

This paper is not to be cited without prior reference to the author

International Council for the
Exploration of the Sea

C.M. 1975/ K:15
Shellfish and Benthos Committee
Att.: Fisheries Improvement
Committee

Studies on laboratory-reared larvae of Pandalus borealis KRØYER:
larval development, growth and feeding under different temperature,
salinity, light and food conditions

=====

by

R. Wienberg
Institut für Hydrobiologie und Fischerei-
wissenschaften der Universität Hamburg,
2 Hamburg 50, Olbersweg 24 und
Institut für Küsten- und Binnenfischerei
der Bundesforschungsanstalt für Fischerei,
2 Hamburg 50, Palmaille 9



INTRODUCTION

Studies on the population dynamics of Pandalus borealis in the North Sea have been carried out at the Institut für Küsten- und Binnenfischerei since 1964. AKER, MELXNER and TIEWS (1972) found large annual fluctuations in the populations of Farn Deep and of Fladen Ground. To understand the reasons for such fluctuations, it was found to be desirable to gain better knowledge on the life history and of the vital requirements of this animal. Special emphasis was given to the development of larval stages.

The first description of the larval development of Pandalus borealis was done by SARS (1900). LÉBOUR (1930), however, discovered that SARS had described Caridion gordonii rather than Pandalus.

The first hatching experiments were conducted by BERKELEY (1930). She obtained first-stage larvae from egg-bearing Pandalus borealis, but failed in reaching later stages. From plankton catches she described 5 further zoea stages and one postlarval. It was not until 1965 that the complete culture of a pandalid, P. jordani, was accomplished by MODIN and COX (1965). In their development these animals passed through 11-13 zoea stages. This number is twice as large as BERKELEY had supposed in her work on the animal's closest relative P. borealis.

MATERIAL AND METHODS

Culture experiments were carried out in 1974 and 1975. In 1974 egg-bearing females were caught for this purpose in Farn Deeps area, in 1975 in the Skagerrak. In 1974 the larvae were placed at a maximum of 50 per glass in 500 ml jars with a daily water renewal. To prevent undue injury during the exchange process, the animals were carefully transferred to an underwater sieve, thus keeping the time out of water at the minimum.

The water used was filtered sea water of 32⁰/oo taken off the coast of Heligoland. At first, until the second larval stage, the animals were fed freshly hatched Artemia nauplia, thereafter with 2-day old nauplia. Using an electronic counter exact quantities of Artemia were fed (counting error less than 1%). As the Pandalus larvae excrete a solid feces, the number of Artemia remaining after 24 hours had to be counted under magnification, so that the feeding rate could be determined.

The following experiments were carried out:

1. Pandalus larvae were cultured at 3⁰C, 6⁰C, 9⁰C and 12⁰C. During the experiments temperatures fluctuated at the 3⁰C trial up to 1⁰C, otherwise not more than 0.1⁰C. The salinity was 32⁰/oo S. A 12 hour day/night period was imposed, the laboratory having been artificial lighted by means of 4 40 Watt cold neon lights. The larvae were fed every day with Artemia nauplii in excess (at first 20 per larva and day, later 50 Artemia per larva and day).

2. Cultures were performed at a salinity of 22, 25, 28, 31, 32 and 34^o/oo S. The temperatures were constant at 6^oC ± 0.5^oC. The other factors were the same as described above in 1.
3. *Pandalus* larvae were kept in total darkness (except 5 minutes of light per day during feeding and control). The temperature was 6^oC ± 0.5^oC, the salinity 32^o/oo S. Food was given in excess.
4. *Pandalus* larvae were fed with different quantities of *Artemia* nauplii. 0, 1, 5, 10, 20 and 50 *Artemia* nauplii per larva and day were given. The other factors were: temperature at 6^oC ± 0.5^oC, salinity 32.5^o/oo and a 12 hour light/dark period.

During these experiments the mortality and the development was checked daily. Exuvia were conserved in a solution of 40% glycerin, 40% ethanol and 20% water. Furthermore the feeding rate was established and the growth recorded. Studies of the exuvia showed the degree of variation in larval development under the various conditions.

The culture of these animals with a daily change of medium was very time-consuming. Therefore in 1975 a new system was constructed for larval culture. A diagram and detailed description of this can be found in appendix 1. The animals were kept in 300 ml glass jars, 20 per glass. A current of approximately 300 ml/hour was established, the water being purified by a gravel-shell filter. Culture temperatures were 9^o and 3^oC., the other factors remained the same as in 1974.

RESULTS

Larval development

In 1974 the complete culture of *Pandalus borealis* from egg to first juvenile adult stage was accomplished. During the development 11 moulting stages were encountered. 4 larvae reached the 11th stage, 2 out of the original 50 in the 12^oC, 2 out of 50 in the 9^oC experiment. Only one of them metamorphosed at 9^oC.

In 1975 there was more success. Using the new closed water recycling system 7 animals out of a total of 100 reached the juvenile adult level at 9°C. Three of these moulted 8 times, 4 moulted 9 times. As in 1974 some larvae showed up to 11 moulting stages, but failed in getting adult.

Examining the exuviae of the larvae, 9 morphological distinct zoeal stages could be described. The drawings and descriptions are given in appendix 2.

In 1975 10 out of 32 larvae skipped the seventh zoeal stage. The sometimes observed 10th and 11th larval stage were practically identical to the 9th zoeal stage.

In 1974 between zoeal stage VIII and IX an extra moulting was witnessed, a moult however, that brought no structural change. As result of this moult, stage X of 1974 corresponds to stage IX of 1975.

These results differ from those of BERKELEY(1930), who considered only 6 larval stages. Furthermore there were many discrepancies in the description of the extremities (segmentation of the antennal scales, number of denticles of the mandible, number of setae on the maxillipeds and pereopods, etc.). The general sequence of development, however, agrees with her findings. On the other hand, there was a high degree of agreement with the works of MODIN and COX on Pandalus jordani: the maximal number of stages being very close of those found in P. borealis (11-12). The morphology of the extremities is in some cases identical to the last microscopic detail. The sequence of development, however, is quite different: P. jordani having independent uropods at stage II, P. borealis not until stage III. The pleopods of P. jordani appear later than in P. borealis.

The following list compares BERKELEY's stages with those of the present study from 1975: B I is equivalent to I, B II to II, B III to III, B IV between V and VI, B V between VII and VIII (no appendices internae), and B VI more or less IX.

Influence of temperature

Cultures at 12°C showed a higher mortality than at 3-9°C, the latter all being more or less the same (Fig. 1 and 2). If however, one considers not the age in days but rather the ontological age, an optimum is seen at 9°C (Fig. 3). 50% of all larvae were dead at 9°C in stage VII, 6°C in stage VI, 3°C in stage III and finally at 12°C in stage II. The animals at 12°C showed only in the first stages a high mortality; thereafter the mortality decreased to such an extent that at the end of the experiment the same number of animals survived at 12°C as at 9°C.

The speed of development was extremely temperature dependent (Fig. 5 and 6). While at 3°C an average of 16.6 days was needed between moults, at 12°C only 7.3 days were necessary (Fig. 4).

A similar temperature dependence was perceptible in the feeding rate. At 3°C only half of that was eaten which at 12°C was consumed (Fig. 7). Whereas the number of *Artemia* nauplia eaten increased with the temperature, the total number of food animals necessary between the larval stages, was, at the tested temperatures, not essentially different (Table 1).

