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LARVAL DEVELOPMENT OF *CARDIUM GLAUCUM* AND *C. HAUNIENSE* (BIVALVIA) FROM THE GDAŃSK BAY

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ABSTRACT

Laboratory studies of larval development of *C. glaucum* and *C. hauniense* were performed in years 1976—1978. Mature gametes were acquired by thermal induction. Larvae obtained by artificial fertilization were cultured till metamorphosis and settling of bivalves at the postlarval stage. Larval development of both species was typical of that characteristic of most Bivalvia and included the free-swimming planktonic stages of trochophore and veliger; the pediveliger stage was also present.

In *C. hauniense*, as compared with *C. glaucum*, the reproductive cells and larval stages were characterized by a smaller size and longer development. At 4 weeks after fertilization, the planktonic larvae went through metamorphosis and changed their life environment; this was associated with big change in their internal structure. In this period, the 24-h mortality was highest, amounting to 65.2 and 53.4% for *C. glaucum* and *C. hauniense*, respectively.

1. INTRODUCTION

The interest in larval development of bivalves has originated in the second half of the 19th century. The initial studies performed on oysters and mussels, and being aimed at obtainment of larvae for culture on an industrial scale, have been unsuccessful. Only in the twenties of the 20th century, Prytcherch (1924) and Wells (1927) have described larval development of American oyster (*Crassostrea virginica*). Blue mussel (*Mytilus edulis*) has been an equally interesting organism; its planktonic stages were described by Borisiak (1909) and Mathews (1913), and fertilization was attained by Field (1922). Many investigators have presumed that there were no prospects of observing larval development under laboratory conditions, and thus they tried to identify larval stages in plankton samples (e.g. Lebour 1937, Jørgensen 1946, Sullivan 1948, Rees 1950, Miyazaki 1962).

Experimental culture of bivalve larvae in the present-day meaning has originated by the end of the forties; the methods for culture of larvae and larval development of 19 species of bivalves have been described by Loosanoff and Davis in 1963.

In recent years reproduction biology and development of bivalves have grown increasingly interesting. This is probably related to the very important part played by these organisms in aquatic ecosystems where they often are the dominant component of bottom fauna. They act as an immense biological filter purifying water masses from suspension, toxic compounds and heavy metal contaminants (Bertine, Goldberg 1972). The sensitive larval

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stages are a good indicator of the contamination degree of reservoirs as well as of the toxicity of contaminants.

For the above-mentioned reasons and on account of a complete lack of information about larval development of *C. hauniense*, we took up studies of this development in both species. The present results, together with the findings concerning the rate of gametogenesis (Wołowicz 1987), fully illustrate the life cycle of *C. glaucum* and *C. hauniense*. At the same time, knowledge of the consecutive larval stages and their description enable identification of these species in plankton samples. An additional goal of these studies involved the development of optimal methods for laboratory culture for further physiological and ecophysiological investigations.

2. MATERIAL AND METHODS

Larvae of both species of cockles were cultured in years 1976—1978. The periods, duration and numbers of cultures, as wll as te numbers of replicates are recorded in Table I. Cultures were carried out at 18°C in sea water (salinity 7.5‰). The mortality

Table I. The periods, duration and numbers of cultures of *C. glaucum* and *C. hauniense*

Cardium glaucum			*Cardium hauniense*		
Period of culture	No. of cultures	No. of replicates	Period of culture	No. of cultures	No. of replicates
24.05. — 8.07.76	3	2	13.05. — 24.06.76	3	2
18.06. — 8.08.77	5	3	21.05. — 21.07.77	5	3
20.06. — 26.07.78	5	3	15.05. — 6.07.78	4	3

of larvae was determined daily by counting the dead larvae and calculating their percentage against that of live larvae on the previous day. This enables the determination of larval mortality during 24-h (24-h mortality) (Wołowicz 1981).

3. RESULTS

LARVAL DEVELOPMENT OF *C. GLAUCUM*

Mature egg cells in the gonads are 86 μm in diameter. Gametes are released as one continuous stream, and less often — in several portions at intervals of some few min; spermatozoa are emitted as a milk-white cloudlet, whereas female gametes are easily recognizable by their grey-white colour and granular texture visible with the unaided eye. The number of eggs released depends on the age of bivalves; according to dissection performed prior to reproduction, young cockles reproducing for the first time have fewer reproductive cells (about 8000) than the 2 or 3 years old individuals (12000—14000). This fact is related to the greater volume of gonads in older cockles.

