EARLY LARVAL STAGES OF THE SEABOB, XIPHOPENEUS KRØYERI
(HELLER)

WILLIAM C. RENFRO and HARRY L. COOK, Fishery Biologists
BUREAU OF COMMERCIAL FISHERIES

ABSTRACT

Five naupliar stages and the first protozoal stage of the seabob (Xiphopeneus krøyeri) have been described from larvae reared in the laboratory. With each molt the larva increases in length and becomes more advanced in its morphology. Differences in body structures among specimens in the same instar were noted and discussed.

METHODS AND MATERIALS

All descriptions and figures are from specimens reared in the laboratory. Gravid females were caught at sea and returned to laboratory aquaria. After spawning, eggs were pipetted from the bottoms of the aquaria into beakers of sea water and the resulting larvae observed continuously. As development proceeded, specimens of each larval stage were measured, photographed, and preserved in buffered 5 percent formalin. Details of rearing trials are included in the appendix.

Microscope magnifications ranged from 10× to 200×. Measurements to the nearest 0.01 mm were made with an ocular grid calibrated against a stage micrometer. We observed, as did Hudinaga (1942), some growth and development of body features occurring between molts. For this reason specimens in the same instar may exhibit differences in the size and shape of body structures. Figures were drawn with the aid of a camera-lucida and represent a conscious effort to illustrate the “typical” or most prevalent form of each stage.

In the ventral aspect many details of the naupliar appendages are obscured. In order to illustrate as clearly as possible all morphological features, dextral appendages have been drawn as though they had been rotated on their axes.

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DESCRIPTION OF THE EGG AND NOTES ON HATCHING

Twenty-six viable eggs had a mean diameter of 0.16 mm. with extremes from 0.15 to 0.17 mm. Although the egg is demersal, sinking readily in still sea water, it is easily buoyed up by slight agitation of the water. The nauplius, surrounded by the embryonic membrane, fills the egg. In later stages its appendages and a well-defined ocellus (naupliar eye) can be clearly seen through the thin, transparent shell (fig. 1). Prior to hatching, rapid, vibrating movements of the nauplius occur at more or less regular intervals.

The emerging nauplius first forces one appendage through the egg shell, then moves this appendage violently to enlarge the opening through which it finally escapes. Immediately after hatching, the nauplius is curled with its appendages drawn in posteriorly along the sides of the body. It soon assumes the normal shape as shown in figure 2.

Figure 1.—Egg containing developing nauplius. Photomicrograph of ventral view.

Figure 2.—Photomicrograph of Nauplius I, ventral view.
At rest, the nauplius lies dorsal surface down. As its appendages beat in unison, it rises a short distance then sinks when movement ceases. Active swimming lasts approximately 2 seconds with a rest period of about 8 seconds. Older nauplii swim longer and rest less.

The yolk granules filling the body give it a grainy appearance. After preservation for several weeks in 5 percent formalin, all color is lost, and the yolk granules become opaque, giving the preserved nauplius a silver, grainy appearance in strong light.

DESCRIPTONS OF STAGES

NAUPLIUS I

The Nauplius I of *X. krøyeri* has a short, pyriiform body (figs. 3 and 4). Body length of 25 specimens measured from the apical to caudal ends but excluding furcal spines averaged 0.26 mm. Measurements across the dorsal surface at the point of greatest width averaged 0.15 mm.

A small but distinct protuberance on the dorsal surface gives all naupliial stages a humpbacked appearance. The medial point of the hump falls between the origins of the second and third appendages. A slight depression is sometimes found posterior to the hump.

The ocellus lies in the longitudinal axis of the body near the anterior end and retains its position and color in all later naupliial stages. In living specimens it is reddish or rust colored but turns black in formalin.

The labrum or upper lip appears as a protrusion of the ventral surface. It is thickest at its posterior end and extends posteriorly to or just beyond the origins of the third appendages.