Table 1: Total number of *Artemia salina* nauplii fed by laboratory reared larvae of *Pandalus borealis* during the experiment at different larval stages and various temperatures.

zoéal stage	temperature			
	12°C	9°C	6°C	3°C
II	130	145	170	152
III	297	295	365	352
IV	468	446	629	602
V	748	722	1 035	857
VI	1 014	1 074	1 365	-
VII	1 274	1 419	1 615	
VIII	1 664	1 743	-	
IX		2 467		
XI	2 630			

Animals of the same ontological stage reached the same lengths at all temperatures up to stage VIII. Thereafter the small number of specimens disallows a definite conclusion (Table 2). The larvae stages of 1974 were found to have been very much smaller than those of BERKELEY. The larvae cultured in 1975 come closer to the values she found, but are still quite a bit smaller in the later stages. Whereas varying temperatures show no effect on the growth, the improved culture method of 1975 may have brought this increased growth. On the other hand the provenience of the mother animal, one coming from the Farn Deeps, the other from the Skagerrak, may have a bearing on this finding.

The author is^{of} the opinion, that in an optimal culture of *Pandalus* one should start with a water temperature of 9°C. After stage II is reached, the temperature should be gradually increased to 12°C. Shortly before reaching metamorphosis, again a temperature of 9°C should be selected.

Influence of light

Animals kept in total darkness showed no differences to those kept at the same conditions (6°C, 32‰ S, feeding in excess) in a 12 h light-dark rhythm: The number of *Artemia* consumed per larva and day was 15.5 at stage I and 26 at stage VI. The average duration of an intermoult period was 11.3 days. Even growth (see Table 2) and mortality rate corresponded nearly completely.

Influence of salinity

The lowest mortality rate and therefore the salinity optimum was found at 31‰. At higher and lower concentrations the mortality was markedly higher. The early stages of development were the most sensitive (Fig. 8). Larval development is only at salinities lower than 28‰ obviously hampered. Whereas all the animals in concentrations over 30‰ were at stage VI at the end of the experiment, those kept at 28‰ were at stages IV, V and VI (3 larvae). Lower than 25‰ concentrations showed a slightly

Table 2: Length of laboratory reared larvae of Pandalus borealis (tip of rostrum to anterior margin of telson) at different larval stages under varying temperature, salinity, food and light conditions.

The indices give the number of measurements if less than 10

Stage	<u>Temperature</u> water renewal				closed system		<u>Salinities, S^o/oo</u>					<u>Artemia nauplii</u> Larva/day					<u>Dark</u>	<u>Berkeley</u> 1930 Plankton
	12	9	6	3	9	3	34	32	31	28	25	50	20	10	5	1		
II	6.1	6.2	6.5	6.0	6.4	6.5	6.1	6.1	6.1	6.0	5.9	6.3	6.2	5.8	5.6	5.4	6.1	7
III	6.7	6.7	7.0	6.8	7.3	7.1	6.5	6.7	6.5	6.4	6.2	6.8	6.8	6.6	6.2	5.7 ₄	6.6	8-9
IV	7.1	7.0	7.2	7.2	7.8	7.9	7.0	7.1	7.0	6.8	6.4	7.1	7.2	7.0	6.5	5.9 ₁	7.2	
V	7.7	7.9	7.9	7.7	-	8.9	7.3	7.4	7.3	7.1 ₇	6.8 ₄	7.8	7.8	7.3	6.8		8.0	9-10
VI	7.9	8.2	8.2	7.9		9.8	8.2	8.3	8.1	7.5 ₃	-	8.2	8.1	7.7	-		8.1	
VII	8.4	8.6	8.6	-		10.3						8.7 ₁	8.7 ₁	-			8.7	14
VIII	8.9	9.3 ₂	-			↓											9.2	
IX	9.3 ₆	9.8 ₁				10.9												
X	9.8 ₄	10.7 ₁				11.4												
XI	10.3 ₂	11.0 ₁				↓												
ad	-	12.0 ₄				12.4												

reduced growth (Table 2). Also at this concentration a markedly lower food consumption was observed. Below 28°/oo the swimming behaviour of the animals was effected: the larvae were no longer capable to remain floating in the medium, but rather sank constantly to the bottom of the container.

Influence of different quantities of food

In the first stage the larvae can exist for only 6 days without food. Thereafter they die very rapidly (Fig. 9). By the ninth day there are no survivors. In contrast, larvae fed 1 Artemia per larva and day were all dead after 50 days. At this time they had gone through 5 moults, which were morphologically identical to unstarved animals.

The mortality up to the third stage is more or less the same whether one feeds 5 or 20 Artemia per larva and day. After this point there is a higher mortality at 5 and 10 than at 20. At 50 Artemia per larva and day there is a higher mortality up to stage III than by 5 Artemia, 50 thus being above the optimum. Thereafter however it is different: after 30 days after hatching the survival is highest among the most strongly fed animals .

Of the 50 Artemia, 20.2 are eaten at stage I and 24.5 at stage V. In the experiments with 20 Artemia per larva and day 17.8 are eaten at stage I, after that all animals almost without exception are found and consumed. When less than 20 Artemia per larva and day were fed all were found and consumed by the larvae.

The moulting pattern is effected by the nutrition, but not to the extent that one would expect based on the temperature tests. The average time between moults with 50 and 20 Artemia per larva and day is practically identical: 10.6 and 11.0 respectively. Even at only 10 Artemia per larva and day the time of 11.5 days is not markedly different. At 5 and 1 Artemia per larva and day with values of 13.4 and 14.7 days one sees a drastic reduction in the development. The growth shows a similar picture: 20 and 50 Artemia produce the same sized animals. 10 Artemia produces a slightly smaller animal, and at 1 Artemia the larvae in stage IV are not even as long as those of stage II with adequate food (Table 2).

SUMMARY

Larvae of Pandalus borealis were cultured in a laboratory up to the juvenile adult stage. The animals moulted all times before getting adult. The animals were kept in 500 ml glass jars with daily water renewal, in a later experiment in a closed system. The larvae were fed Artemia nauplia.

The optimal culture temperature was shown to be 9°C., above and below which a higher mortality can be seen especially in the first stages. The rate of development increases with the temperature: at 3°C nearly 17 days are needed between moults, at 12°C on the other hand only 7. With decreased temperature the number of Artemia consumed is reduced, but the number needed to reach the same ontological stage is approximately the same.

Animals kept in constant darkness showed the same mortality rates, feeding rates, moulting frequency and growth as those kept in a 12 hour light/dark rhythm.

In these experiments a salinity of 31‰ was found to be optimal. Development and growth as well as feeding rate were disturbed at salinities under 28‰. At these concentrations the swimming behaviour of the larvae is disturbed.

