RNA synthesis in the early embryogenesis of a fish
(Misgurnus fossilis)

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Synthesis of ribonucleic acids in early embryos has been extensively studied
during recent years in a number of laboratories and has been shown to begin
shortly after fertilization (Kafiani, Tatarskaya & Kanopkayte, 1958; Wilt, 1963;
Brown & Littna, 1964; Decroly, Cape & Brachet, 1964; Glišin & Glišin, 1964;
Kafiani & Timofeeva, 1964, 1965; Nemer & Infant, 1965). Early embryos of
Xenopus (Brown & Gurdon, 1964; Brown & Littna, 1964, 1966) and of sea
urchins (Wilt, 1963; Glišin & Glišin, 1964; Nemer & Infant, 1965) synthesize
up to gastrula stage predominantly or exclusively polydisperse RNA of a non-
ribosomal nature usually referred to as DNA-like RNA (dRNA).

The occurrence of continuous dRNA synthesis in early embryogenesis is in
apparent conflict with the periodicity of the ‘morphogenetic function’ of cell
nuclei found by one of us (Neyfakh, 1959, 1961, 1964, 1965) in embryos of a
number of animal species. In fact, for a certain time after fertilization of eggs
with a regulatory type of development, the nuclei remain morphogenetically
inactive. Microsurgical (Harvey, 1940; Briggs & King, 1959), chemical (Gross
& Cousineau, 1963; Lallier, 1963; Gross, Malkin & Moyer, 1964; Neyfakh,
1965) or radiation-induced (Neyfakh, 1959, 1961; Neyfakh & Rott, 1958;
Shapiro & Lander, 1960) enucleation of the egg does not visibly affect early
development up to the late blastula stage. After the initial period of inactivity,
a period of ‘morphogenetic activity’ of the nuclei begins which assures the
process of gastrulation. The occurrence of dRNA synthesis starting immediately
or shortly after fertilization is hard to reconcile with the proposal of a direct
relationship between the morphogenetic and the biochemical (dRNA-syn-
thesizing) functions of cell nuclei. This work seeks to analyse this apparent
contraction, to further understanding of the molecular basis of early
embryogenesis.

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To approach this problem we used the method of quantitative evaluation of RNA synthesis in embryos described previously (Kafiani & Timofeeva, 1964, 1965). The relative rate of dRNA synthesis (‘dRNA-synthesizing activity’) was estimated at different stages of development in normal embryos of loach (*Misgurnus fossilis*) and in embryos partially or nearly wholly deprived of nuclear genetic material (haploid and ‘anucleate’ embryos obtained by inactivation of one or both of the gametes with X-rays).

It was with loach embryos that morphogenetic function of nuclei was studied for the first time using the method of radiation-induced inactivation of nuclei; it was shown that the nuclear activity controlling the onset and the progress of gastrulation begins at the mid-blastula stage (Neyfakh, 1959). RNA synthesis was found to be sharply accelerated at about the same time (Kafiani & Timofeeva, 1964, 1965).

The present work shows that the activation of dRNA synthesis occurs not only on a per embryo but also on a per cell base. The extent of activation depends on the quantity of genetic material in the nuclei. These facts confirm the occurrence of the true activation, or the onset of genome transcription in the cell nuclei at the mid-blastula stage. On the other hand RNA synthesis during the preceding period of development (synchronous cleavage of the egg) exhibits peculiarities which suggest that this ‘early’ synthesis of RNA is at least partly independent of the nuclei.

**MATERIAL AND METHODS**

*Material.* Mature eggs of loach were obtained 40 h after injecting the females with 200 i.u. of Choriogonin (Gedeon Richter, Hungary). Eggs were fertilized, left to develop in tap water at 21 °C and staged as described previously (Neyfakh, 1959).

*X-ray irradiation.* Eggs were irradiated with a dose of 40 kr, and sperm with 80 kr using apparatus RUP-1 (190 kV, 15 mA, 5 kr/min).

*Introduction of the label.* Since egg membranes are poorly permeable to usual precursors RNA synthesis was studied using $^{14}$C carbonate. It was introduced in the eggs as described by Cohen (1954) and Flickinger (1954). Equal quantities of eggs at desired stages (from the same clutch of developing eggs) were incubated in stoppered flasks in a slightly acid medium (pH 6.0–6.5) containing Na$_2^{14}$CO$_3$. In different series of experiments isotope concentration varied from 20 to 40 $\mu$Ci/ml of final medium. Temperature (21 °C) and duration of incubation (60 or 90 min) were kept constant in each series. Penicillin and streptomycin (100 and 50 i.u./ml respectively) were added to prevent bacterial contamination.