Two furcal spines arising at the posteroventral end of the body generally project directly backward but curve upward in some specimens. Viewed ventrally they are seen to curve inward. Three pairs of appendages are inserted ventrally on the anterior half of the body. The anterior pair, or first antennae, are unbranched. The middle appendages, or second antennae, are branched into ventral endopods and dorsal exopods. The posterior appendages, or mandibles, are also branched into ventral endopods and dorsal exopods. All appendages bear setae which have been assigned arbitrary numbers to facilitate their description in the text. Starting with the anterior, proximal seta on each dactyl appendage, the setae are numbered counterclockwise in the figure. It must be emphasized that setae are numbered on appendages which are represented as having been rotated around their axes. A given seta does not always retain the same number in subsequent figures. That is, with addition or loss of setae on an appendage, the setae are renumbered.

Each first antenna originates at the anteroventral edge of the body and curves outward. It possesses six setae. Setae 1, 2, and 3 are inserted on the anteroventral edge of the appendage. Seta 1 may not always be distinct; its position may merely be indicated by a slight protuberance. Setae 4 and 5 are terminal, and seta 6 arises from the posterodorsal surface near the end. On most specimens a short, spikelike spine, which may be the bud of another seta, projects from the ventral surface near the end of the first antenna.

The second antennae arise immediately posterior to the origins of the first antennae and are directed obliquely backward. The endopod of each second antenna appears as an extension
of the basal portion and bears four setae. Setae 1 and 2 arise along the ventral midline, while setae 3 and 4 are terminal. A small, spikelike spine projects from the ventral surface at the distal end. The exopod of each second antenna is inserted on the dorsal surface. It is slightly longer than the endopod and bears five setae. Setae 1, 2, and 3 originate along the midline on the ventral surface, and setae 4 and 5 are terminal.

The posterior appendages, or mandibles, have their origins on the ventrolateral edges of the body about halfway between the anterior and posterior ends. Each endopod is directed posteriorly and bears three setae. Seta 1 is inserted on the posteroventral surface near the distal end, and setae 2 and 3 are terminal. The exopod branches from the dorsal surface of each mandible and bears three setae of nearly equal length. Setae 2 and 3 are terminal, and seta 1 is subterminal. Setation of the endopods and exopods of the mandibles remains constant in all subsequent naupliar stages.

**NAUPLIUS II**

Twenty-five Nauplius II specimens averaged 0.27 mm. in length and 0.15 mm. in greatest width (figs. 5 and 6). The labrum has a pronounced fold posteriorly, and a second fold, the labium or lower lip, can be seen behind the labrum in the lateral view. The two furcal spines are longer, straighter, and inserted farther apart than those of Nauplius I.

Shapes of the appendages are not changed, but all are slightly longer. Some setae, generally the longer ones, become plumose with the addition of setules along their lengths; however, this condition varies among specimens in this stage.

The spikelike spine on each first antenna of Nauplius I has lengthened to become seta 4, while the terminal and dorsolateral setae are shorter.

The endopod of each second antenna retains the setation of Nauplius I except that the two terminal setae are shorter. Each exopod of the second antennae gains a short sixth seta terminally. Setae 4 and 5 have short, cylindrical shanks at their bases. These basal shanks are also found occasionally on other long setae of second nauplii. Setae 1, 2, 3, 4, and 5 are generally plumose.

As previously stated, setation of the mandibles remains constant in all naupliar stages.

**NAUPLIUS III**

Nine Nauplius III specimens averaged 0.29 mm. in length and 0.15 mm. in width (figs. 7 and 8). Both the labrum and labium are larger. Four pairs of ventral appendages, which will appear externally in the next stage, can be seen beneath the cuticle in lateral view.

Three pairs of small furcal spines have been added, two pairs laterally (spines 1 and 2) and one pair medially (spine 4). The furcal spine count thus becomes 4+4. The posterior half of the body appears slightly more slender, and the caudal end shows definite bifurcation.

All longer setae are plumose in this stage, and the basal setae, which first appeared in the preceding stage, are longer and occur more frequently. Setation of the first antennae is unchanged.
dorsal surface. A pair of "frontal organs" appear as slight protuberances at the anterior margin of the body. The labrum narrows posteriorly, and the labium can now be seen in the ventral view.

Four pairs of biramous appendages (the first and second maxillae and the first and second maxillipeds) are now prominent on the ventral surface of the posterior half of the body.