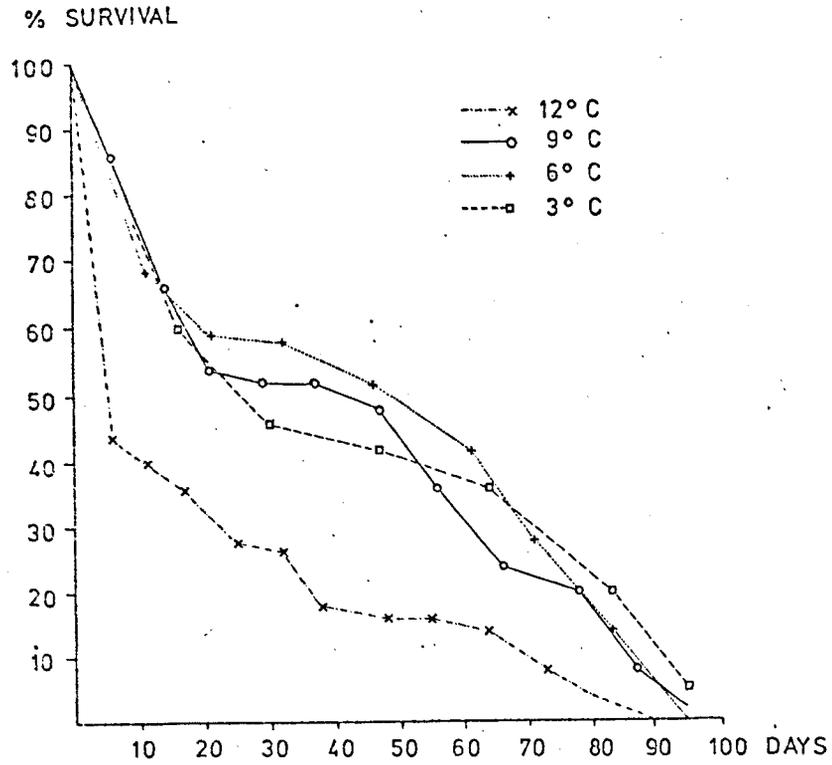
The food requirement in the experiments was 20 Artemia per larva and day, below which a higher mortality rate was seen, the development was hampered, and the linear growth was lessened.

REFERENCES

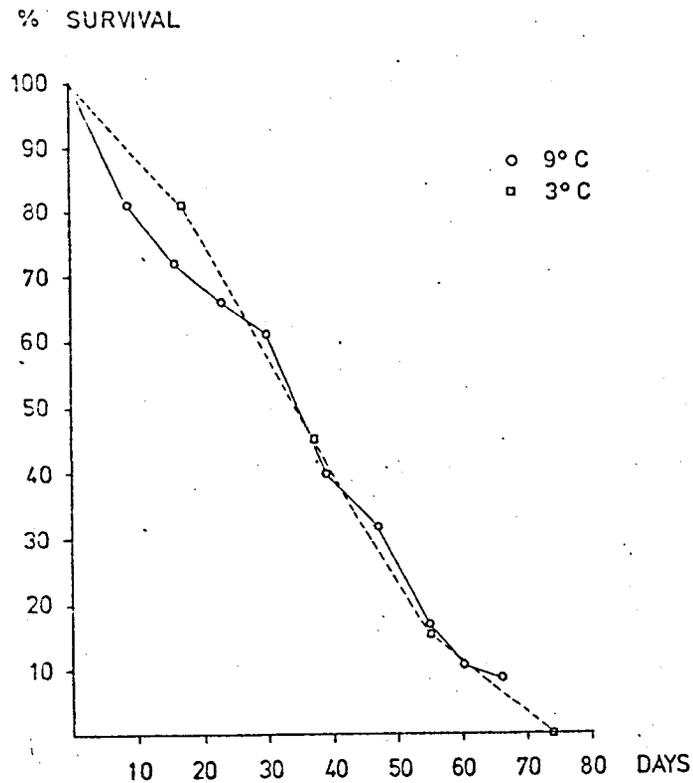
- AKER, E., MEIKNER, R.: On the size and sex composition of Pandalus borealis catches from Farn Deeps and Fladen Ground area between 1965 and 1972. ICES, Shellfish Cmttee, C.M.1972/K:9: 1-16
- BERKELEY, A.A., 1930: The postembryonic development of the common Pandalids of British Columbia. Contr. Canad. Biol. Fish. 6 (6-7):79-163
- LEBOUR, M.V., 1930: The larval stages of Caridion with a description of a new species, C. steveni. Proc. Zool. Soc. Lond. 1930: 181-194

MODIN, J.C. and K.W.COX, Larval development of laboratory reared
1965: Ocean Shrimp, *Pandalus jordani* RATHBUN.
Crustaceana 13 : 197-219

SARS, G.O., 1900: Account of the development of *Pandalus*
borealis.
Rep. Norw. Fish. Mar. Invest. 1 (3):
1-45



1

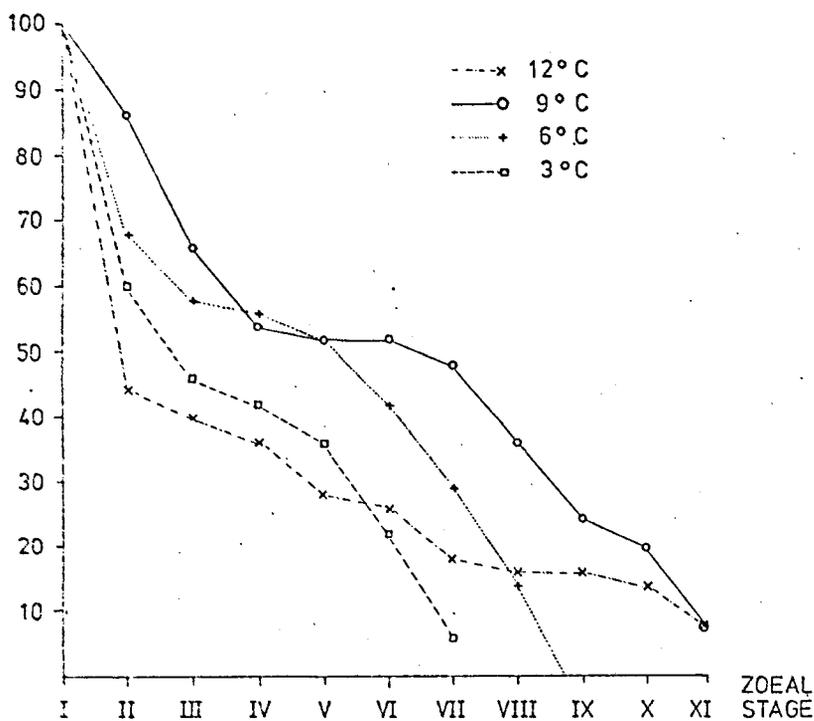


2

Figure 1 and 2
Survival of laboratory reared larvae of Pandalus borealis at different temperatures in relation to the time.

Fig. 1: Experiments made in 1974.

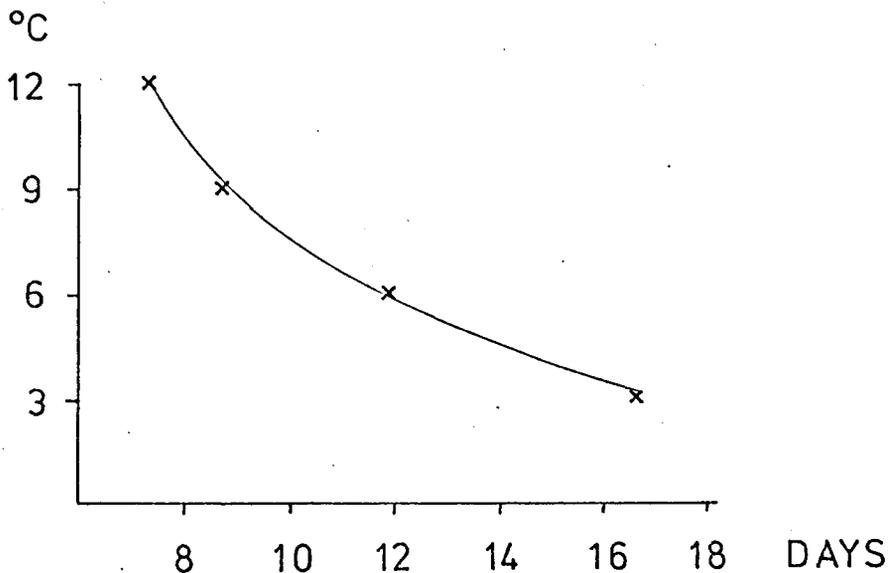
Fig. 2: Experiments made in 1975.



