching trays without substrate, the spring 1986. After 50% hatching on 17 June, 100 alevins of normal appearance were still kept in the trays. These trays were constructed as choice chambers with dark and light compartments (see Fig.3). The temperature varied between 12,7 and 15,6 °C, with a mean value of 14 °C. Each choice chamber had its own separate water supply from a common reservoir, and the flow rate through each one was kept steadily at 1 l/min. A continuously illuminating fluorescent light gave a light intensity at the water surface of each choice chamber of 8.0 W/m².

The alevins could freely swim below the elevated centre partition and choose either darkness or illumination. This centre partition, fixed three cm above the bottom, parallel to the water flow direction, was lowered every third day. Number of alevins in each compartment was counted, and mean values from the three trays were calculated. 50% emergence to the water surface was estimated by eye. To ensure that the alevins did not habituate to a specific compartment, the reversible lid was arbitrarily placed at the right or left side of the choice chamber every third day.

On 4 July the alevins in all trays suffered from high mortalities, probably caused by acid flood water, and the experiment was consequently terminated.

The following abbreviations will be used:

ATR = Astroturf reared
GR = gravel reared
FSR = flat screen reared
dC = day degrees

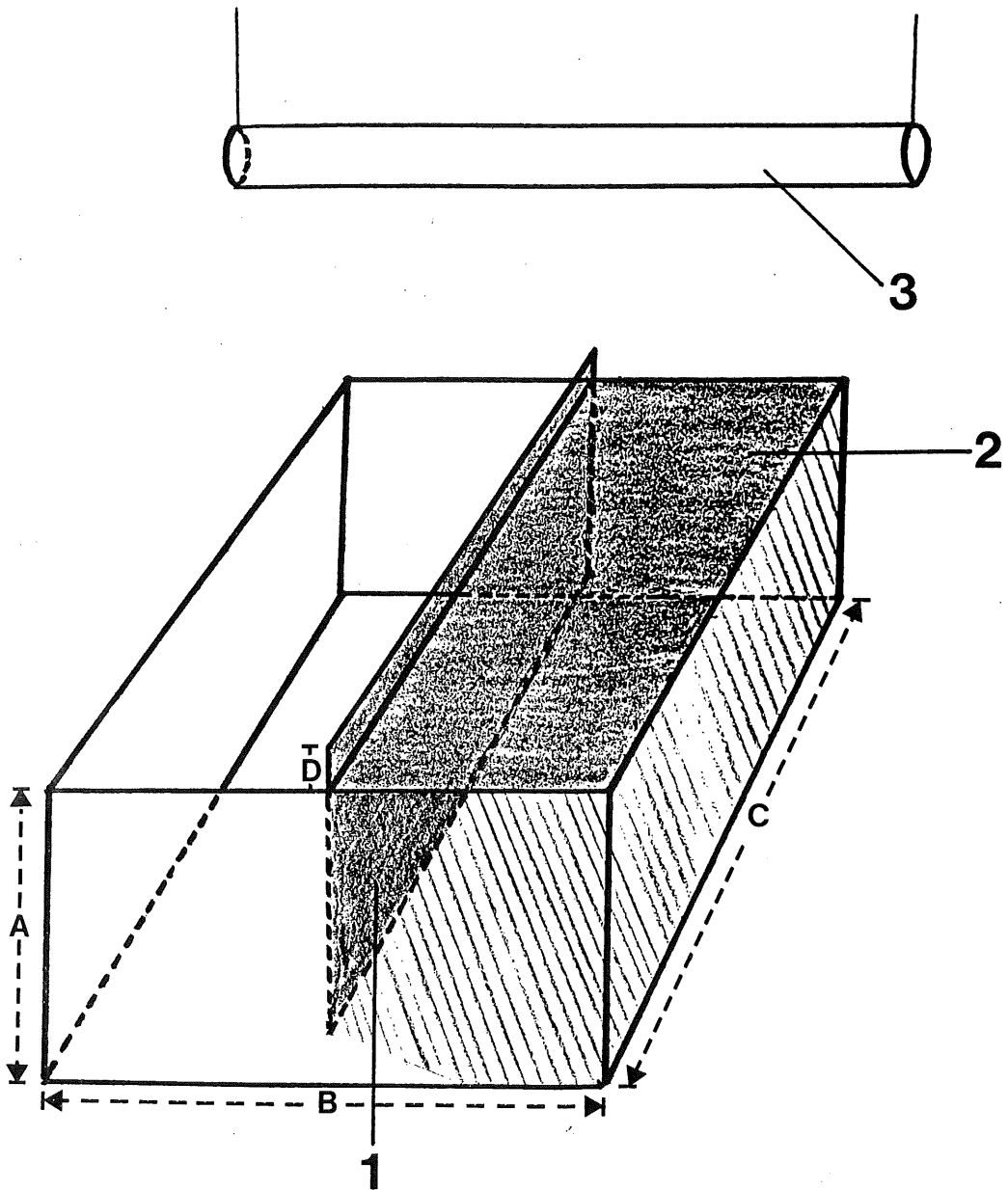


Fig. 3: Choice chamber. Same water supply principle as in Fig. 1.

A = 20.0 cm, B = 39.0 cm, C = 36.0 cm, D = 3.0 cm.

- 1) Vertical centre partition, can be elevated and fixed 3 cm above the bottom.
- 2) Reversible lid.
- 3) Light.

RESULTS

Atlantic salmon

About 50% of the GR alevins had disappeared from the surface of this substrate two days posthatching. They searched down in the crevices during darkness, and some were observed near the bottom along the plexi-glass walls. No alevins were observed at the gravel surface from day 8 to day 20. 50% of the alevins had emerged during darkness to the gravel surface on day 25.

The ATR alevins stayed quiet between the bristles of this substrate for the three first weeks posthatching. The first alevin was observed to place its head at the top of the bristles on day 20. 20% and 50% of the alevins were situated at the surface of this substrate on days 29 and 38, respectively.

The FSR alevins showed high swimming activity between days 8 and 23 (Nortvedt 1986b). This rapid burst activity brought them across the bottom and suddenly up along the wall to the water surface from day 8 (Tab. 1).

Tab. 1: Maximum swimming heights (0 - 7) above the bottom of GR, ATR and FSR Atlantic salmon, during five minutes in darkness (D), followed by five minutes under illumination (L). F = Fed, U = Unfed.

DAY	dC	GR(U)		GR(F)		ATR(U)		ATR(F)		FSR(U)		FSR(F)	
		D	L	D	L	D	L	D	L	D	L	D	L
2	14									2	0		
8	55									7	4		
14	93									7	5		
20	131		2							5	7		
29	190			3	7					0	7	0	7
35	230		7		7	7	0			1	1	0	7
38	251	7	2	3	7	0	0	7	3	0	7	0	7
43	285	4	3	7	7	7	0	7	1	0	0	7	0
50	335	5	7	7	7	7	0	7	2	7	7	7	7
53	357	7	7	7	7	7	7	7	7	7	7	7	7
59	400	7	7	7	7	7	0	7	7	7	7	7	6
68	465	7	2	7	7	7	2	7	7	7	7	7	3

The timing of 50 % emergence to the water surface occurred between days 50 and 59 among the Atlantic salmon alevins. Emergence was less conspicuous during feeding and most conspicuous during darkness.

The first observation of surface swimming among the GR alevins was made during illumination on day 35 (Fig. 4). Emergence behaviour in darkness appeared from day 38, and 50% emergence occurred on day 59. However, a low mean swimming height above the bottom on the emergence day (Fig 7c), resulted from the very heterogeneous emergence pattern (Fig 4).