After the release of eggs into waters, their size increases to a diameter of 96 ± 11.3 μm (mean value ± SD) and — together with the 40—50 μm thick gelatinous layer — to a diameter of 182.8 ± 18.2 μm. Spermatozoa are

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9—10 μm in length, and have a spiral shaped head. After release into water, they are very active.

After fertilization, the vitelline membrane shrinks (Fig. 1A). Cleavage is total, undifferentiated and spiral, of the determinate type. At 2 h after mixing of egg cells and spermatozoa (18°C), some eggs release polar bodies (Fig. 1B, C) and some undergo their first cleavage (Fig. 1D). The length of one blastomer is 50 μm, and of the other one — 38 μm. The 4-cell stage is observed 4 h after fertilization (Fig. 1E). The smaller blastomer cleaves evenly and the bigger one — unevenly; three micromers and one macromer are formed. Despite the differences in cell size, the subsequent cleavage is synchronous. At 8 h after fertilization the 8-cell stage appears; two cells are bigger than the remaining ones. As a result of consecutive cleavages, the number of cells increases, and their size diminishes. After 18—20 h bare granulae, 100 μm in diameter, are formed (Fig. 1F). On their anterior surface there appear cilia impairing to the gastrula a rotary motion within the gelatinous layer which often persists till the veliger stage. At 40—42 h after fertilization trochophores are formed (Fig. 1G); their length is 103.2 ± 6.8 μm, and their breadth amounts to 91.2 ± 3.2 μm, or — with the gelatinous layer — to 151.2 ± 12.0 μm. The trochophore has an enlarged apical region with fine cilia forming the prototroch and an apical tuft with longer cilia. The prototroch acts as a locomotor organ; therefore, larvae are usually visible during rotary motion. Subsequently, on the trochophore apex some apical flagellae appear. The internal structure is simple; gland cells secreting the material for the larval shell and cells from which the gaster will be formed are visible. The remaining space is filled with mesoderm cells. After subsequent 8 h gland cells begin to secrete the material for the larval shell. After three 24-h periods, the larval shell encloses the soft parts of the larva, and the trochophore is transformed into a veliger. The characteristic properties of this stage (also referred to as prodissoconch I) involve the body enclosed by the larval shell and the velum enabling pelagic larvae to move freely (Fig. 1H). The veliger is of a "D" shape, since the shell hinge is straight; this is the straight-hinge stage (Fig. 1I). The veliger is 103.7 ± 6.2 μm in length and 92.5 ± 2.7 μm in breadth; at 3 weeks after fertilization it is 178.7 ± 12.9 μm in length and 161.9 ± 11.2 μm in breadth. The mean daily increase in length is 4 μm (Fig. 2). The straight-hinge stage lasts till the time when larval length becomes two times bigger than the hinge length, i.e. when the larva is 130.3 ± 4.1 μm in length and 116.1 ± 4.2 μm in breadth; this corresponds to about 6 days (from the 4th till the 10th day after fertilization). Now the shell assumes a rounded shape (Fig. 1J); the inflection of the curve between the 14th and 16th day of life (visible in Fig. 2) is related to a change in body proportions. The relationship between the length and breadth can be described by the equation:

$$y = 0.9248\,x - 4.3706 \qquad \text{(Fig. 3)}$$

By the end of this stage the adductor muscles and mantle appear; the velum comprises muscle fibres which — together with the velum — disappear during metamorphosis, and a tuft of long flagellae being the locomotor organ