3

Figure 3

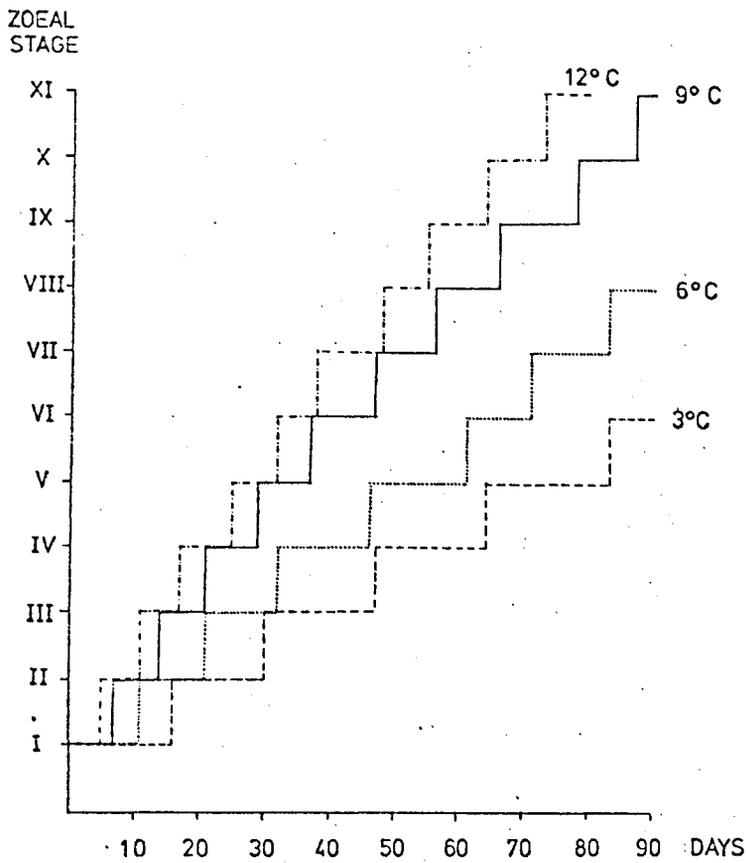
Survival of laboratory reared larvae of Pandalus borealis at different temperatures in relation to the ontogenetic age.



4

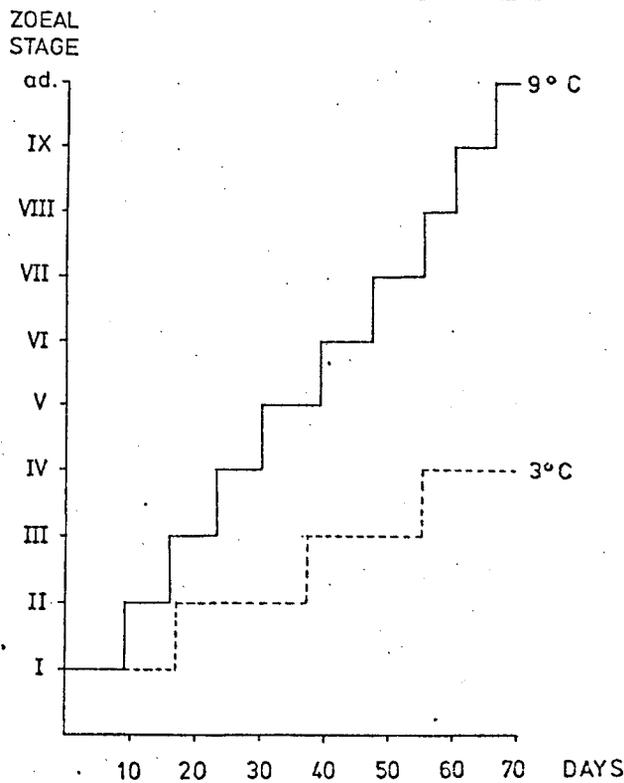
Figure 4

Average time needed between moults of laboratory reared larvae of Pandalus borealis at various temperatures.



- 13 -

5



6

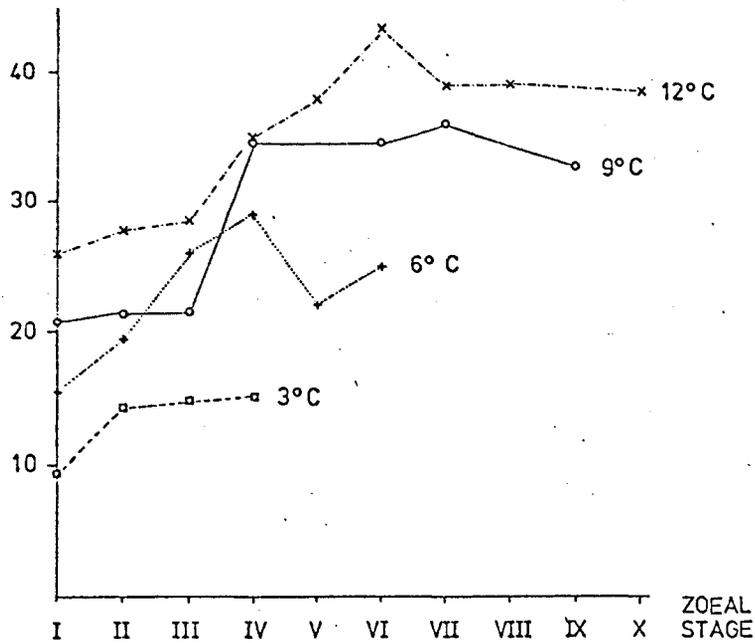
Figure 5 and 6

Stage of development of laboratory reared larvae of Pandalus borealis at different ages and temperatures.

Fig. 4: Experiments made in 1974.

Fig. 5: Experiments made in 1975.

ARTEMIA
NAUPLII



7

Figure 7

Feeding rate of laboratory reared larvae of Pandalus borealis at different developmental stages and varying temperatures.

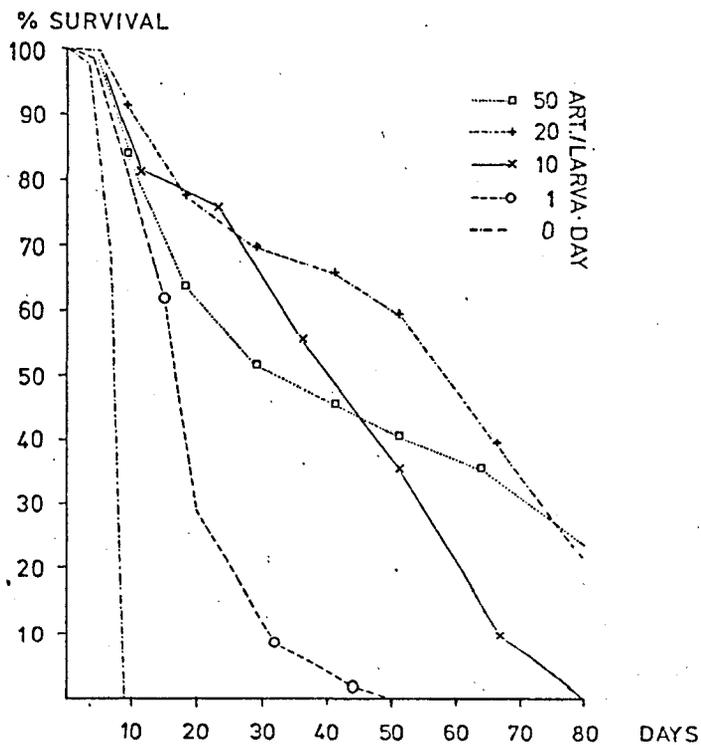


Figure 8

Survival of laboratory reared larvae of Pandalus borealis fed with different quantities of Artemia salina nauplii.