Definite, lobelike furcal processes are now apparent, and with the addition of one pair of lateral spines and another pair medially, the furcal spine count is 6+6.

Setation of the first antennae does not change. On the endopods of the second antennae, setation is unchanged except for the addition of a terminal spikelike spine inserted ventrally. The exopod of each second antenna acquires an additional seta, making its total setae count eight.

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Setae 1, 2, 3, and 4 are longer, and seta 7 is shorter than in the last stage.

On the endopod of each second antenna the spikelike spine, which was present in the preceding two stages, has lengthened to become seta 3. The exopod of each second antenna gains a small seta (seta 7) terminally, and seta 6 has become longer.

The bases of the mandibles in some specimens appear to be swollen.

**NAUPLIUS IV**

Measurements of 13 Nauplius IV specimens showed their average length to be 0.34 mm. and average width 0.16 mm. The body is more elongate and slender posteriorly (figs. 9 and 10). Paint outlines of a carapace have appeared on the
Setation of the mandibles remains unchanged, but a prominent rounded lobe appears at the base of each. This is the rudiment of a masticatory organ, and combined with the appearance of the maxillae and maxillipeds, is the most characteristic feature of Nauplius IV.

**NAUPLIUS V**

Seven specimens of Nauplius V averaged 0.39 mm. in length and 0.16 mm. in greatest width. The body is more elongate, the carapace more prominent, and the frontal organs more sharply defined than in the preceding stage (figs. 11 and 12). The labrum is further narrowed posteriorly and the labium is now bilobed.

The maxillae and maxillipeds have lengthened and now bear two or three terminal setae on each branch.

The caudal furcae are further separated by a sulcus which has developed between them. With the addition of a pair of spines inserted medially, furcal spine count is 7+7.

![Figure 11: Nauplius V, ventral view.](image)

**Figure 12:** Nauplius V, lateral view.

On each first antenna there are now three dorso-lateral setae as a result of the addition of setae 7 and 9.

On the endopod of each second antenna a small seta (seta 2) is present near the base of seta 3, and the small, terminal bud which was present in the last stage has lengthened to form seta 4. Each exopod gains an additional seta to make its total nine.

As in previous stages, setation of the mandibles is unchanged, but the endopods are frequently transparent. The rudimentary masticatory organ at the base of each mandible is further enlarged and is shaped somewhat like a strawberry. Transparent, toothed structures are faintly discernible on its posterior surface.

**PROTOZOA I**

Measured from the anterior margin of the carapace to the ends of the furcae, eight Protozoa I specimens averaged 0.69 mm. Six averaged 0.32 mm. in greatest carapace width and 0.36 mm. in carapace length (figs. 13, 14, and 15).

Although the Protozoa I does not move as rapidly as the Nauplius V, it is much stronger, swimming almost continuously with its ventral surface up. All appendages except the mandibles appear to aid in locomotion, and occasionally protozoa were observed to bend the abdomen beneath the cephalothorax and flip themselves when meeting an obstacle.

The carapace, which is somewhat flattened, fits loosely on the dorsal surface. The dorsal protuberance present in the nauplii persists but is not so prominent in this stage. The anterior edge of the carapace is divided into two lobes each of which
Figure 13.—Photomicrograph of Protozoa I, ventral view.

EARLY LARVAL STAGES OF THE SEA BIRD
bears a well-developed frontal organ ventrally. The compound eyes as well as the ocellus can be seen beneath the carapace.

Behind the carapace the body is slender and segmented. The caudal end is divided into two lobes, each bearing seven furcal spines. These furcae are separated by a semicircular notch through which the anus opens. In the posterior portion of the body the intestine can be seen, flanked by long muscle fibers.

The labrum now has a stout, anterior spine, bears fine setae on its posterior margin, and partially obscures the mandibles. The masticatory processes of the mandibles are longer and curve inward, terminating in a ring of teeth (fig. 16). The larger teeth are prominent structures posterior to the labrum. Within each mandible a second ring of teeth is present. A small lobe directed laterally arises from the ventral surface of each mandible. The two lobes of the labium lie posterior to the mandibles and bear fine setae on their medial surfaces.