*Extraction and purification of RNA.* Total RNA of embryos was extracted with sodium dodecylsulphate (SDS) and phenol in the cold by a procedure similar to that used by Brown & Litna (1964). Embryos were quickly homogenized in ice-cold tris-HCl buffer, 0.01 M (pH 6.5) containing 0.01 M-MgCl$_2$, the homogenate made 1% in respect to SDS and mixed for ½–1 min at 10–15 °C.
The lysed material was deproteinized three times with water-saturated phenol at 3–5 °C. Nucleic acids were precipitated from the aqueous phase with ethanol after addition of a small amount of potassium acetate.

For the determinations of RNA-synthesizing activity, the total nucleic acid precipitate was dissolved in a small volume of cold water and made 2 M with sodium chloride. The precipitate of ‘salt-insoluble RNA’ (siRNA) formed overnight (–10 °C) contained ribosomal RNA (rRNA) and other kinds of RNA (including dRNA) except transfer RNAs (tRNA). The latter, as well as DNA, polysaccharide and other contaminants, remained in the supernatant. The siRNA precipitate was freed of traces of these contaminants by three more reprecipitations and washings with 2 M-NaCl. The RNA preparations contained less than 0.3 % protein (Lowry, Rosebrough, Farr & Randall, 1951) and were free of DNA. The label in siRNA preparations was 90–95 % sensitive to RNase treatment. A lower proportion of counts (60–80 %) was, however, sensitive to RNase in siRNA from early cleavage eggs.

For sucrose gradient centrifugations, total RNA preparations were used. To obtain these, initial crude nucleic acid preparations were treated for 30 min at 37 °C with DNase (Worthington), 5 μg/ml, in 0.01 M tris-HCl buffer (pH 7.8) containing 0.01 M-MgCl₂. DNase was then eliminated with three successive phenol-SDS deproteinizations, and total RNA precipitated with ethanol.

Sucrose-gradient centrifugation (Britten & Roberts, 1960). Two to 3 mg RNA dissolved in 0.5 ml of 0.1 M acetate buffer (pH 5) with 0.01 M-EDTA was layered on a 5–20 % sucrose gradient prepared in the same buffer. After 12 h centrifugation at 24000 rev./min in the SW-25 rotor of the Spinco L ultracentrifuge at 10–12 °C, the bottom of the tube was pierced and fractions collected.

Radioactivity measurements. After determining RNA content in aliquots or fractions from u.v.-absorption (at 260 μm) RNA was precipitated with cold 5 % trichloroacetic acid (TCA). The precipitate was collected on nitrocellulose filters (RUFS, Czechoslovakia, pore diameter 0.9–1.2 μm), and washed with cold TCA and ethanol. Radioactivity was counted in a liquid-scintillation spectrometer (Lie Belin, France) with a non-polar scintillation mixture: 0.4 % 2,5-diphenyloxazole and 0.01 % 1,4-bis-2-(5-phenyloxazolyl)benzene in toluene.

RESULTS

Figure 1, A and B, show typical sedimentation patterns of total RNA preparations from loach eggs at mid-gastrula stage, obtained after 14CO₂ incorporation during 1 h (A) and 5 h (B). It is seen that the bulk of RNA (u.v.-absorption, solid line) forms three peaks, two of which represent the large and small components of rRNA (28 S and 18 S), while the third peak (4–5 S) corresponds to low molecular weight RNAs, mainly tRNA.

The distribution of labelled RNA (dotted line) is quite different and reveals the existence of a polydisperse population of newly formed RNA molecules.
sedimenting along the entire gradient with a few distinct peaks. The first peak, in the upper portion of the gradient, contains labelled RNAs of low molecular weight including transfer RNA. Since the latter rapidly turn over their terminal nucleotides, the incorporation of the label in this region of the gradient probably does not wholly correspond to the synthesis of RNA. However, a significant part of the labelled RNA in this peak sediments faster than u.v.-absorbing material. This suggests that this broad peak includes some other labelled RNA species besides tRNA. This is confirmed by the sedimentation pattern of a siRNA preparation obtained at the same developmental stage (Fig. 2). Here,