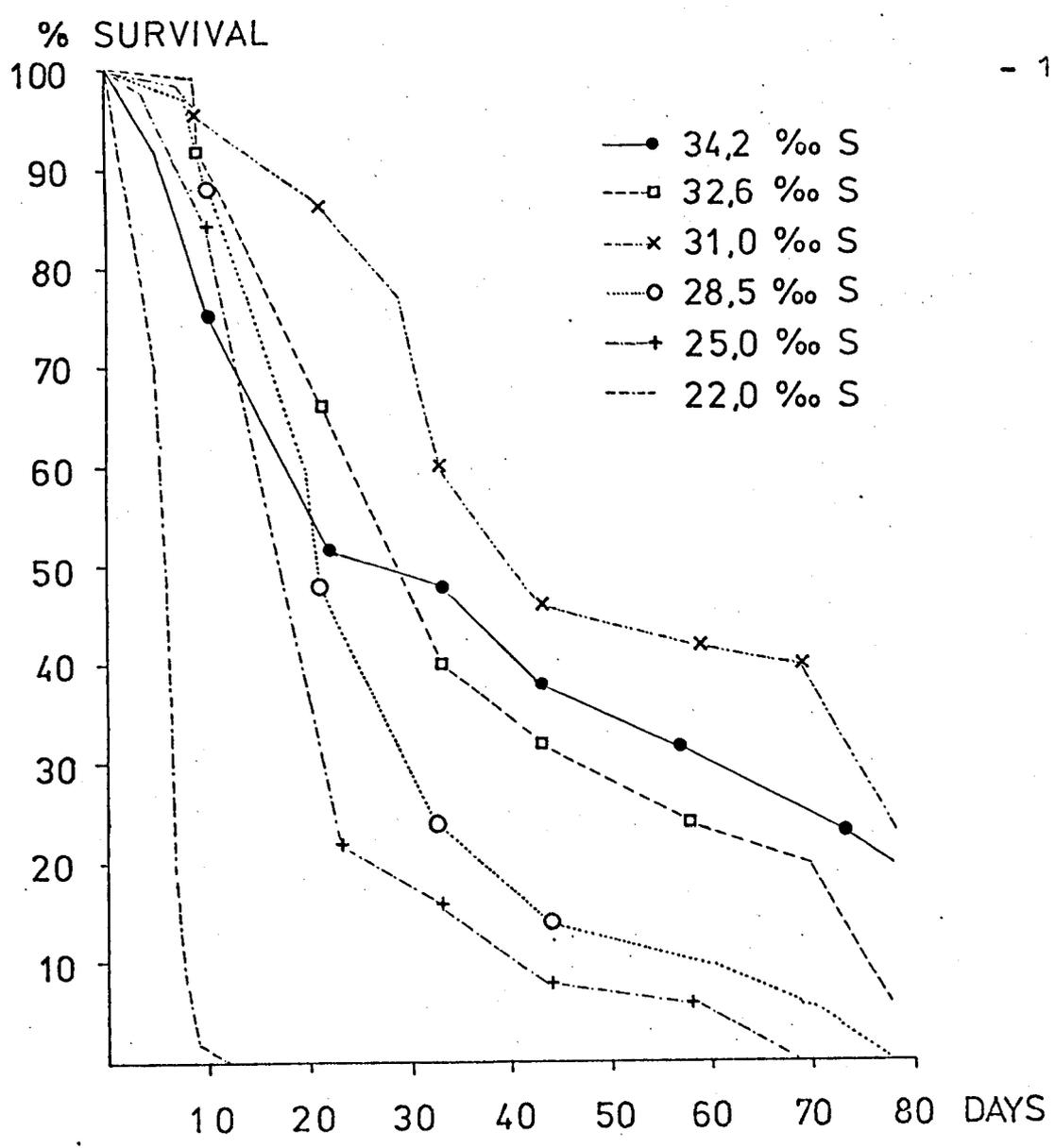
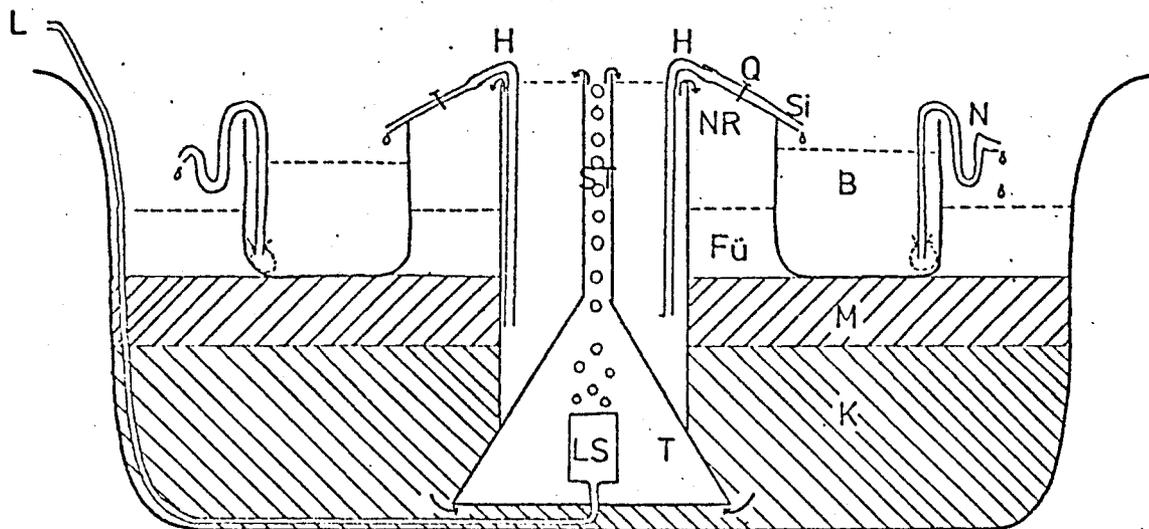


Figure 9
Survival of laboratory reared larvae of Pandalus borealis at different salinities.

Culture apparatus for *Pandulus* larvae.

Filtered water is dropped into the glass jar (B), in which the larvae are kept. Using a water-leveler (N), water is sucked from the bottom of the jar without changing the water level. The water then reaches the outer water (Fü) and passes through a 3 cm thick layer of crushed seashells (M) and a 10 cm thick layer of coarse gravel (K) (diameter 2-3 mm) into the filter-funnel (T). Air bubbles force the water through the funnel tube (ST) and into the surrounding reserve tube (NR), which is securely fastened to the funnel. Most of the water runs from here into the surrounding outer water (Fü) and thus ensures an adequate current and oxygen supply in the filter. A small amount of the water is brought via the siphon (H) through the silicon hose (Si) into the glass jar. This can be regulated by means of a tap (Q).