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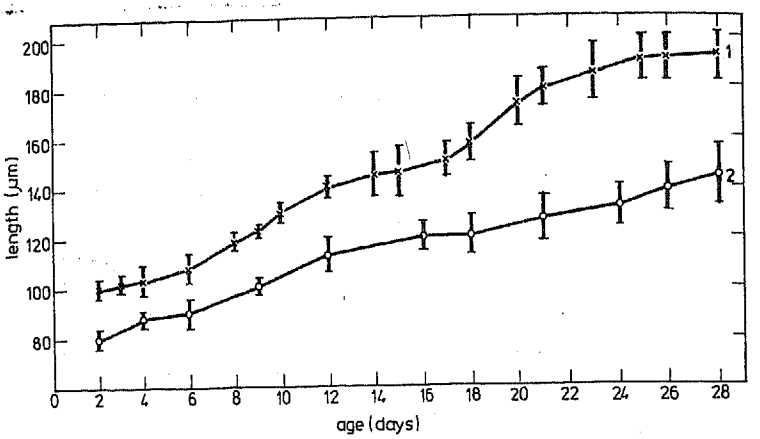

Fig. 2. Growth rate of *Cardium glaucum* (1) and *C. hauniense* (2) larvae

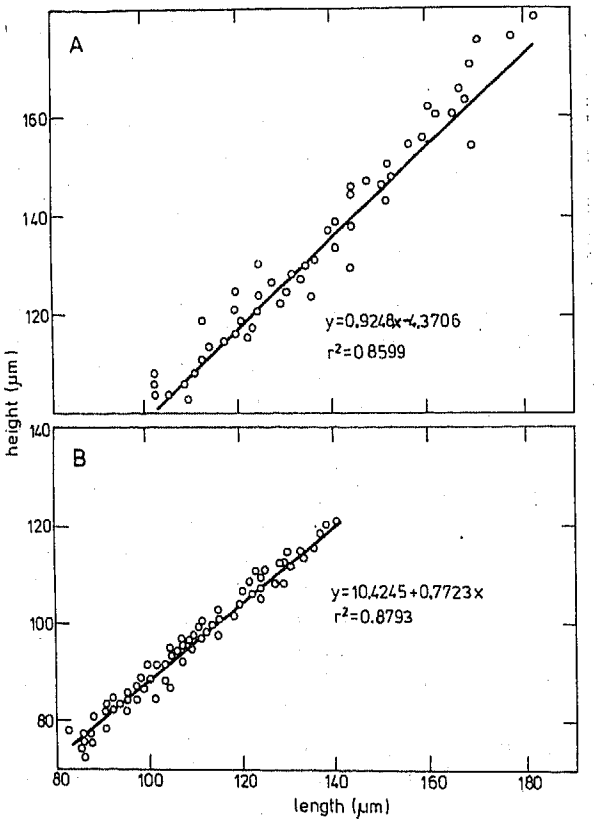

Fig. 3. Relationship between length and breadth of *C. glucum* (A) and *C. hauniense* (B) larvae in veliger stage

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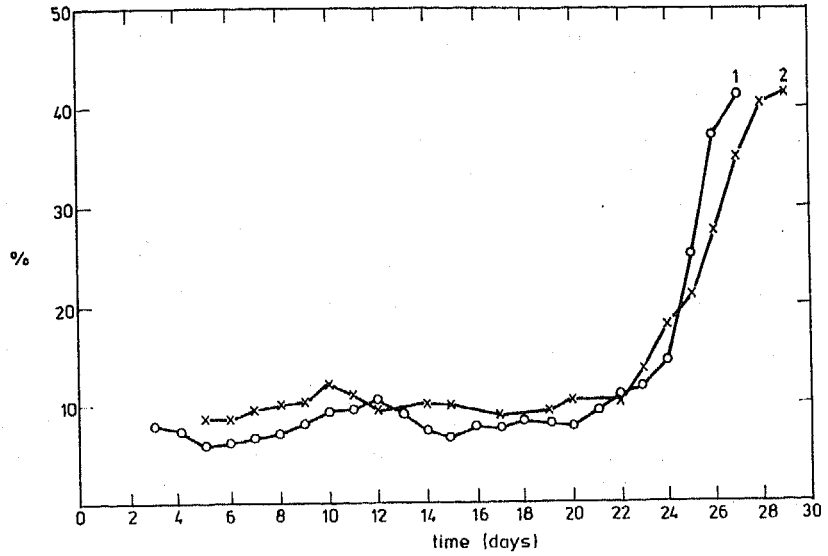