Extensive surface swimming in darkness among ATR and FSR alevins occurred for the first time on days 35 and 50, respectively (Figs.5,6). However, 50% emergence occurred on days 53 and 50. Mean swimming heights indicated the same results (Fig. 7 a,b), but the alevins swam closer to the bottom after emergence. None of the Atlantic salmon groups became photopositive during the present investigation.

Rainbow trout

About 70% of the FR alevins had disappeared from the surface of this substrate six hours after hatching, and none were left the third day posthatching. They searched down in the crevices the same way as the Atlantic salmon alevins did. The first alevin emerged to the gravel surface again on day 27, and 50% of the alevins appeared at this surface on day 30. They emerged during darkness.

The observations revealed early jumping and restlessness at the bottom among the ATR and FSR alevins. None of the ATR alevins were observed to rest at the top of the bristles before 50% emergence to the water surface. This was probably caused by their small size. The early activity of the FSR alevins (Nortvedt 1986b), brought them up along the aquarium walls from day three (Tab. 2).

Tab. 2: Maximum swimming heights (0-7) above the bottom of GR, ATR and FSR rainbow trout, during five minutes in darkness (D), followed by five minutes under illumination (L). F = Fed, U = Unfed.

DAY	dC	GR(U)		GR(F)		ATR(U)		ATR(F)		FSR(U)		FSR(F)	
		D	L	D	L	D	L	D	L	D	L	D	L
0	2									0	1		
3	21									0	5		
6	40									4	5		
13	85									1	2		
18	120									1	2		
23	154					7	0			2	7		
28	183					0	0			2	7		
30	204	7	7	2	3	0	0	7	7	7	7	7	7
33	226	7	7	7	7	7	7	7	7	7	7	7	7
39	269									7	7		

The timing of 50% emergence to the water surface occurred between days 30 (204 day degrees) and 33 (226 day degrees) among all the groups (Fig. 8). Both species snapped air at the water surface. They did not control buoyancy the first day this behaviour was observed. 50% of the rainbow trout alevins became photopositive on day 39. That means that they actively turned their heads against the light. Before this day, most of the alevins sank down from the water surface some minutes and turned away from the light. However, following some minutes of exposure, they swam to the water surface again after day 30. Above 90% of the alevins stayed in the upper 2 cm of the water column from day 39.

When the GR and ATR alevins emerged, their activity in the intermediary part of the water column was low (Figs. 9, 10). The first peak of mean emergence among the ATR alevins was not representative to the overall emergence trend, because this contribution came from only one alevin (Fig. 8). The fed ATR alevins emerged three days before the unfed. No such difference was observed among the GR alevins, as far as mean swimming heights were concerned, but percentage occurrence in definite heights above the bottom indicated that the unfed alevins emerged three days before the fed.

Although Fig. 8 indicated that the unfed FSR alevins emerged three days before the fed, the percentage occurrence measure did not show clear differences between these groups. The FSR alevins emerged earlier during illumination, but less well defined than in darkness (Fig. 11).

The results from the photoresponse experiment showed that 50% emergence occurred the 1 July (196 dC) during both darkness and illumination. Approximately 35% of the alevins chose the light compartment that day (Tab. 3).

Tab. 3: Mean (\pm SD) percentage choice of the light compartment in a choice chamber.

DATE:	17 June	22 June	25 June	28 June	1 July	4 July
%	0.0	3.7(2.0)	0.0	32.3(4.0)	34.7(6.4)	63.7(11.0)

Above 50% of the still living rainbow trout alevins were photopositive on 4 July.

DISCUSSION

Early surface swimming before 50 % emergence among the Atlantic salmon alevins (Figs. 4-6) was caused by several action patterns. These were the stress behaviour of the FSR in lack of ventro lateral support, the unsynchronized emergence within the groups and the lack of individual buoyancy control after their first day of emergence.

These heterogenous emergence patterns were illustrated by the measures of mean swimming heights and the percentage occurrence in specified heights above the bottom. But the best measure of 50 % emergence was that of 50 % occurrence in the upper half volume of the water column. Bams (1982) and Carey and Noakes (1981) measured emergence from the substrate/ water interface as proportion of fry leaving some evenly spaced plastic tubes on the surface of the substrate. However, this interesting method will not reveal that the Atlantic salmon alevins stayed closer to the bottom after they became neutrally buoyant, than did the rainbow trout alevins.

The early emergence behaviour during darkness among the ATR Atlantic salmon alevins was caused by only some few individuals until day 53, and the surface swimming among the GR alevins on day 35 was caused by their stress behaviour due to illumination. This behaviour ceased from day 40 among the Atlantic salmon alevins (Nortvedt 1986b). Consequently, one cannot conclude that the substrate reared alevins developed faster, and thereby initiated an earlier emergence.

This is in agreement with Bams (1969), who stated that the average time of emergence of sockeye salmon (Oncorhynchus nerka) was predetermined by previous selection, and that the individual alevins had no control over it. So even if the FSR alevins had higher activity than the ATR alevins (Nortvedt 1986b) and thereby higher respiratory rates during the first weeks of their life (Nortvedt 1986a), this metabolic demand and the differentiation of the body took precedence over growth (Bams op.cit.). Predetermined time of emergence was therefore unaffected by the rearing conditions in the present investigation. This conclusion

was confirmed by the behaviour of the rainbow trout alevins, whose timing of emergence was even closer synchronized among the groups (Fig.8). Dill (1977) also found that alevins of both species left the bottom in the gravel-free situation at an age similar to emergence of conspecifics raised in gravel.

However, Taranger et al. (1985) found a higher DNA content, which indicate a higher cell number, in favour of ATR Atlantic salmon alevins. Whether this gain caused an increase in muscle cells or differentiation of the central nervous system, essential to behaviour, was not investigated. Such investigations should be performed in the future, together with studies on behaviour of alevins in a large scale rearing situation. This would clarify if Bams' statements holds under real rearing conditions.

Why were then the Atlantic salmon alevins appearing earlier at the gravel surface than at the top of the Astroturf bristles, and five days before the GR rainbow trout alevins? This is possibly explained by the reduced water flow through the gravel, compared to the other rearing environments (Nortvedt 1986a). This environmental factor was possibly acting as a guiding factor, which influenced the predetermined emergence under conditions of potential oxygen deficit in the micro environments of the Atlantic salmon alevins. The rainbow trout alevins moved more rapidly down in the crevices during their early development, and emerged much earlier to the water surface. But evidently, the rainbow trout alevins were not influenced the same way by this guiding factor. This reflects their smaller size, and consequently their lower oxygen demands at early stages of development. Besides, Peterson and Metcalfe (1981) found that there was a tendency for smaller Atlantic salmon fry to emerge later. They argued that smaller fry were able to use smaller crevices to move upward through the gravel.

The term guiding factor was introduced by Bams (op.cit.), who also stated that gravity acted as a guiding factor during both intra gravel migratory activity and later "swim-up" activity to the water surface, besides the internal factors' action of continuing development. He found that pre-migrants, not normally moving through the gravel, could be experimentally induced to do so by shutting off or greatly reducing the waterflow. In

another investigation (Bams 1982), it was observed that the time of emergence of chum salmon (O. keta) was marginally affected by density and increased flow, but slowed considerably with increasing gravel depth, even though the growth was higher.

Evidently, emergence to the water surface was influenced by illumination in the present investigation. This was most conspicuous among the Atlantic salmon alevins (Figs. 4-6), who mainly emerged during darkness. When light was turned on, they sank to the bottom. This behaviour was also noted amongst the rainbow trout alevins, but after day 30 (204 dC), their adaptation to this stimulus increased from day to day. More than 50 % of the alevins were photopositive on day 39 (269 dC). They turned their heads against the light, and slowed down the activity (Nortvedt 1986b) in the upper part of the water column.