Description of the larval Development of laboratory reared
Pandalus Borealis

FIRST ZOEAL STAGE

Rostrum - slender, spinyform, without denticles .

Eyes - immobile, not stalked.

Antennule - basal portion unsegmented, bearing distally a conical projection representing the outer flagellum, tipped with one long, one short and two medium size setae.

Antenna - Scale distally divided into 5 segments, fringed with 15 plumose setae. At the base of the segments one stout simple spine. Basal portion of the antenna undivided, bearing distally at the base of the flagellum a spine. Flagellum half as long as scale, distally with a spinous seta.

Mandibles - left mandible with 4, right with 3 incisivi and 3 praemolares between incisor- and molar progress. Left instead of praemolares one short stout spine in the same position.

Maxillula - proximal lobe, the coxopodite, with 4 long heavy plumose setae and one smaller one. Median lobe, basipodite with 9 serrated stout spines. On the lateral margin of the basipodite is the endopodite with 3 terminal and 2 subterminal plumose setae.

Maxilla - coxopodite with 14 plumose setae on the proximal lobe and 4 on the distal lobe. Basipodite: two lobes with 7 spinous, serrate, plumose and also simple setae on each, fringing the terminal margin. The oval lamelliform exopodite is fringed with 10 heavily plumose setae.

1st maxilliped - coxopodite with 6 setae on the inner margin, basipodite with 14 respectively. Endopodite divided into 4 portions, bearing 10 setae together, those 4 of the distal segment not being plumose. Exopodite not segmented, provided with 5 long heavily plumose natatory setae.

2nd maxilliped - coxopodite on the inner margin with 2 little spines and distally 2 long plumose setae, basipodite with 8 plumose and spinous ones. Endopodite divided into 5 portions, provided with 16 setae all together. Exopodite twice as long as endopodite, bearing 13 swimming setae.

3rd maxilliped - similar to second, but endopodite nearly as long as exopodite. Number of setae: endopodite 12, exopodite 15 natatory setae, protopodite only on the distal lobe, the basipodite, 4 sparsely plumose ones.

Pereiopods - fleshy rudimentary appendages, first to third biramous, fourth and fifth uniramous. (Not to be found on exuviae).

Pleopods - no pleopods.

Telson - not distinct from sixth abdominal segment. Terminal margin with 14 plumose setae. Uropods can be seen as undeveloped bud like rudiments enclosed of the telsons integument (not on exuviae).

SECOND ZOEL STAGE

- 18 -

In this and the following stages descriptions will only be given of those appendages showing structural changes to the proceeding stages.

Eyes - mobile, stalked.

Antennule - basal portion consists of three segments. Basal segment with one large ventral spine, one long plumose seta and several short terminal ones. The distally following segment is shorter, bears 2 long plumose setae at the inner margin and several terminal ones. The terminal segment is provided with 7 plumose long and some short setae. The little inner flagellum bears only one long heavily plumose seta, the bigger outer flagellum 7 terminal and two subterminal setae, only one terminal being plumose.

Antenna - scale with 26 heavily plumose setae. Distal segments of the scale begin to disappear. Flagellum with two segments, bearing 3 short setae on the distal greater one. Basal portion of the antenna consists of two segments.

Mandibles - left one with 4 serrate incisivi and one new more spiny one. 7 little praemolares. Right one nearly unchanged. Molares have increased in number on both mandibles.

Maxillule - coxopodite with 10 terminal and subterminal plumose setae of different length. Basipodite with 8 stout terminal and 2 more slender subterminal spines. Endopodite remains unchanged in this and all following larval stages.

Maxilla - exopodite has increased in size and number of setae, now 16 to 17 heavily plumose ones.

1st maxilliped - slight increase in number of setae: protopodite with 9 on the basal and 18 on the distal portion, exopodite with 7 swimming setae. Endopodite unchanged.

2nd maxilliped - coxopodite bears only 1 plumose seta. Exopodite with 14 setae.

3rd maxilliped - endo- and exopodite of same length. Exopodite bears 16 natatory setae.

Pereiopods - first and second in size and setation very similar to 3rd maxilliped. Exopodite of the third smaller than endopodite. Fourth and fifth are uniramous, bearing 3 and 5 setae resp. on the two distal segments.

Fleopods - simple little buds.

Telson - 16 plumose setae on terminal margin. Uropods not free.

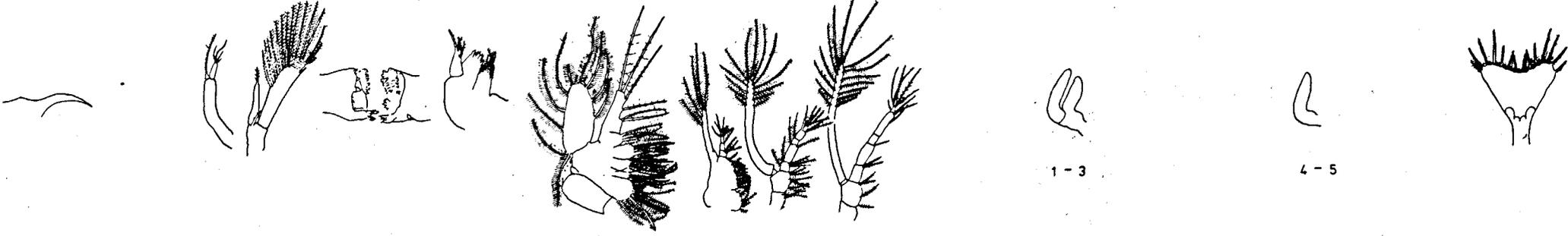
THIRD ZOEAL STAGE

Rostrum - on the base, on carapace, 1 or 2 little teeth.

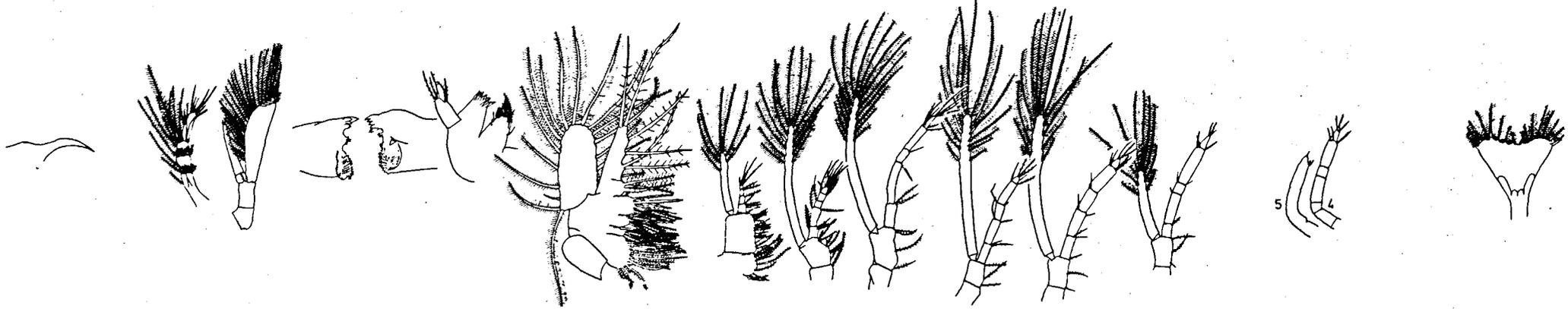
Antenna - segmentation of the scale decreases to 2 or 3 indistinct little distal joints. Flagellum distinctly divided into 5 segments, some more indistinct joints are to be seen.