Fig. 4. Mortality of *C. glaucum* (1) and *C. hauniense* (2) larvae in laboratory culture

and exerting a sensory function. In older veligers the mantle takes over the function of secreting the material for the shell proper; this is the stage of veliconch or prodissoconch II. The terms prodissoconch I and II refer to the manner of formation of the veliger — enclosing shell and to its kind, but not to the structure of larva. On the surface of the veliconch fine rings appear; they are marks of the daily length gain (Fig. 1K). The shell hinge develops and its umbo is singled out; in the internal structure the food and gill filaments appear. The veliger stage lasts about 3 weeks, and after 21—26 days of pelagic life the *C. glaucum* larvae begin metamorphosis. This process involves transition of larvae from a planktonic to a settled mode of life as well as big changes in their internal structure. Prior to metamorphosis the larvae are 178.9 ± 14.6 μm in length and 163.6 ± 15.4 μm in breadth, whereas after this process they are 189.8 ± 12.9 μm in length and 167.6 ± 11.2 μm in breadth. At this time the mean larval mortality amounts to 79.6% (Fig. 4). During metamorphosis the velum disappears, whereas the gills and siphon develop. In some few individuals the velum and foot continue to function; they are pediveligers. The mantle secretes the material for the postlarval shell-dissoconch, but the veliconch remains visible. After 6 weeks the bivalves attain a mean length of 320 μm (Fig. 1L), and on the shell surface ribs typical of family Cardiidae appears.

LARVAL DEVELOPMENT OF *C. HAUNIENSE*

The diameter of the egg cells in gonads is 63.8 ± 4.3 μm (together with the gelatinous layer — 97.4 ± 2.4 μm), and after swelling in water it is 72.1 ± 1.9 μm (together with the gelatinous layer — 110.2 ± 7.6 μm). Eggs often stick

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together in aggregates and then the development of many larvae can be observed simultaneously (Fig. 5A). Spermatozoa are 8 μm long. Similarly as in *C. glaucum*, the first cleavage of the egg cell occurs 2 h after fertilization; the length of the bigger and smaller blastomer is 46 and 32 μm, respectively. The diameter of a formed gastrula amounts after 24—26 h to 77.2 ± 10.2 μm (together with the gelatinous layer — 129.2—11.0 μm). Trochophores develop at 48—50 h after fertilization; they are 81.1 ± 3.6 μm in length and 72.5 ± 2.2 μm in breadth. The first veligers observed 96 h after fertilization are 87.8 ± 4.3 μm in length and 78.0 ± 4.8 μm in breadth. The straight-hinge stage lasts 8 days; on the 12th day the larvae are 113.2 ± 7.8 μm in length and 97.1 ± 6.5 μm in breadth. At this time the umbo is singled out. The shell secreted by the mantle assumes the shape characteristic of this species, i.e. its posterior part becomes greatly elongated, whereas the anterior part remains mildly rounded (Fig. 5B). From this time the larvae of *C. glaucum* and *C. hauniense* can be distinguished by the shell shape. The relationship between the length and breadth of veligers can be described by the equation:

$$y = 10.4245 + 0.7723\,x \qquad \text{(Fig. 3)}$$

After 28—30 days of pelagic life the larvae go through metamorphosis; at this time they are 142.8 ± 12.3 μm in length and 127.4 ± 11.8 μm in breadth. The pediveliger stage is observed more frequently than in *C. glaucum*.

Young *C. hauniense* individuals often ascend the walls of culture vessels with the aid of the byssus and foot. The growth rate of *C. hauniense* larvae is between 2.7—3.4 μm/24 h (Fig. 2).

Owing to an addition of antibiotics to the culture, the 24-h mortality of larvae remains within the range of 3.5—12.0% averaging for the culture of *C. glaucum* and *C. hauniense* 7.8 and 8.9% per 24 h, respectively (Fig. 4). In the course of 3 days during metamorphosis the mean 24 h mortality of *C. glaucum* and *C. hauniense* increases to 65.2 and 53.4%, respectively. The high degree of hazard involved in this period is testified to by the fact that whereas about 15 and 12% of larvae of *C. glaucum* and *C. hauniense*, respectively, live till metamorphosis, only 3.2 and 2.1% of them, respectively, survive this process.