![Sucrose-gradient centrifugation patterns of total RNA isolated from loach eggs at the mid-gastrula stage after incubation with $[^{14}C]$carbonate (24 μc/ml) for 1 h (A) and 5 h (B). ——, u.v.-absorption (at 260 mμ); ----, TCA-precipitable radioactivity.](image)

Fig. 1. Sucrose-gradient centrifugation patterns of total RNA isolated from loach eggs at the mid-gastrula stage after incubation with $[^{14}C]$carbonate (24 μc/ml) for 1 h (A) and 5 h (B). ——, u.v.-absorption (at 260 mμ); ----, TCA-precipitable radioactivity.
RNA synthesis in a fish embryo

the 4–5 S peak of u.v.-absorption is lacking due to elimination of tRNA, while there is a significant amount of labelled RNA of somewhat higher molecular weight.

Most of the radioactive RNA sediments move rapidly, the 'heaviest' fractions being found in greater proportions at shorter durations of $^{14}$CO$_2$ incorporation (cf. Figs. 1A and B). But even after prolonged incorporation, the distribution of the label does not correspond to that of rRNA. This is true also for earlier stages of development (Timofeeva & Kafiani, 1965, 1966).

From the sedimentation behaviour of labelled RNAs of early loach embryos we conclude that, up to mid-gastrula stage, rRNA is not synthesized to any significant degree. Consequently siRNA preparations freed of tRNA contain the label predominantly, if not exclusively, in polydisperse RNA, or dRNA, which may include messenger RNA. A typical sedimentation pattern of an siRNA sample shown in Fig. 2 illustrates the character of the RNA preparations used throughout the present work.

In order to study the dynamics of transcription during early development in loach, we followed variations in the rate of dRNA synthesis at cleavage and blastula stages, up to the onset of gastrulation. Figure 3 summarizes the results of three separate experiments showing the peculiar course and reproducibility of the curves obtained. In each experiment equal quantities of eggs from the same batch were pulsed at different stages with $^{14}$CO$_2$, under identical conditions, then siRNA isolated from each egg sample and specific radioactivity determined.
as described in Methods. In Fig. 3 (as well as in Figs. 4 and 5) the values obtained are plotted against hours of development, the latter representing mid-points between the beginning and the end of incubation with [14C]carbonate.

Fig. 3. Incorporation of 14CO₂ into siRNA of loach eggs at different stages of development. The curves illustrate the results of three separate experiments in which equal quantities of eggs were incubated at stages indicated under following conditions: (1) 45 min., 20 μc/ml; (2) 60 min., 40 μc/ml; (3) 60 min., 20 μc/ml.

Since incorporation conditions were similar for all developmental stages, since siRNA content (2 μg per egg) remains constant over the period studied (Timofeeva & Kafiani, 1964), and since, finally, the rate of RNA labelling in conditions defined is not limited by 14CO₂ incorporation into free nucleotides of developing eggs (Kafiani & Timofeeva, 1964, 1965) we consider observed changes in specific radioactivities of siRNA to be a measure of variations in the rate of RNA synthesis on a per embryo basis. The capacity of an embryo to incorporate a given quantity of the label into siRNA per unit time (e.g. 1 h) is therefore designated as ‘dRNA-synthesizing activity’.

The curves in Fig. 3 have a clear-cut break at about 6 h of development. Up to this time dRNA-synthesizing activity remains very low, increasing abruptly within a narrow time interval between the 6th and 7th h. It was conceivable that the increase in the over-all rate of dRNA synthesis in the embryos was due to a corresponding increase in the number of nuclei rather than to their activation.
RNA synthesis in a fish embryo

Figure 4 shows, however, that the rates of increase of dRNA synthesis and of cell number are quite different. In fact, from the 3rd until the 6th h, when cleavage proceeds in a synchronous manner with a 30 min period (Neyfakh & Rott, 1958; Rott & Sheveleva, 1967) the cell number increases about 30-fold while dRNA-synthesizing activity increases only twofold. After the 6th h the rate of dRNA synthesis increases much faster than the cell number. As a result the dRNA-synthesizing activity calculated per cell (see curve 3, Fig. 4) shows, at about the 7th h, a marked rise indicating a real activation of dRNA synthesis.

The left-hand, descending part of curve 3 of Fig. 4 requires special consideration, as it implies that RNA-synthesizing activity is very high at the time of morphogenetic inactivity of cell nuclei. This would seem paradoxical if the nuclei are supposed to be the sole site for RNA synthesis. This paradox might be resolved, however, if the ‘early’ RNA synthesis were partly or entirely independent of the cell nuclei.