Mandibles - one additional serrate spine appears on the incisor progress of left one. Some slender spinules appear

FIRST ZOEAL STAGE

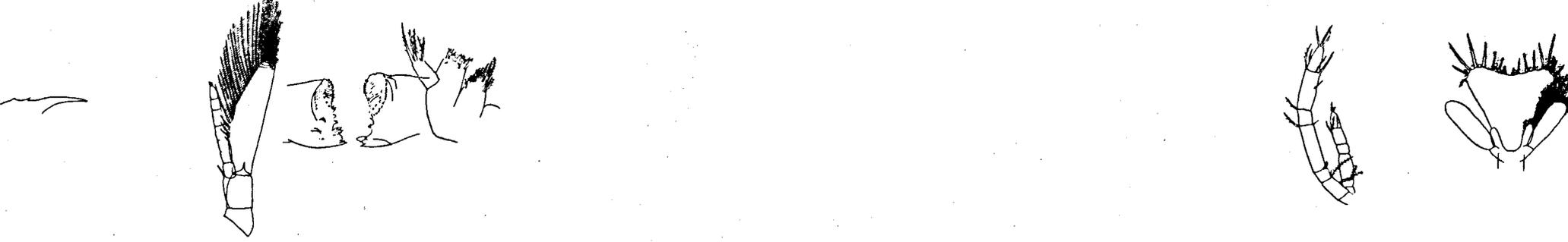


SECOND ZOEAL STAGE



-19-

THIRD ZOEAL STAGE



ROSTRUM

ANTENNULE ANTENNA

MANDIBLES

first
MAXILLAE

second

first second third
MAXILLIPEDS

first second third
PEREIPODS

fourth and fifth
PEREIPODS

TELSON

between praemolares and the molar area.

Maxillula - slight increase in number of setae or spines on coxo and basipodite.

Maxilla - proximal lobe of coxopodite with 16 instead of 14 setae. Exopodite proximal somewhat extended, fringed with 19 to 21 heavily plumose setae.

Pereiopods - fourth one now very similar to the endopodites of the first to third one. Fifth resembles to the fourth of the previous stage in size and setation, but it bears one seta on the distal margin of the basipodite.

Telson - distinctly divided from 6th abdominal segments. Uropods are free now, the outer ventral pair reaching two third of the length of the telson, bearing 25 heavily plumose setae. The inner dorsal pair reaches the maximum length of one half of the ventral ones, fringed with 8 to 9 shorter plumose setae.

FOURTH ZOEAL STAGE

Rostrum - 3 teeth on the base.

Antennule - Basal segment with 6 little setae on the base of the outer margin and 5 long plumose ones along the inner margin. Outer flagellum undivided with 6 terminal and 3 subterminal simple setae.

Antenna - scale distally now unsegmented with a rounded distal end. 30 plumose setae. Flagellum has increased in length, not in number of segments. The segments of the distal end bear 1 to 2 very little spinules each.

Maxillula - setation increases. Coxopodite has 14 terminal and subterminal setae of different length, basipodite 4 subterminal and 10 terminal serrate spines.

Maxilla - proximal segment of coxopodite with 18 setae now. Exopodite proximal distinctly expanded, fringed with 25 long heavily plumose setae.

1st maxilliped - number of setae of the protopodite and endopodite increases : coxopodite 11, basipodite 23. On the endopodite 3 additional setae appear on the outer margin.

3rd maxilliped - 23 to 27 setae on the two distal segments of the endopodite, that is twice the number of those at the 3rd stage.

Pereiopods - increase of setation similar to 3rd maxilliped. The second one has a terminal chela on its endopodite. Fourth and fifth one now of nearly the same length as the third.

Pleopods - first abdominal segment with still no pleopod. The others are biramous, not segmented, without setae, without appendices internae.

Telson - whilst in previous stages an equilateral triangle in shape, the distal margin gets a bit shorter, the lateral ones longer. Distal margin with still 14 setae. On each of the lateral sides 1 short stout spine. Uropods increase in size and setation. The ventral one is as long as the telson (setae thought dissected), the dorsal one reaches three quarters of that length. They are densely fringed with 32 and 16 plumose setae respectively.

FOURTH ZOEAL STAGE

FIFTH ZOEAL STAGE

-21-

SIXTH ZOEAL STAGE



ROSTRUM

ANTENNULE

ANTENNA

MANDIBLES

first

second

MAXILLAE

first

second

third

MAXILLIPEDS

first

second

third

fourth

fifth

PEREIPODS

PLEOPODS

TELSON

FIFTH ZOEAL STAGE

Rostrum - 4 to 5 dorsal teeth.

Antennule - number of plumose setae on the inner margin of the basal portion has increased to 7 to 8. Outer flagellum not segmented, equipped with 4 groups of simple setae, one terminal and two subterminal, with 2 to 4 setae in each group.

Antenna - scale fringed with about 34 plumose setae. Flagellum with 8 to 9 segments, each bearing 1 to 3 little setulae on its distal margin. Flagellum as long as scale.

Maxillule - coxopodite with 15 setae of different length, basipodite with 10 terminal and 5 subterminal spines.

Maxilla - proximal extension of exopodite increases in length. Exopodite: 32 long plumose setae. Basal segment of coxopodite: 20 setae.

Thoracopods - the endopodites increase in proportion to the length of the larva. The two terminal segments get much more setose. The chela of the 2nd pereopod is more developed, but still shows no articulation for manipulation.

Telson - somewhat more spatula shaped. One pair of spines is located on the lateral margins about one third of the length of the telson from its distal margin. Another pair is near the distal margin. There are 12 terminal setae. The ventral and dorsal uropods bear 35 and 23 heavily plumose setae respectively.

SIXTH ZOEAL STAGE

This stage is very similar to the previous one.

Rostrum - 7 to 8 teeth.

Antenna - 1 to 2 more setae on the scale. Maximum number of segments of the flagellum was 14.

Antennule - inner flagellum tipped with two more little simple setae, outer flagellum two segmented, distal segment bearing 6 simple setae, proximal one three groups of setae, one at the distal end and two subterminal ones on the inner lateral margin. Each group of setae consists of 2 to 3 setae.

Fleopods - first one uniramous unsegmented, the others are segmented now.

Telson - 3 pairs of lateral spines, one near the terminal margin. Dorsal and ventral uropods bear 25 resp. 35 plumose setae on the margin and a lot of little simple setae on the dorsal and ventral surfaces.

SEVENTH ZOEAL STAGE

Rostrum - 8 to 9 teeth.

Antennula - basal portion with a new group of seven plumose setae near the proximal end. Inner flagellum three segmented, distal segment tipped with one heavily plumose and 3 little simple setae.

Antenna - scale with 35 to 38 plumose setae. Flagellum reaches nearly twice the length of the scale, consists of maximal 21 segments, each provided with 1 to 6 little setulae on its terminal margin.

Mandible - left one: four long spinules occur on the base of the incisor progress. Between these and the molar progress are 4 more denticles. Right mandible with 5 little praemolar progresses. On the anterior margin of the molar region a well developed cutting edge.

Maxillula - the coxopodite bears now 18 setose and serrate setae of different length, the basipodite 12 terminal and 8 to 10 subterminal spines.