Such a reorientation was also observed by Stuart (1953) on trout alevins. But when a current was introduced after reorientation, they responded to this stimulus, and showed no longer any reaction to the direction of light. Ali (1959) found that the increased photopositiveness with age of four *Oncorhynchus* species coincided with their development of the retinal elements and the capabilities of retinomotor responses.

The lack of this photopositiveness among the Atlantic salmon alevins in the present investigation agreed with the observations of Woodhead (1957), who even observed that rainbow trout and brown trout alevins became heedless to light after a period of high photo-orthokinesis. This points to the fact that light probably inhibited emergence before the visible apparatus of the alevins could properly handle this stimulus. But, that the continuing development, guided by current and gravity, ensured the timing of emergence. Indeed, the observations of the present investigation revealed that light did not initiate emergence among the Atlantic salmon alevins.

This is in agreement with Bams (1969), Gustafson-Marjanen and Dowse (1983) and Heard (1964), who observed that sockeye and pink salmon (O. gorbuscha), Atlantic salmon, and sockeye, respectively, emerged during darkness. Godin (1980) also found

mainly nocturnal emergence among pink salmon. However, the fry's tendency to emerge during daylight increased progressively during the emergence period. Mason (1976) found no clear preference for nocturnal or daylight emergence among coho fry (O. kisutch), but the latter increased with time. Evidently, the different salmon species react differently to light. In fact, Hoar et al. (1957) observed that coho fry were indifferent to light of moderately high intensities, schools of chum and pink salmon fry showed a marked preference for light, whereas sockeye fry retreated to darker areas. These differences were related to schooling behaviour and alarm reactions of the different species.

However, my observations are not in agreement with Carey (1985) and Carey and Noakes (1981). They stated that light both initiated the downward movement in the substrate and the later emergence of brook charr (Salvelinus fontinalis) and lake charr (S. namaycush), and rainbow trout, respectively. I doubt these observations, made with the aid of a small penlight, and else only when experimental lights were on. The proposed 'testing' by the fish of the photic environment at different substrate depths appear to me to be an effect of the sampling intervals or the stratification of the turf substrates. I will therefore not support their conclusion that phototactic reversal is a precondition for rainbow trout emergence.

My observations were probably also biased with respect to the timing of emergence during illumination. The sudden and short recording sequence was certainly too short a period to ensure the cones of the eyes to contract (light adapt) completely. Cones of Atlantic salmon yearlings light-adapt in 45 minutes (Ali et al. 1961). However, the pure-cone retina of the early stage Atlantic salmon alevins had differentiated among older alevins (Blaxter and Staines 1970), and older Oncorhynchus alevins with developed rods were capable of scotopic vision (Ali 1959). They were then not dependent of complete light adaptation to form schools or capture prey by "the silhouette method". In fact, 25 % of the dark-adapted emerged coho fry schooled after five minutes of exposure to light of 4300 lux (Ali op.cit.).

However, the uncertainty of the temporal light adaptation, led to the photoresponse experiment with rainbow trout alevins in the present investigation. The 50 % emergence in both darkness and under illumination before 50 % photopositiveness, confirmed the conclusion that even among the rainbow trout alevins, the phototactic reversal were not a necessary precondition for emergence.

The 50 % emergence in this experiment after 196 dC were assumed to be within the range of the 50 % emergence among the rainbow trout alevins in the first experiment (204-226 dC), because the alevins were only observed every third day. The exact timing should be studied in an hour-by-hour investigation in the future. It is concluded that hypothesis H fits the behaviour of the Atlantic salmon and rainbow trout alevins. Hypothesis H is consequently rejected.

Feeding depressed the surface swimming of all the groups of Atlantic salmon, and the day of 50 % emergence was delayed and less conspicuous among these alevins. However, this behaviour was probably caused by their instantaneous confusion (Milinski 1984) at the time of food presentation. No clear differences between timing of emergence were observed among the fed and unfed rainbow trout alevins. Although the feeding and emergence patterns may interfere, it is concluded that neither will the cost of feeding delay the timing of emergence, nor will fed alevins emerge earlier than unfed.

The emergence patterns differed between the two species. The most conspicuous differences were the timing of emergence and their subsequent positions and swimming activity in the water column. This reflects their different rates of development and evolutionary strategies. The rainbow trout exploits a greater part of the water column at later stages, whereas the Atlantic salmon parrs stay closer to the bottom. This could be caused by their different ways of hunting the prey. Rainbow trout has the opportunity to wait for the visible prey in the upper part of the water column. The Atlantic salmon save energy near the stream bottom. They probably utilize the contrast and silhouette of the prey when they suddenly leave the bottom in an energy

demanding vault, and seize the prey. Moreover, bottom dwelling could be a hiding strategy.

Nortvedt et al. (1985) showed that no effects could be gained by rearing rainbow trout alevins on Astroturf. This was caused by their ability to keep balance on their small yolk sacs, and their early emergence from the substrate, as observed in the present investigation. However, the substrates do serve a function to fry in modern aquaculture farms today. They function as hiding places for the fry before first feeding and habituation to light.

The rainbow trouts have been reared for over a century. This has probably changed their behaviour during domestication. The Atlantic salmons have only been reared since middle of the 60's in Norway, and its possible that future ethologists and farmers will experience a change in their bottom dwelling strategy, with a different utilization of the water volume.

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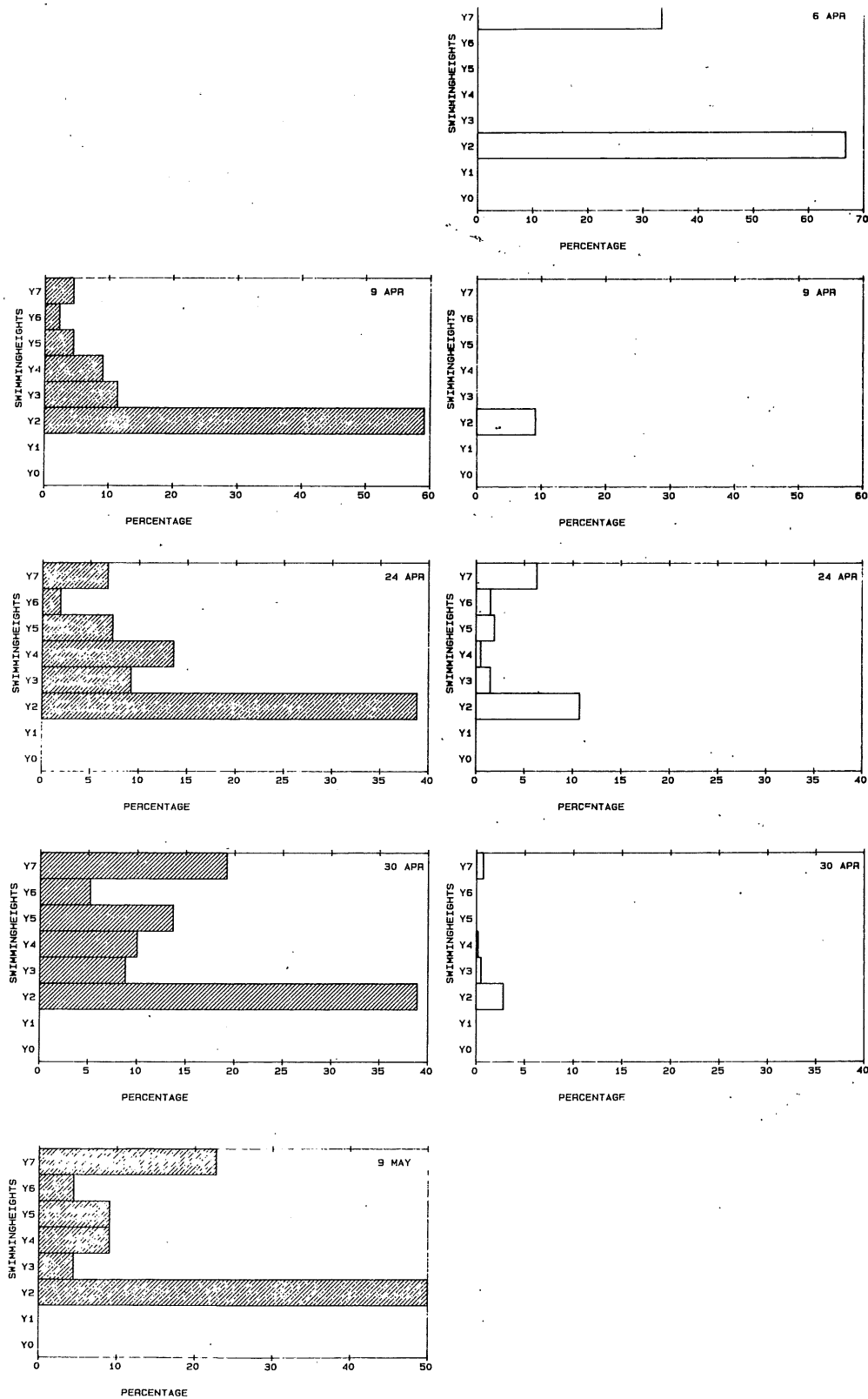