We attempted to clarify this point by measuring the rate of RNA synthesis in embryos with a reduced quantity of nuclear genetic material. The dRNA-synthesizing activities were compared in diploid embryos, gynogenetic haploids (obtained by fertilizing normal eggs with X-ray-irradiated sperm) and ‘anucleate’ embryos (obtained either by combining X-ray-irradiated gametes or by irradiating the zygotes). Morphologically, haploid embryos develop normally...
at least till late gastrula, the 'haploid syndrome' appearing considerably later. In 'anucleate' embryos cleavage still occurs, resulting in a blastula-like mass of cells virtually devoid of chromosomes (Shapiro & Lander, 1960).

![Graph showing incorporation of $^{14}$CO$_2$ into siRNA of diploid (2$n$), gynogenetic haploid (1$n$) and 'anucleate' (0$n$) embryos.](image)

Figure 5 and Table 1 show that until 5–6 h diploid and haploid embryos incorporate $^{14}$CO$_2$ into siRNA at nearly the same rate while at 6–8 h diploid embryos incorporate label into siRNA about twice as fast as do haploid ones. This difference is not due to the smaller number of cells in the latter, as they contain at this time even more cells than do diploid embryos (Rott & Sheveleva, 1967). This higher rate of cell multiplication probably accounts for the compensation in the over-all production of dRNA shown by the reapproachment of the 1$n$ and 2$n$ curves in Fig. 5 by the beginning of gastrulation.

Appearance of a direct dependence of RNA-synthesizing activity of embryos on their ploidy testifies to the onset of nucleus-directed RNA synthesis. The lack of such correlation over the first 6 h of development suggests that RNA synthesis is independent of the nuclei at this time. The sites for the 'early' RNA
synthesis might reside in the cytoplasm, which would account for the decrease of the left-hand part of curve 3 in Fig. 4 as a result of division of egg cytoplasm into progressively smaller units.

This proposal is supported by experiments with 'anucleate' embryos. The data summarized in Fig. 5 and Table 1 show a quite definite incorporation of $^{14}$CO$_2$ into siRNA in such embryos. Early RNA synthesis rises gradually, increasing fivefold by 10 h, but fails to display the activation characteristic of nucleated embryos. Despite the low level of incorporation most part of it appears to reflect actual RNA synthesis since it is 80% sensitive to RNase in control and 60% sensitive in anucleate embryos.

Table 1. dRNA synthesis in diploid, haploid and 'anucleate' embryos

<table>
<thead>
<tr>
<th>Time of introduction of $^{14}$CO$_2$</th>
<th>Specific radioactivity (counts/min per mg siRNA)</th>
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</thead>
<tbody>
<tr>
<td>Hours of development at 21 °C</td>
<td>Stage</td>
</tr>
<tr>
<td>--------------------------------------</td>
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<tr>
<td>1 1/2-2 1/2</td>
<td>1st–3rd division</td>
</tr>
<tr>
<td>4-5 1/2</td>
<td>Morula–early blastula</td>
</tr>
<tr>
<td>6-7 1/2</td>
<td>Mid-blastula</td>
</tr>
<tr>
<td>7 1/2-9</td>
<td>Mid-late blastula</td>
</tr>
<tr>
<td>9 1/2-11</td>
<td>Early gastrula</td>
</tr>
</tbody>
</table>

In order to get some information on the nature of the early incorporation into siRNA we tested its sensitivity to actinomycin D. The antibiotic could be introduced in the eggs only if applied at high concentrations (up to 100 µg/ml) immediately after fertilization (at the time of swelling). Cleavage occurred in such eggs but development was arrested at late blastula stage. $^{14}$CO$_2$ incorporation into the RNase-sensitive portion of siRNA preparations isolated from the eggs at 6 h of development after 3 h incubation with the isotope was found to be inhibited with actinomycin by about 50% both in normal (diploid) and 'anucleate' embryos, when compared to respective untreated controls. This suggests that at least a part of the $^{14}$CO$_2$ incorporation into the siRNA of normal early cleavage eggs represents DNA-dependent RNA synthesis. Furthermore the result supports the proposal about the cytoplasmic location of early RNA
synthesis since a comparable RNase and actinomycin-sensitive incorporation can be demonstrated in embryos virtually devoid of nuclear genetic material. The results obtained with actinomycin D should, however, be interpreted with caution because of uncertainty of the actual concentration of the antibiotic in the cells and its possible indirect effects.