4. DISCUSSION

As earlier mentioned, the number of egg cells is smaller in young *C. glaucum* individuals than in those 1 or 2 years old. This probably results from the smaller volume of gonads in young individuals. The lower number of gametes in 1 year old female is compensated by the big numbers of these females (54.4% of the population), as compared with the 2 and 3 years old ones (18.1 and 3.5% of the population, respectively) (Wołowicz 1984). Lucain and Martin (1974) report that under laboratory conditions a *C. glaucum* female produces about 13000 egg cells, whereas von Oertzen (1972) estimates the mean number of *C. lamarcki* (*C. glaucum*) eggs at

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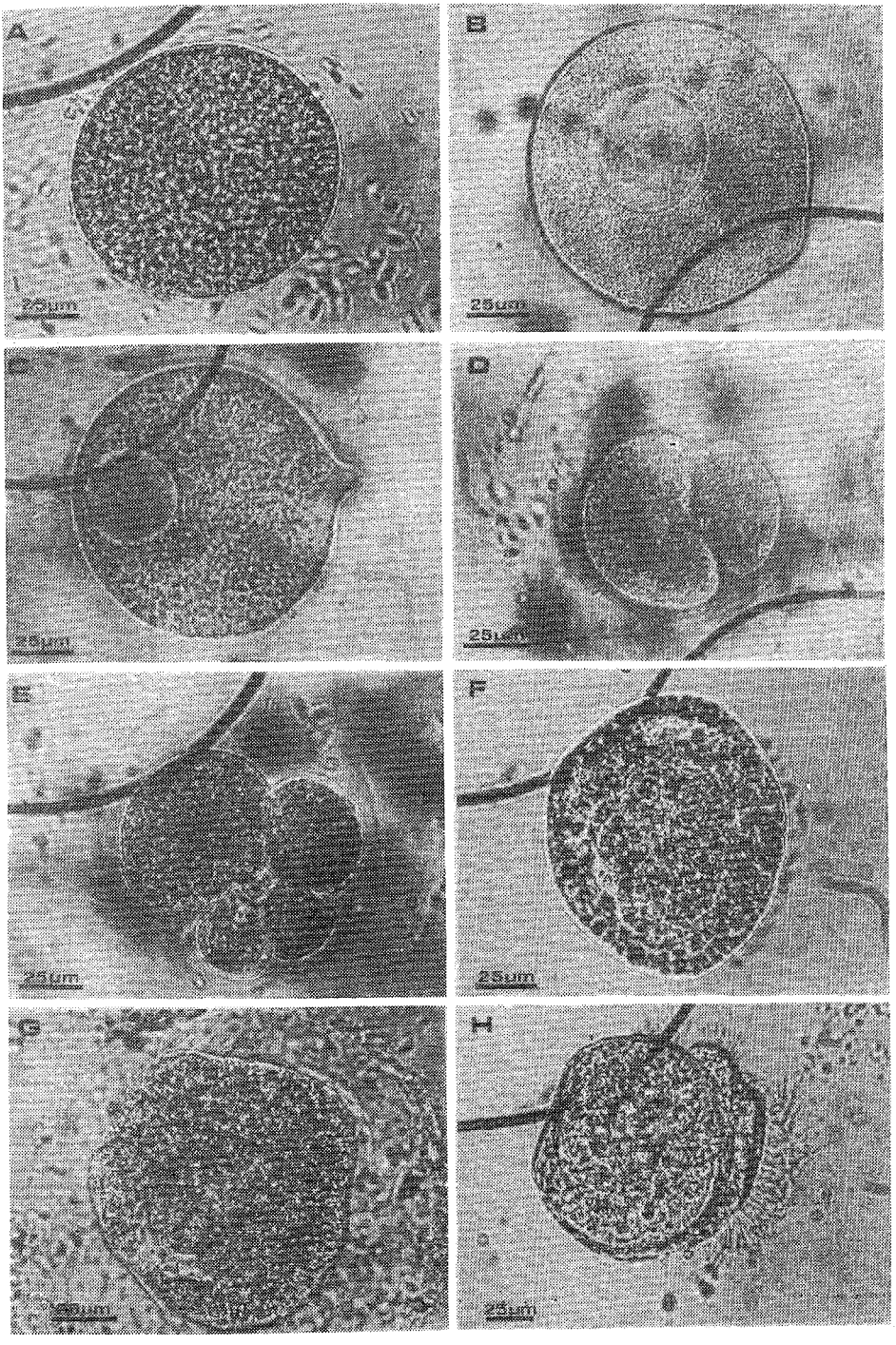