Fig. 4: Trend of emergence of unfed GR Atlantic salmon, expressed as percentage occurrence in specific heights above the bottom. Each row of figures represents one day, with five minutes swimming in darkness (hatched bar), followed by five minutes under illumination (plain bar). Units along the vertical independent axis are 2.4 cm. Y1/Y2 interface represents gravel surface.

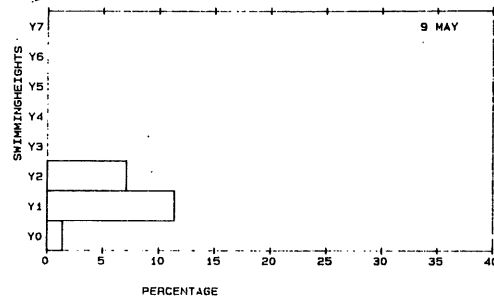
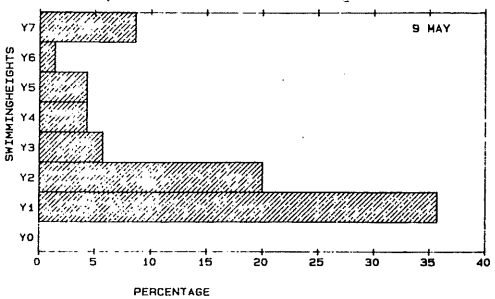
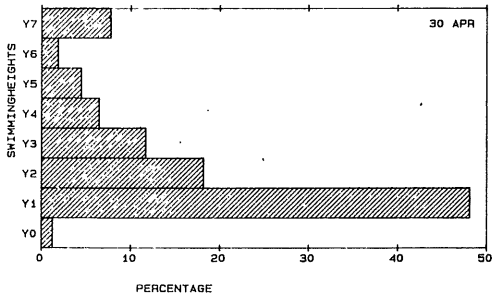
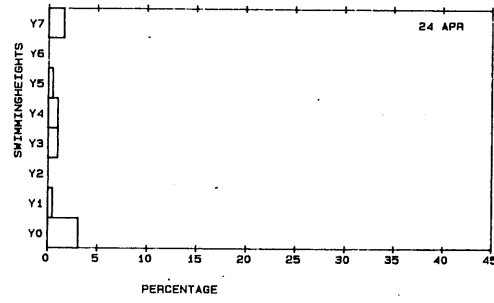
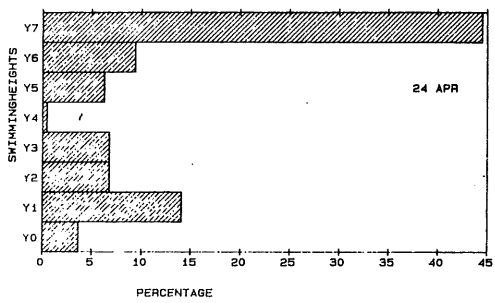
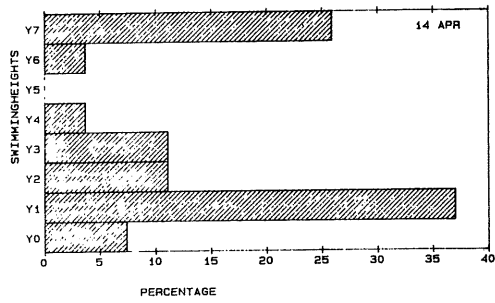
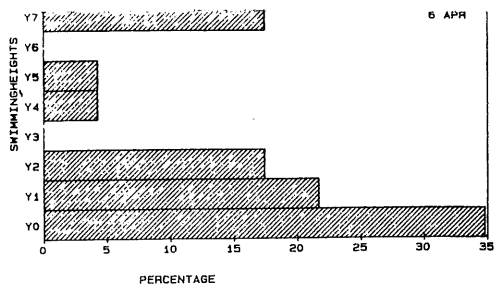


Fig. 5: Trend of emergence of unfed ATR Atlantic salmon, expressed as percentage occurrence in specific heights above the bottom. Y0/Y1 interface represents Astroturf surface. See also Fig. 4.