DISCUSSION

The present paper gives some characteristics of RNA synthesis in early embryogenesis of a teleost fish (Misgurnus fossilis).

Sucrose-gradient analysis showed that synthesis of ribosomal RNAs does not occur to any significant extent at least until mid-gastrula stage, and the embryos synthesize predominantly or exclusively polydisperse RNAs of a non-ribosomal nature designated as dRNA. Selective inhibition of expression of ribosomal cistrons seems to be a general phenomenon in early embryonic development since it has been demonstrated also in pre-gastrula stages of *Xenopus laevis* (Brown & Gurdon, 1964; Brown & Littna, 1964, 1966) and sea urchins (Glišin & Glišin, 1964; Nemer & Infant, 1965; Guidice & Mutolo, 1967).

A quantitative approach (Kafiani & Timofeeva, 1964) was applied here for evaluating changes in the activity of the embryonic genome in transcription of genetic information during pregastrular development. It consists of comparing specific radioactivities of RNA of the eggs after pulsing them, at different stages, under standard conditions, with a precursor (\(^{14}\)CO\(_2\)) which is rapidly incorporated into the free nucleotide pool. In view of the non-specific nature of the precursor and possible terminal incorporation into tRNA, thoroughly purified RNA preparations were used freed of tRNA and other contaminants by repeated precipitations with sodium chloride. Such RNA preparations contained rRNA and dRNA of which only the latter was labelled. Specific radioactivities of the RNA preparations corresponded to the approximate rate of dRNA synthesis and were considered a measure of 'dRNA-synthesizing activity' of the embryos.

dRNA-synthesizing activity changes strikingly during the early development of loach. It remains very low for the first 6 h of cleavage and increases abruptly at 6–7 h of development (mid-blastula), suggesting operation of a trigger mechanism. The large extent of the activation suggests, furthermore, that the triggering involves a large part of the cell population.

The sharp activation of nuclear RNA synthesis in loach at the mid-blastula stage has been shown previously (Kafiani & Timofeeva, 1964, 1965). In the present paper additional evidence is given that this activation really involves nuclear genetical material: (a) the increase in dRNA-synthesizing activity calculated per cell, and (b) the appearance of a correlation between the rate of dRNA synthesis and ploidy of embryos.

Similar activation of RNA synthesis has been found in *Rana pipiens*...
RNA synthesis in a fish embryo

(Bachvarova, Davidson, Allfrey & Mirsky, 1966) and in *X. laevis* (Brown & Littna, 1966) at the late blastula stage, which correlates with the onset of morphogenetic activity (Neyfakh, 1964). In starfish, transcription of templates supporting gastrulation is reported to begin at early mid-blastula stage (Barros, Hand & Monroy, 1966). An abrupt activation of RNA synthesis was found in mouse embryos at the morula-early blastocyst stage (Monesi & Salifi, 1967). Stimulation of genome transcription appears therefore to be a characteristic event in early embryogenesis.

In loach, the activation of RNA synthesis coincides with important cytological changes: the beginning of fusion of caryomeres (Pankova, 1963), and a drop in the mitotic index and lengthening of mitotic cycle due to lengthening of interphase (Rott & Sheveleva, 1967). Since RNA synthesis occurs mainly during interphase our data are in accord with the cytological observations.

By the 7th h of development an important change in the developmental potency of loach embryos occurs, the blastoderms becoming able to differentiate in artificial media (Kostomarova & Neyfakh, 1964).

Finally, at the 6th h of development morphogenetic function of the cell nuclei starts (Neyfakh, 1959). Concomitant activation of dRNA synthesis in the nuclei is unlikely to be a coincidence and suggests that the beginning of active gene transcription forms a biochemical basis for nuclear function in directing gastrulation.

The correlation between the dRNA-synthesizing and morphogenetic activity of the nuclei seems, however, to be confined to the time of their commencement. Morphogenetic activity exhibits periodicity, the first period lasting for 2 1/2 h (from 6 to 8 1/2 h) followed by an ‘interruption of morphogenetic function’ which lasts until the 14th h. This is not so, however, with RNA synthesis, which goes on with increasing speed after being switched in at the 6th h. The reasons for the discrepancy between biological and biochemical function remain obscure.