Segmentation of all appendages occurs for the first time in this stage, although segments are indistinct in many cases. Each first antenna is divided into six or seven segments. Except for the appearance of a small bud terminally, setation of each first antenna is unchanged from that of the last stage.

On each of the second antennae the basal portion, or protopod, is divided into 3 segments, the endopod into 2 segments, and the exopod into 9 or 10 segments. The first segment of the endopod bears two pairs of setae on its anteroventral margin: one pair proximally and the second distally.

Figure 14.—Protozoa I, ventral view.

Figure 15.—Protozoa I, lateral view.

Figure 16.—Protozoa I, right mandible, posterior view.
The distal segment bears five terminal setae. The exopod of each second antenna bears five setae on its anteroventral margin, one each arising from the fifth, sixth, seventh, eighth, and ninth segments. Its 10th segment bears four terminal setae. The fifth and seventh segments also have a single seta on their posterodorsal surface.

The protopod of each first maxilla (fig. 17) is unsegmented but has two lobes on its anterior margin. The proximal lobe bears eight short, thick setae, and the distal lobe bears three stout setae, which are barbed terminally. The endopod is composed of two segments bearing three setae each. The exopods of the first maxillae are present as small, spherical knobs, each of which bears four setae.

The protopod of each second maxilla (fig. 18) shows no segmentation but has seven small lobes on its anterior margin. The first four lobes are sometimes coalesced to form one large lobe. The first or proximal lobe bears six setae while the remainder bear three or four. Two setae also arise from the distal end of the protopod. The endopod is composed of three segments: the proximal bearing two setae; the middle, one; and the distal, three. The exopod is a small knob which bears five setae.

The protopod of each first maxilliped (fig. 19) is composed of three segments. The proximal segment has four lobes on its anterior margin, each bearing one or two setae. The second and third segments of the protopod also bear one or two setae. Each endopod has five segments, the first four bear one to three setae on their anterior margins and the fifth possesses five terminal setae. The exopod of each first maxilliped is unsegmented and bears four lateral and three terminal setae.

The second maxillipeds (fig. 20) closely resemble the first maxillipeds. Their protopods consist of four segments, each of which bears one or two setae. Each endopod is composed of six segments with the first five segments bearing one or two setae on their anterior margins and the sixth bearing three terminal setae. The exopod of each
second maxilliped is unsegmented and bears three posterolateral and three terminal setae.

Posterior to the second maxillipeds is a pair of small third maxillipeds. The exopods are considerably longer than the endopods and bear two terminal setae.

MORPHOLOGICAL VARIATION AMONG SPECIMENS WITHIN AN INSTAR

The development of these normally planktonic larvae was probably slower in the laboratory than in nature. For example, molting in some specimens continued for 15 minutes or more in the laboratory. In the sea, this process might be completed in much less time. It is possible, therefore, that the morphological variations discussed here were observable only because normal developmental rates were retarded.

Hudinaga (1942, p. 331) stated: “It may be said that in Crustacea the body-length increases only by molting, but in some species there is a slight difference in the length immediately after one moult and before the next, an outstanding example of which is the zoa stage of *P. japonicus*.”

During our rearing trials individual nauplii were isolated in small containers and observed periodically. Slight elongation of some body parts was observed, but actual, periodic measurements of the moving larvae were not attempted. The spines and setae of all preserved specimens were measured to the nearest 0.01 mm. These measurements were examined to determine the extent of variation in morphology among specimens in the same instar. The results showed: (1) Nauplius I. Fourteen specimens had one pair of furcal spines 0.04 to 0.05 mm. long and 10 specimens possessed one pair of furcal spines measuring 0.06 mm. The 10 specimens with larger furcal spines also had longer setae on all appendages. (2) Nauplius II. Ten specimens with furcal spines 0.06 to 0.08 mm. long had, in almost every case, longer setae than did 13 specimens with furcal spines 0.04 to 0.05 mm. in length. (3) Nauplius III. Three groups of specimens were distinguished (table 1); three with four pairs of furcal spines, four with three pairs, and two with two pairs. Specimens with fewer and shorter furcal spines also had shorter setae. Of interest was the fact that the furcal spines missing in the two groups having shorter setae were those spines which are added at this instar. (4) Nauplius IV. Four specimens with four pairs of furcal spines had, in most instances, shorter setae than the remaining five specimens with six pairs. (5) Nauplius V. Of seven specimens one had four pairs of furcal spines, one had five pairs, and five specimens had seven pairs. In general the specimens with fewer furcal spines had shorter setae.