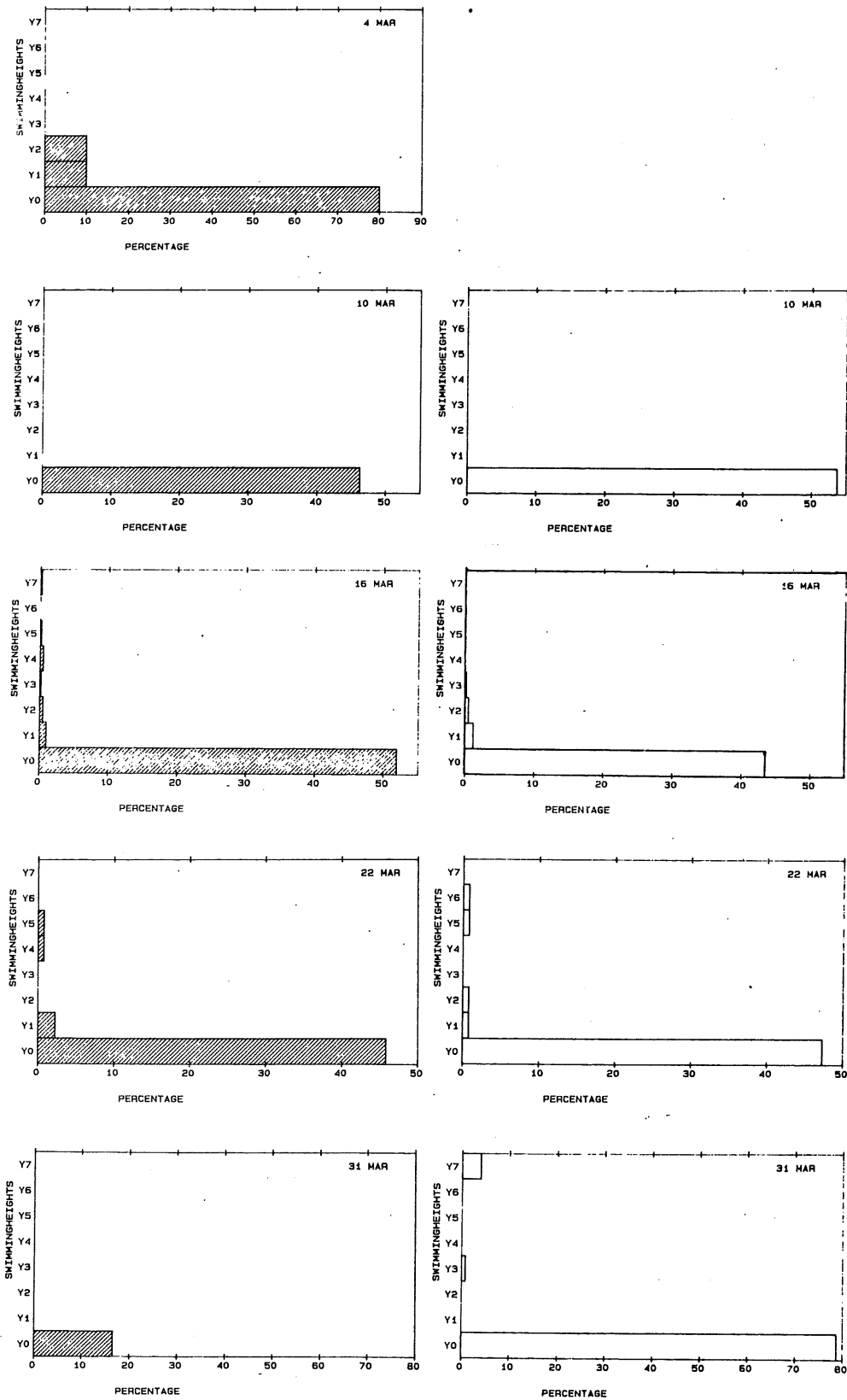


Fig. 6: Trend of emergence of unfed FSR Atlantic salmon, expressed as percentage occurrence in specific heights above the bottom. See also Fig. 4.