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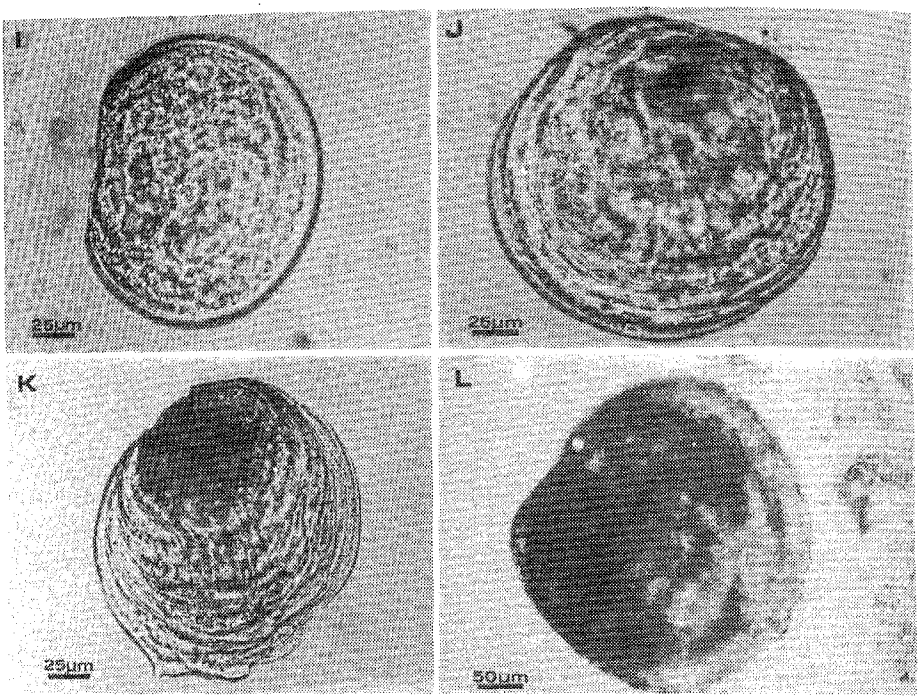

Fig. 1. Development of *Cardium glaucum*; A — fertilized egg cell, B — release of polar body — first stage (2 h after fertilization), C — final stage of polar body release, D — first cleavage of egg cell (2 h after fertilization), E — four-cell stage (4 h after fertilization), F — gastrula (18—20 h after fertilization), G — trochophore (40—42 h after fertilization). H — veliger with visible velum, I — straight-hinge stage (5 days after fertilization), J — singling out of umbo in veliger stage (16—18 days after fertilization), K — veliconcha with visible rings of 24-h increases in length, L — settled larva after metamorphosis (about 30 days after fertilization)

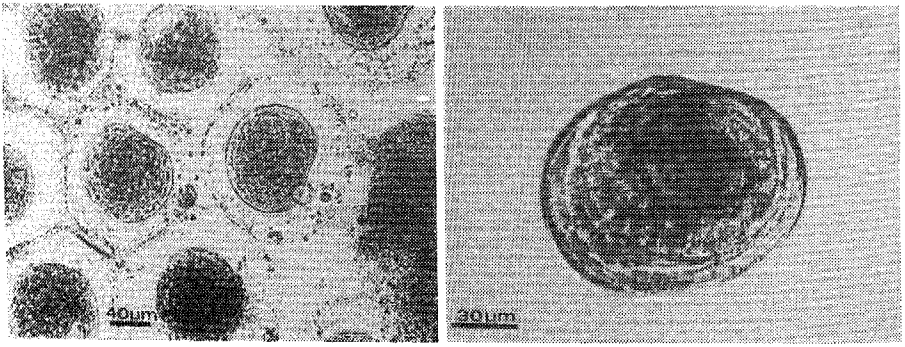

Fig. 5. Development of *Cardium hauniense*; A — within the gelatinous layer (4—5 days after fertilization), B — stage from which *C. hauniense* larvae can be morphologically distinguished from larvae of *C. glaucum* (about 28 days after fertilization)

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20000 per female. Because of the long reproduction period, it was impossible in the present studies to determine the number of eggs in *C. hauniense*. At the laboratory, from a 4—5 mm long female up to 3000 eggs were obtained. Artificial fertilization affords larvae for which a culture density of 20 larvae/cm^3 is accepted as optimal (Le Roux 1975, Lucas et al. 1976). Higher density causes slowing down of the growth rate (Loosanoff 1954).