Obviously, individual nauplii in the same instar differ considerably in their body dimensions. Several possible causes for these observed differences might be considered: (a) The nauplii with shorter and fewer furcal spines and setae may be malformed specimens which die before reaching the next instar. (b) The differences are the result of individual variation, some nauplii simply being smaller and less well developed than others. (c) These tiny larvae, covered with a thin cuticle, continue to develop and lengthen, during the period between molts.

Another cause for variation observed among individuals in the same stage of development lies in the molting process. Loss of the exoskeleton was observed to begin at the posterior end of the nauplius. The furcal spines and the posterior cuticle were shed first followed by the setae and exoskeleton of the mandibles, the second antennae, and the first antennae. In most cases, the body exoskeleton was lost in pieces. The molting of right and left appendages did not always occur simultaneously. Because molting of all parts was not instantaneous, a number of our specimens had only partially shed their exoskeletons. In one Nauplius IV specimen, for example, the right
TABLE 1.—Nauplius III, mean length of furcal spines and setae in specimens with different furcal spine counts
[0.01-mm units]

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<th>2+2</th>
<th>3+3</th>
<th>4+4</th>
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<tr>
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<tr>
<td>First antennae:</td>
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<tr>
<td>Seta 1</td>
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</table>

1 Not measured.
2 Absent.

Second antenna had molted, while the left second antenna retained the exoskeleton of the previous instar, thus the right had more setae than the left. Occasionally the exoskeleton of an appendage had loosened but was not completely shed at the time of preservation. Its new setae, which were visible beneath the old cast, were very small.

Listed below are variations from the described forms:

**NAUPLIUS I**

The slight depression posterior to the dorsal hump was not present on a few of the specimens studied.

The labrum varied in size from slight to very prominent.

Seta 1 on the anteroventral margin of each first antenna was absent in 2 of 25 specimens.

Seta 1 on the endopods of the second antennae was not present in 3 of 25 specimens.

**NAUPLIUS II**

Some specimens, preserved in the process of molting, exhibited appendage setation characteristic of Nauplius II while retaining the Nauplius I setation on the corresponding appendage of the opposite side. Frequently, the cast of an appendage had only partially slipped off and obscured the new setae beneath it.

Addition of setules to the setae varied in individual specimens and among the different specimens. That is, some specimens had plumose setae on one appendage while corresponding setae on the opposite appendage or on another specimen lacked setules.

The shanks present at the bases of setae 4 and 5 on the exopods of the second antennae were also found randomly on all longer setae.

The terminus of seta 4 on the exopod of each second antenna was split in occasional specimens of Nauplius II and later stages. This seta is always the longest seta on the exopod although its number may change.

**NAUPLIUS III**

In three specimens a small median spine between the furcae was noted.

On two specimens having three pairs of furcal spines, seta 7 on the exopods of the second antennae was absent. Variation in the number of furcal spines has previously been discussed.

**NAUPLIUS IV**

Four individuals possessed four pairs of furcal spines, five had six pairs, and one specimen was too badly damaged to determine the spine count.

Seta 8 on the exopods of the second antennae was absent in two of six specimens which were otherwise in good condition.

**NAUPLIUS V**

Seta 2 on the endopods of the second antennae was missing in three of seven specimens.

**PROTOZOOEA I**

No significant morphological differences were noted among the eight specimens examined.