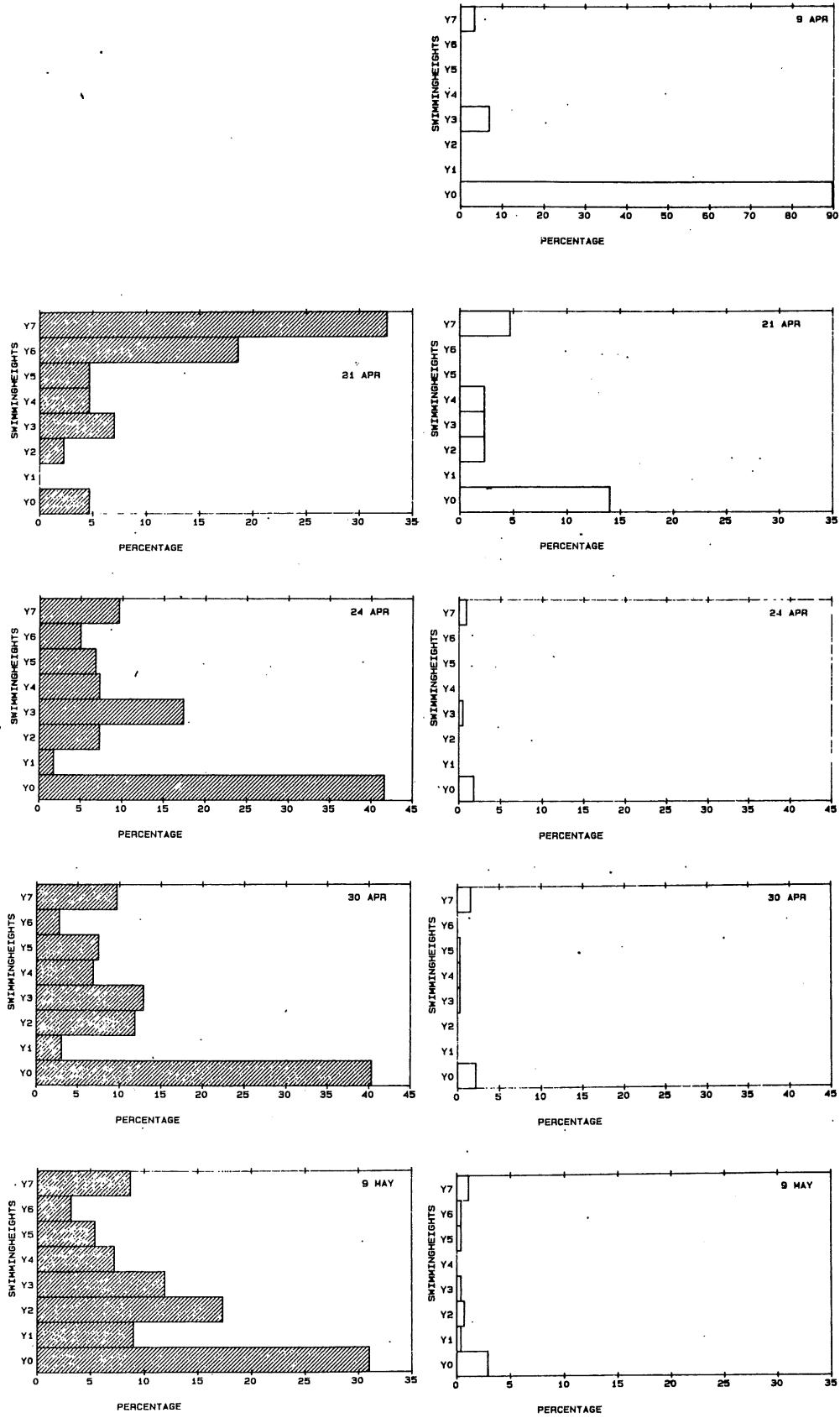


Fig. 6 cont'd

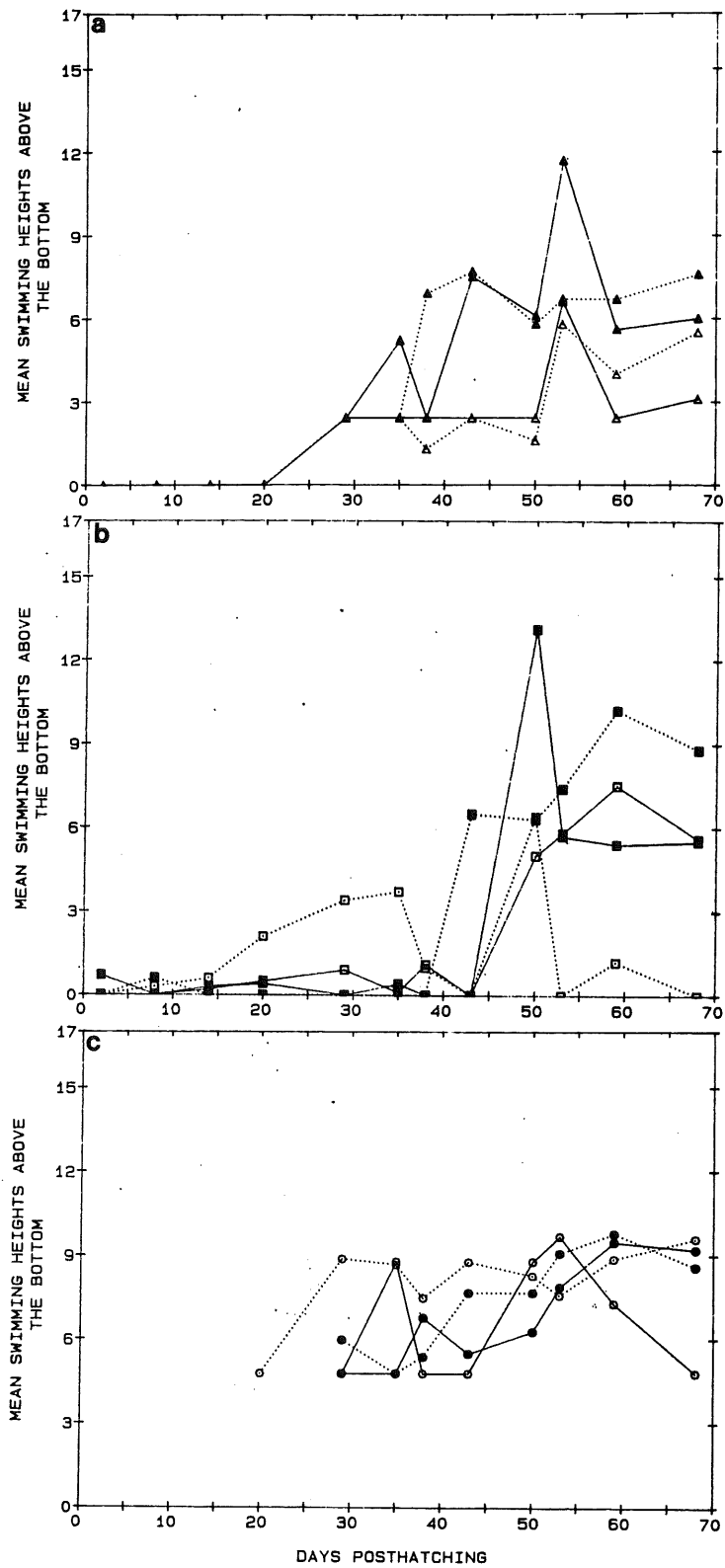


Fig. 7: Mean swimming heights above the bottom of Atlantic salmon, plotted against days posthatching. Dotted line, fed; single line, unfed. Closed symbols denote darkness; open symbols, illumination.

- a) ▲ △ = ATR
- b) ■ □ = FSR
- c) ● ○ = GR

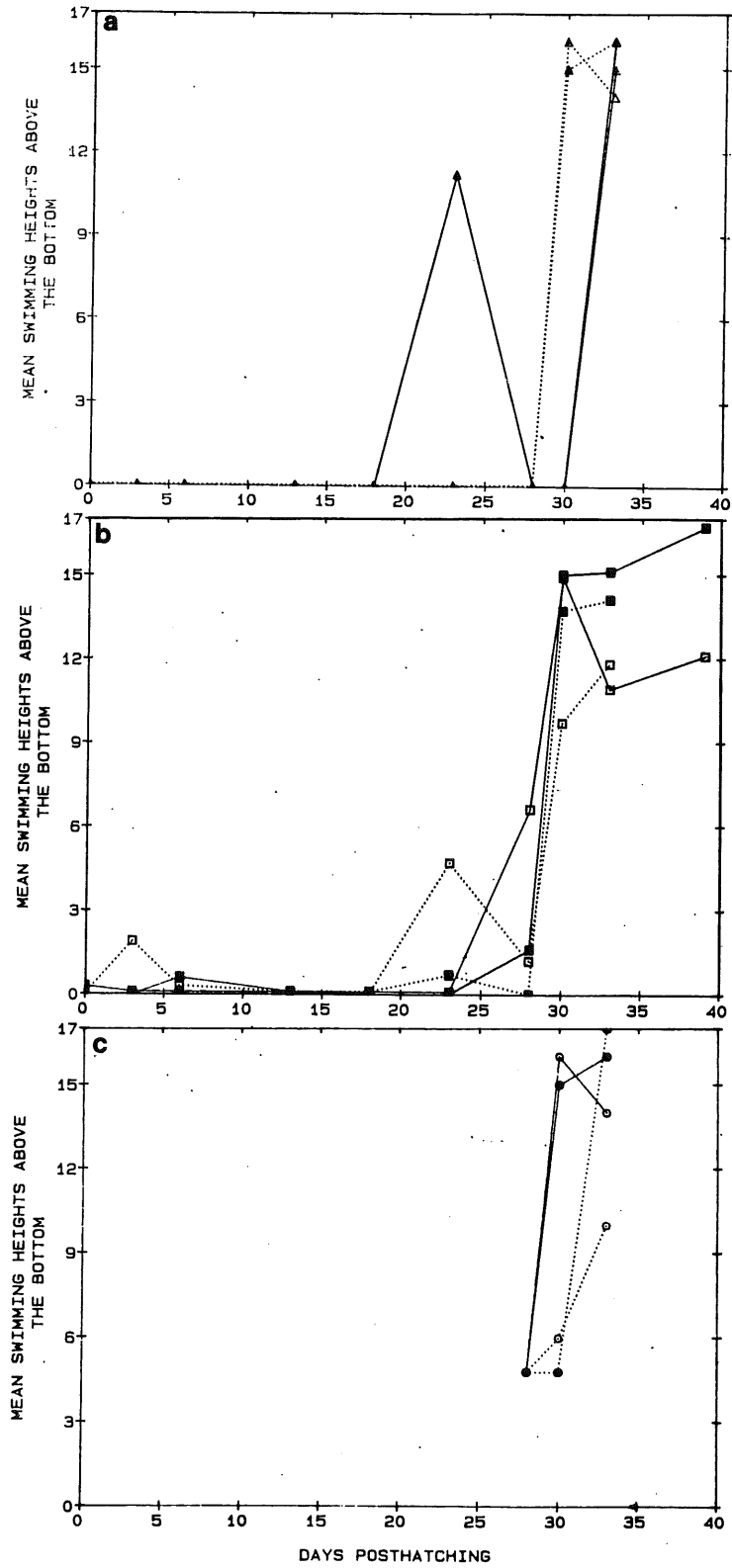


Fig. 8: Mean swimming heights above the bottom of rainbow trout, plotted against days posthatching. See also Fig. 7.