Larval development of *C. edule* from England (Creek 1960) and of *C. glaucum* from the Sea of Azov and Aral Sea (Karpevič 1964) was compared with that of *C. glaucum* and *C. hauniense* from the Gdańsk Bay (Table II). Comparison of the different developmental stages and of their duration indicates that the rate of development is highest for cockles from the Sea of Azov and Aral Sea, which go through metamorphosis on the 9th and 10th day after fertilization, respectively. Larval development of cockles from the Gdańsk Bay is much slower and approaches that of *C. edule* from the coast of England. Lucain and Martin (1974) have observed metamorphosis of *C. glaucum* from the Mediterranean Sea after 25—28 days from fertilization, at a length of 165—180 μm. Kingston (1974) reports a length of 317—351 μm, but as a criterion of metamorphosis he accepts the appearance of ribs on the shell (in *C. glaucum* from the Gdańsk Bay ribs appear at a length of 320 μm).

Temperature and salinity exert a strong effect on the size of gametes and larval development rate in bivalves. It is found experimentally that the optimal temperature for the culture of larvae of both species is 18—20°C. It approaches the environmental temperature in the period of larval development; moreover, it allow for an optimal larval growth rate and highest survival (Brenko, Calabrese 1969, Le Roux 1975). Under laboratory conditions fertilization is possible between 15—25°C. At 35°C egg cells have been found to be incapable of fertilization; in case of larvae, their growth is slowed down or inhibited, and deformed larvae die prior to metamorphosis. At temperature lower than 10°C, larvae are characterized by slight growth. *C. edule* larvae cultured at 10°C go through metamorphosis after 39 days from fertilization, at 15°C — after 26—30 days, and at 20°C — even after 20—24 days. Between 15—20°C the growth rate of *C. edule* larvae remains fairly constant (Kingston 1974). The growth rate of *C. glaucum* larvae between 15—30°C increases in proportion to temperature elevation, and above 30°C it diminishes (whereas the growth rate of *C. edule* decreases even above 20°C). Russell (1971) suggests that this is due to the origin of *C. glaucum* from warm waters. Being an eurythermal and euryhaline species, *C. glaucum* easier becomes adapted to diverse living conditions.

The size of gametes (mainly egg cells) depends on water density, i.e. on salinity of the reservoir (Thorson 1936). At the highest salinity, the reproductive cells and larval stages are smallest (Table II), whereas from metamorphosis (when cockles already have postlarval shell) the larval growth rate is higher in saline than in brackish reservoirs.

Under natural conditions *C. glaucum* larvae settle by the end of July. In September cockles are 2—3 mm in length, and the monthly increases

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Table II. Larval development of *C. edule*, *C. glaucum* and *C. hauniense* from different water bodies

Water body / Stage	*C. edule* North Sea temp. 10 — 15°C Creek (1960)		*C. glaucum* Azov Sea temp. 17—18°C $S = 12‰$ Karpevič (1964)		*C. glaucum* Aral Sea temp. 22—24°C $S = 10‰$ Karpevič (1964)		*C. glaucum* Baltic Sea temp. 18°C $S = 7‰$ Present paper		*C. hauniense* Baltic Sea temp. 18°C $S = 7‰$ Present paper	
	Length (µm)	Time after fertilization	Length (µm)	Time after fertilization	Length (µm)	Time after fertilization	Length (µm)	Time after fertilization	Length (µm)	Time after fertilization
Egg cells	50 (100)*	—	50 — 55	—	60 — 75 (120)*	—	86	—	64 (97)*	—
Gastrula	60	23	—	4 — 8	—	4 — 7	100	18 — 20	77 (129)	24 — 26
Trochophore	80	48	—	9 — 12	—	30 — 35	103 × 91	40 — 42	81 × 72	48 — 50
Veliger	100 — 120	3 days	95 × 114 to 185 × 162	24 — 30	105 × 75 to 100 × 115	40 — 45	103 × 92 to 179 × 164	45	88 × 78 to 113 × 97	96 — 100
Metamorphosis and settling	270	3.5 weeks	190 — 220	9 days	200 — 225	10 days	190 × 174	25 — 26 days	143 × 127	28 — 30 days

* with gelatinous layer.

in length amount to 1—1.5 mm. The period of autumn promotes intense growth, and in November *C. glaucum* attains a length of 4—5 mm. These values are analogous to those reported for *C. edule* by Creek (1960). Individuals beginning their first reproduction in July of the next year are more than 5 mm long.