**SUMMARY**

There are five naupliar stages during the early larval development of the seabob. With each molt the larva increases in length and becomes more advanced in its morphology. Differences in various body structures among specimens in the same instar are discussed. A characteristic which is usually sufficient to separate naupliar stages is the addition of one seta on the exopods of the second antennae with each molt. This and other characteristics are summarized in Table 2.
Table 2.—Counts of furcal spines and setae

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<td>Nautilus V</td>
<td>7+7</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Protozan I</td>
<td>7+7</td>
<td>9</td>
<td>9</td>
<td>11</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

LITERATURE CITED

DOBIIK, SHELDON

HUDINAGA, MOTOSAKU

APPENDIX 1

NOTES ON REARING

Trial 1

The first seabob to spawn viable eggs was caught October 7, 1959, with a 10-foot otter trawl 6 miles northeast of the Galveston Jetties in a depth of 5 fathoms. This female was returned to the laboratory and placed in a plastic barrel filled with seawater filtered through a plankton net. Thirteen hours later, eggs were found in the container. The eggs were pipetted from the container bottom and distributed among seven 4-liter beakers filled with water from the spawning container. These beakers were sampled for larvae periodically during the next 110 hours.

Hatching began shortly after introduction of the eggs into the beakers and continued for 2 days. As development proceeded, specimens of each instar were examined and preserved for future study. Water temperatures in the beakers ranged from 19.6° to 25.0° C. during the trial, and salinity measured 29.5°/oo. Mortality in all instars proved high, and no more than 40 specimens reached the Protozoa I stage.

At the conclusion of this trial, preliminary descriptions of each instar were begun. It soon became apparent, however, that too few specimens of Nautilus III and IV in good condition were available to complete the figures and descriptions.

Trials 2 to 6

Through the spring, summer, and fall of 1960, repeated attempts to rear seabob larvae failed. On five different occasions gravid females were captured and returned to the laboratory. Some aborted their eggs in gelatinous masses, while the eggs of others were round and smooth but proved nonviable. Sometimes viable eggs were spawned and appeared to develop normally for a time, only to stop for no apparent reason. Destruction of the eggs by micro-organisms, chiefly bacteria and ciliates, frequently caused hatching failures. Entanglement of the larvae in detritus also seriously hindered the rearing trials.

After each failure, efforts to improve conditions in the rearing containers were made. These included: addition of antibiotics, irradiation with ultraviolet light, filtration, centrifuging, and preheating the medium to rid it of micro-organisms. Artificial sea water was tried as a medium also. Despite these efforts, all rearing trials failed during 1960.

Trial 7

On April 25, 1961, 2 dozen gravid females, collected from 2 to 3 fathoms northeast of the Galveston Jetties, were returned to the recently completed circulating sea-water laboratory. Here they were distributed among five small glass aquaria and three circular, wooden tanks, 4 feet in diameter and 3 feet deep. Water circulating in the aquaria and two of the tanks was filtered through glass wool, then through a cellulose filter, and finally irradiated with ultraviolet. The third wooden tank received sea water filtered through an 18-inch layer of coarse sand. Water temperature ranged from 23.0° to 24.0° C., and salinity was 22.6°/oo.

Spawning took place in all the containers within 6 hours after introduction of the females. Eggs were siphoned from the spawning aquaria, distributed among containers in which the treated
water was circulated, and observed continuously. Hatching began approximately 10 hours after spawning and continued for 41 hours. Although none of the resulting larvae reached the protozoa stage during this trial, the additional nauplial specimens obtained permitted completion of the early larval descriptions.

The following table, constructed from notes made during the two successful trials, indicates intervals between molts.

<table>
<thead>
<tr>
<th></th>
<th>Trial 1</th>
<th>Trial 2</th>
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<tbody>
<tr>
<td>Nauplii well-developed and moving sporadically inside egg</td>
<td>11</td>
<td>11</td>
</tr>
<tr>
<td>Nauplius I first found</td>
<td>111/4</td>
<td>12</td>
</tr>
<tr>
<td>Nauplius II</td>
<td>17</td>
<td>25</td>
</tr>
<tr>
<td>Nauplius III</td>
<td>51</td>
<td>25</td>
</tr>
<tr>
<td>Nauplius IV</td>
<td>56</td>
<td>44</td>
</tr>
<tr>
<td>Nauplius V</td>
<td>57</td>
<td></td>
</tr>
<tr>
<td>Protozoa I</td>
<td>58</td>
<td></td>
</tr>
<tr>
<td>Hatching ceased</td>
<td>52</td>
<td>41</td>
</tr>
</tbody>
</table>

**Table A-1: Chronological development of larvae**