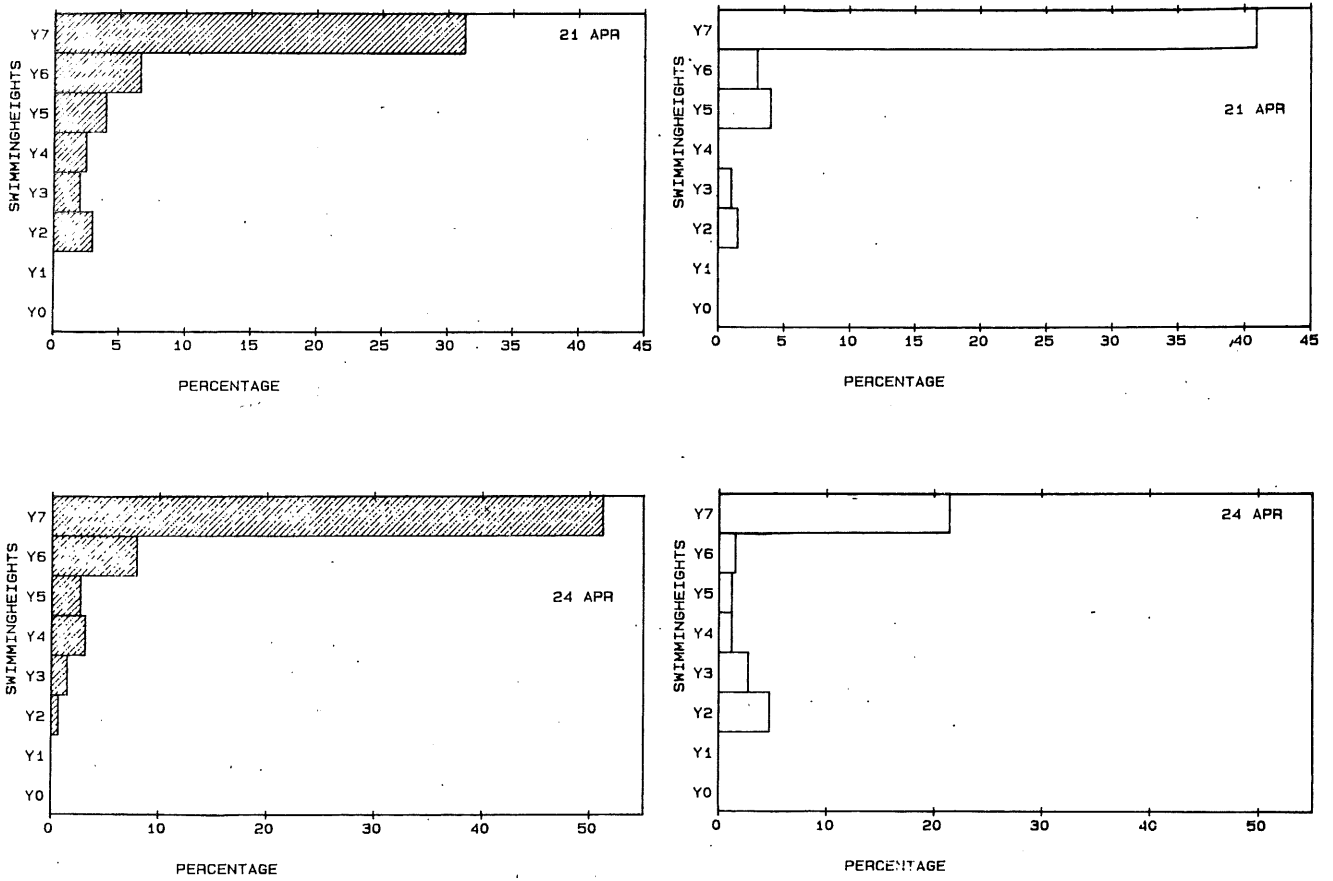


Fig. 9: Trend of emergence of unfed GR rainbow trout, expressed as percentage occurrence in specific heights above the bottom. See also Fig. 4.

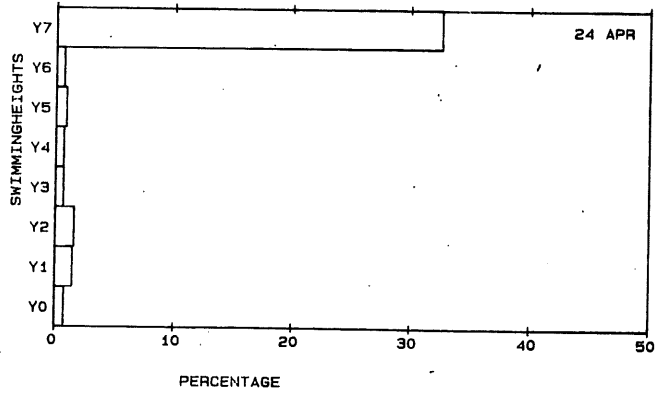
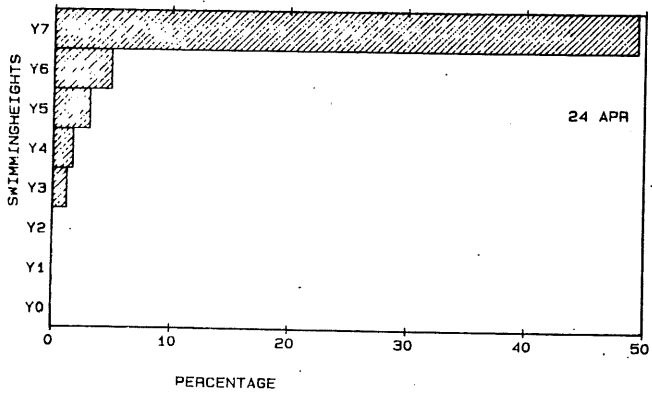
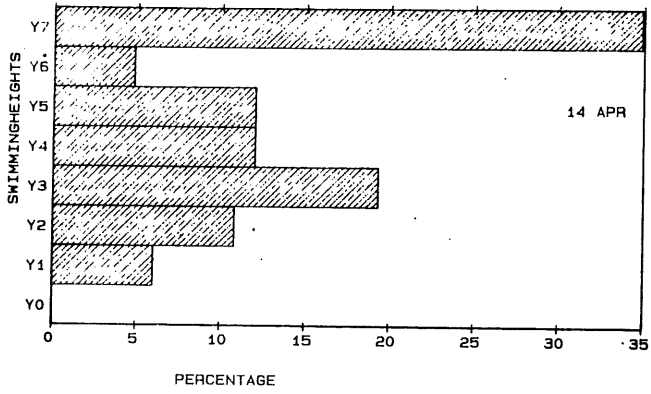


Fig. 10: Trend of emergence of unfed ATR rainbow trout, expressed as percentage occurrence in specific heights above the bottom. Y0/Y1 interface represents Astroturf surface. See also Fig. 4.