As for the first period of morphogenetic inactivity of the nuclei (up to 6 h postfertilization), the observed limited RNA synthesis seems to be at least partly nuclear-independent. This view is supported by the fact that the rate of RNA synthesis in early cleavage eggs correlates neither with cell number nor with the ploidy of embryos. The ‘early’ RNA synthesis is presumed to occur in some cytoplasmic DNA-containing structures. Such a possibility has been suggested for anucleate halves of sea-urchin eggs (Baltus, Quertier, Ficq & Brachet, 1965). Loach-egg cytoplasm contains sufficient DNA to support measurable RNA synthesis, since as shown previously the DNA content of an egg is \( 6-10 \times 10^{-3} \) µg while that of a sperm cell is \( 2.4 \times 10^{-6} \) µg, the ‘extra’ DNA corresponding to the nuclear DNA of about 1000 diploid cells (Timofeeva & Kafiani, 1964). We have, however, no direct data concerning the exact localization of nuclear-independent ‘early’ RNA synthesis nor are we able to answer the question whether cell nuclei are totally inactive during early cleavage.

In conclusion, the data presented show that there are two clearly distin-
guishable functional states of cell nuclei during early embryonic development of loach. The nuclei are virtually inactive in transcription of genetic information during early cleavage, and at this time they are also inactive morphogenetically. At the mid-blastula stage the nuclei progress into another state characterized by a high rate of gene transcription and morphogenetic activity.

**SUMMARY**

1. RNA synthesis during early embryogenesis of loach (*Misgurnus fossilis*) was studied using $^{14}$CO$_2$ incorporation into the 2 M-NaCl-precipitated fraction of total embryonic RNA.

2. From fertilization until mid-gastrula stage the RNA preparations contain label in non-ribosomal RNAs (dRNA) which have a high degree of size heterogeneity.

3. A quantitative method was used for evaluating relative dRNA-synthesizing activities of embryos at different stages of development by measuring specific radioactivities of NaCl-precipitated RNA preparations isolated from eggs pulsed with $^{14}$CO$_2$ under standard conditions.

4. The dRNA-synthesizing activity is very low for early (synchronous) cleavage stages and increases slowly compared to cell division. At this time the rate of RNA synthesis is nearly equal in diploid and haploid embryos. A detectable RNA synthesis occurs also in ‘anucleate’ embryos. It is concluded tentatively that at least a part of the ‘early’ RNA synthesis occurs independently of the cell nuclei, in some DNA-containing cytoplasmic structures.

5. At the mid-blastula stage, dRNA synthesis is sharply accelerated per embryo as well as per cell, the rate of synthesis becoming directly dependent on cell ploidy. It is concluded that after an initial period of cleavage an activation, or onset of gene transcription, occurs in the cell nuclei which may be the basis of their morphogenetic function.

**Синтез РНК в раннем эмбриогенезе рыбы**

(*Misgurnus fossilis*)

1. Изучался синтез РНК в раннем эмбриогенезе выюна по включению $^{14}$CO$_2$ в осаждаемую 2М хлористым натрием фракцию суммарной РНК яиц.

2. От оплодотворения до стадии средней бластулы препараты РНК содержат метку в РНК нерибосомального типа (дРНК), в высокой степени гетерогенных по размеру молекул.

3. Для оценки относительной дРНК-синтезирующей активности зародышей на разных стадиях развития использован количественный метод, основанный на определениях удельной радиоактивности осаждаемых хлористым натрием препаратов РНК, выделенных из яиц, импульсно меченных $^{14}$CO$_2$ в стандартных условиях.
RNA synthesis in a fish embryo

4. В течение раннего (синхронного) дробления дРНК-синтезирующая активность очень мала, и растет медленно по сравнению с клеточными делениями. В этот период скорость синтеза РНК в гаплоидных и диплоидных зародышах почти одинакова. Измеримый синтез РНК имеет также место в "безъядерных" зародышах. Делается заключение, что по крайней мере часть "раннего" синтеза РНК происходит независимо от клеточных ядер, в каких-то ДНК-содержащих цитоплазматических структурах.

5. На стадии средней бластулы синтез дРНК резко ускоряется как в расчете на зародыш, так и на клетку, причем темп синтеза приобретает прямую зависимость от плодности клеток. Делается вывод, что после начального периода дробления в ядрах клеток имеет место активация или начало транскрипции генов, которое может являться основой их морфогенетической функции.

REFERENCES


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