Under natural conditions, settled *C. hauniense* individuals are observed by the end of June. In July the spat are 0.80—1.35 mm in length and 0.65—1.15 mm in breadth, whereas in August they are 1.65—2.00 mm in length and 1.35—1.85 mm in breadth (Wołowicz, Wiktor 1975). The growth rate of *C. hauniense* is small; in the beginning of reproduction their length is 3—5 mm and remains the maximal one for the major part of them. Mass mortality of 3—4 mm long individuals (up to 80%) occurs in June and July, during reproduction. An analysis of the gonads suggests that the major part of cockles die after their first reproduction.

5. SUMMARY

C. glaucum and *C. hauniense* larvae were cultured from fertilization till metamorphosis and settling of cockles at the postlarval stage. At 4 h after artificial fertilization the first cleavages took place, leading to the formation of blastulae and then — of gastrulae. At 40—50 h after fertilization there appeared trochophores, and after three 24 h periods — veligers whose length amounted to 103.7—178.7 μm and 87.8—113.3 μm for *C. glaucum* and *C. hauniense*, respectively. In contrast to *C. glaucum*, the development of *C. hauniense* till the veliger stage proceeded within the gelatinous layer which well protects the sensitive larvae. The metamorphosis of larvae of both species took place after 4 weeks of pelagic life; the mean length of settling cockles was 189.8 and 142.8 μm for *C. glaucum* and *C. hauniense*, respectively. Differentiation of *C. hauniense* larvae from those of *C. glaucum* on the grounds of their morphological properties was possible at 2 weeks after fertilization, when the larval shell was replaced by the shell secreted by the mantle (dissoconch). In both cultures the 24-h mortality fluctuated between 3.5—12%, and during metamorphosis it increased to more than 50%/24 h. After metamorphosis, young *C. glaucum* individuals settled on the bottom of the culture vessels, whereas many *C. hauniense* individuals remained attached by the byssus to the culture vessel walls or ascended them with the aid of the foot.

6. STRESZCZENIE

Hodowlę larw *C. glaucum* i *C. hauniense* prowadzono od zapłodnienia do metamorfozy i osiadania małży w stadium postlarwalnym. Po 4 godzinach do sztucznego zapłodnienia obserwowano pierwsze podziały komórkowe, które prowadziły do powstania blastul, a następnie gastrul. W 40—50 godzin od zapłodnienia w hodowli pojawiały się trochofory, a po trzech dobach veligery o długości od 103,7 do 178,7 μm — *C. glaucum* i 87,8—113,2 μm — *C. hauniense*. W przeciwieństwie do *C. glaucum* rozwój *C. hauniense* do stadium veligera odbywał się w osłonce jajowej, która dobrze chroni delikatne larwy. Metamorfoza larw obu gatunków ma miejsce po 4 tygodniach życia pelagicznego, długość osiadających małży wynosiła 189,8 μm — *C. glaucum* oraz 142,8 μm — *C. hauniense*. Rozróżnienie larw planktonowych na podstawie cech morfologicznych możliwe było po dwóch tygodniach od zapłodnienia, z chwilą, gdy muszla została zastąpiona przez muszlę wydzielaną przez płaszcz-dissoconch.

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W obu hodowlach dobowa śmiertelność larw wahała się od 3,5 do 12%, natomiast w okresie metamorfozy wzrastała do ponad 50%/dobę. Po metamorfozie młode osobniki *C. glaucum* osiadały na dnie naczyń hodowlanych, natomiast liczne *C. hauniense* przytwierdzały się bisiorem do ścian naczyń hodowlanych lub wspinały się po nich posługując się stopą.

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