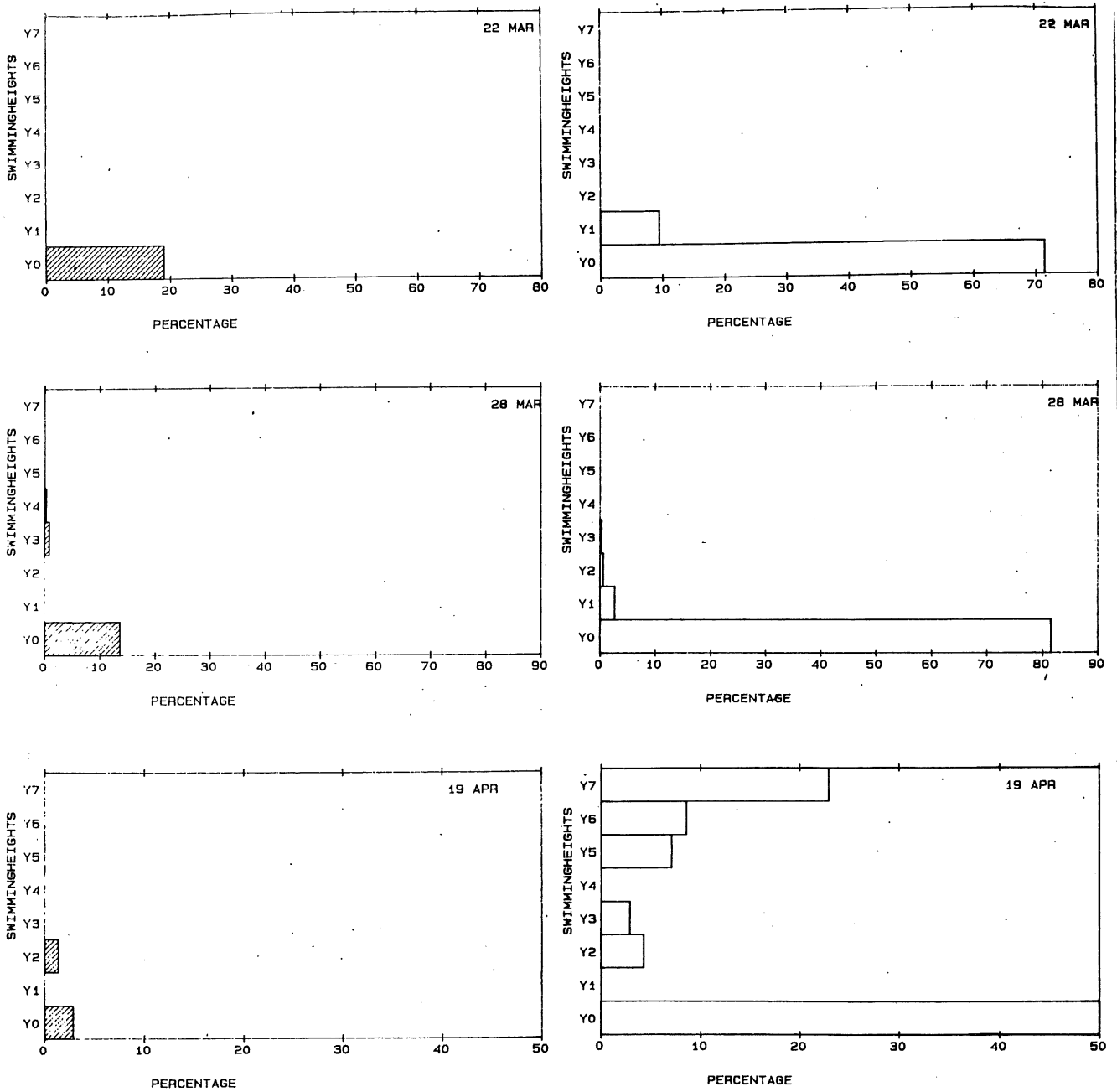


Fig. 11: Trend of emergence of unfed FSR rainbow trout, expressed as percentage occurrence in specific heights above the bottom. See also Fig. 4.

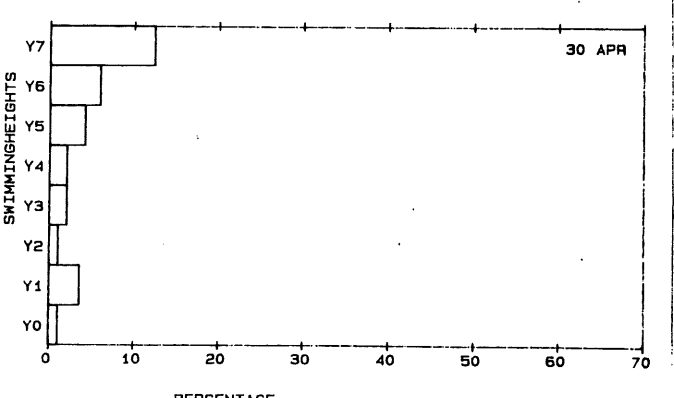
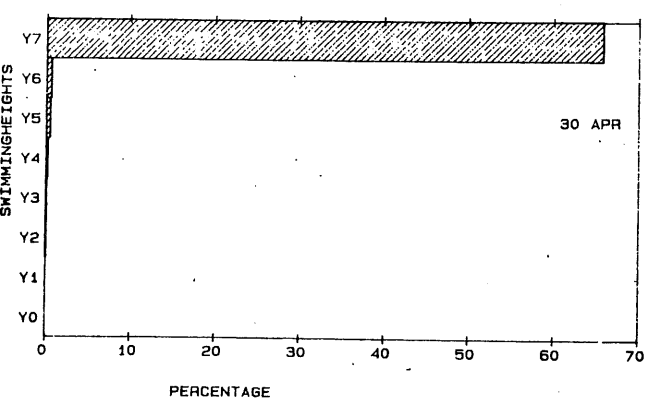
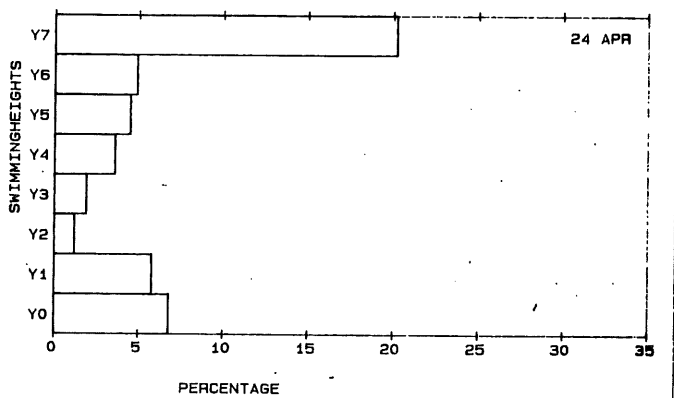
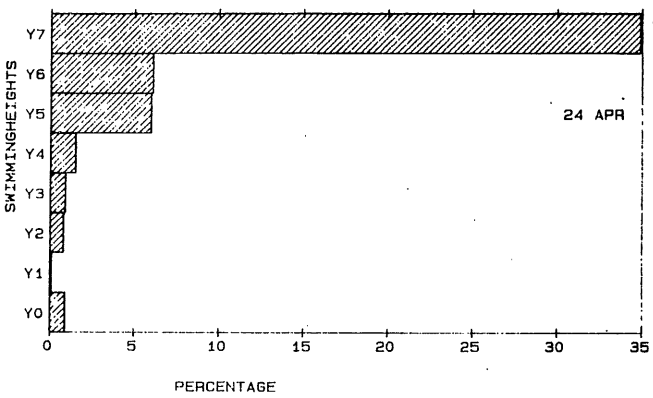
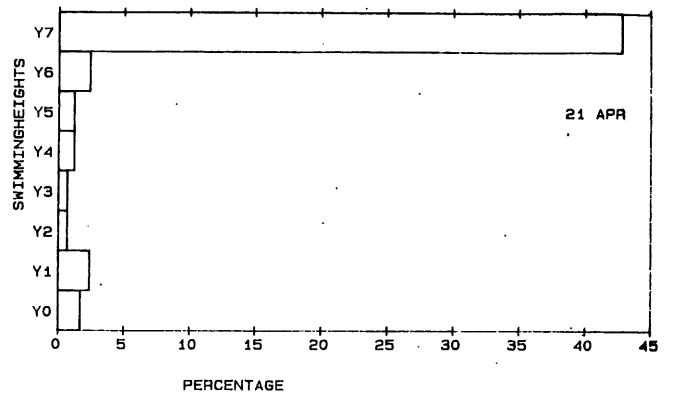
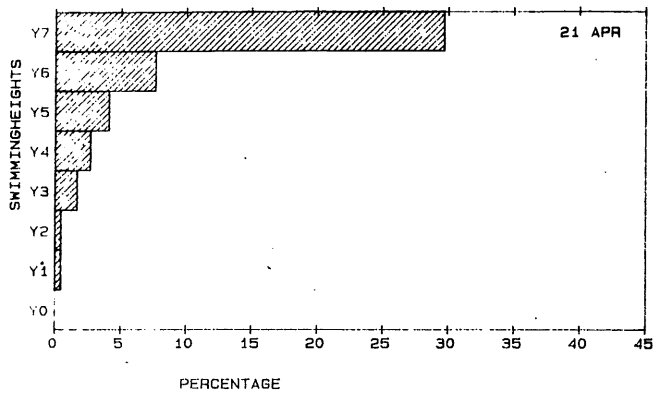


Fig. 11 cont'd