Maxilla - coxopodite, basal portion, provided with 21 to 24 setae, both portions of the basipodite with 11 setae each. The proximal extension of the exopodite extends to the base of the coxopodite. Exopodite fringed with 40 to 45 heavily plumose setae.

1st maxilliped - protopodite gets much more setose, 33 to 38 setae on both portions.

3rd maxilliped - the two distal segments of the endopodite with about 5 to 8 additional setae, exopodite with 19 to 21 natatory setae.

1st and 2nd pereopod - on the first a little claw is developing too from propodal and dactylar segment of the endopodite. Endo- and exopodite of nearly same length. Endopodites about one third shorter than pereopods 3 to 5. Exopodites with about 19 and 17 natatory setae respectively.

3rd pereopod - exopodite, equipped with 15 swimming setae, as long as that of the 2nd pereopod, two thirds of the length of the third endopodite. Setation of the endopodites, especially the propodites, increase markedly.

4th and 5th pereopod - nearly identical to the endopodite of pereopod 3.

Telson - lateral margins almost parallel. Ventral and dorsal uropods setation has increased to 40 and 30 respectively.

EIGHTH ZOEAL STAGE

Very similar to the preceding stage. Significant morphological changes occurred on:

Rostrum - 10 to 12 teeth.

Antennule - outer flagellum three segmented, bearing five groups of olfactory setae.

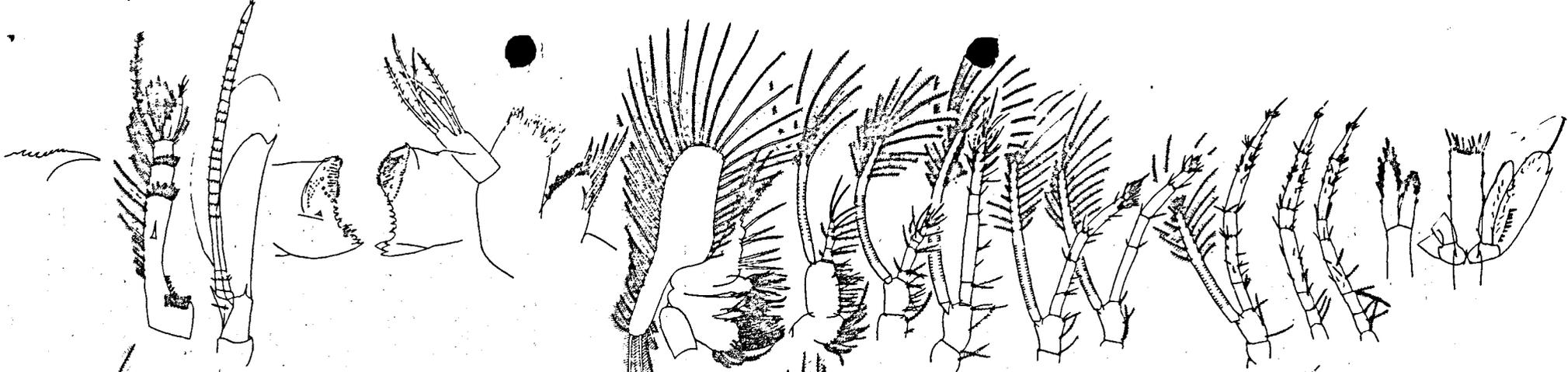
Mandibles - on the base of the incisor progress of the left mandible 5 stout spines. Right one with 6 praemolar progresses.

Maxilla - exopodite with 45 to 50 setae.

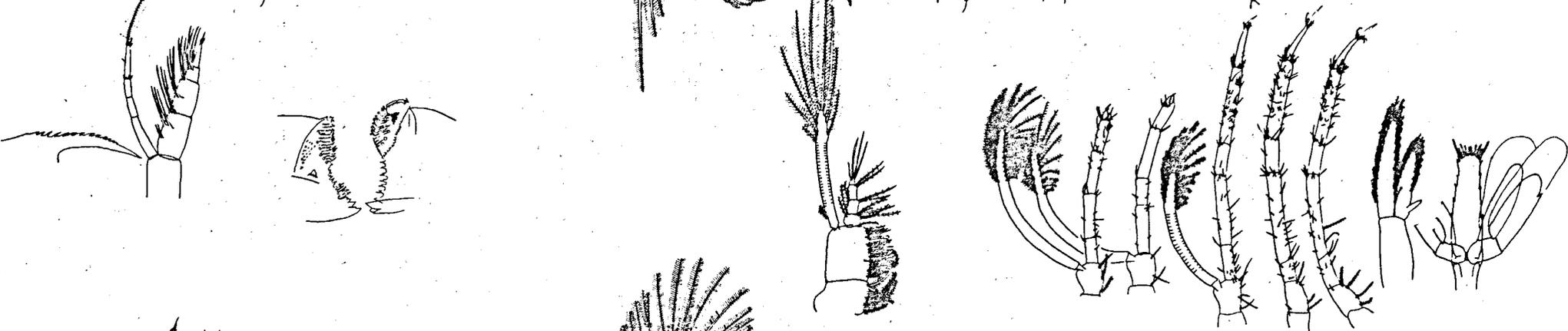
Thoracopods - some additional setae.

Pleopods - get heavily setose, appendices internae present, first one without the latter and still uniramous but well developed.

SEVENTH ZOEAL STAGE

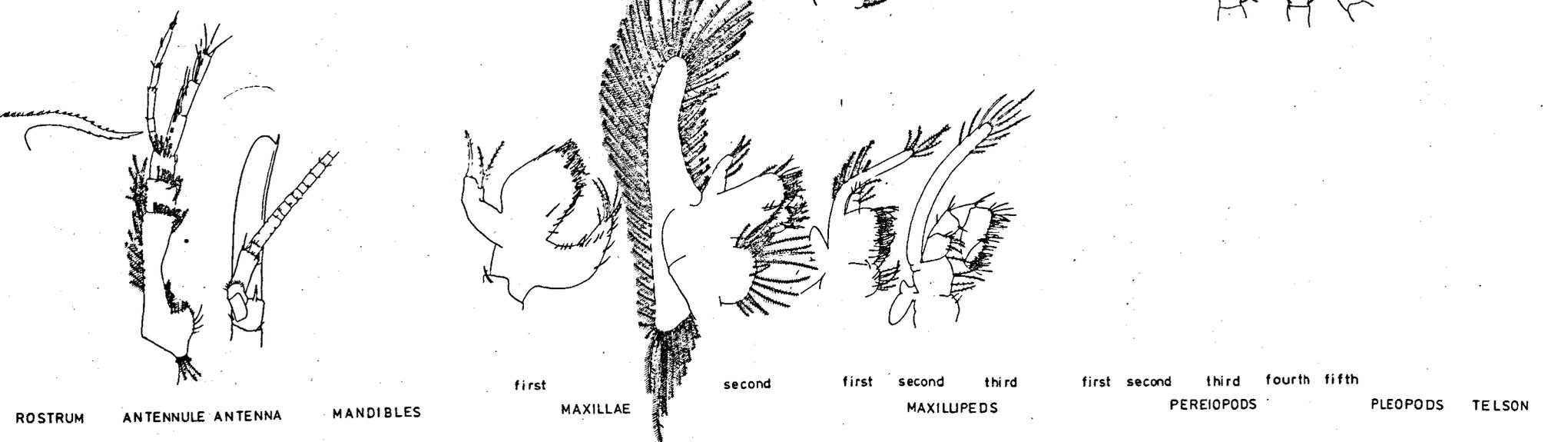


NINTH ZOEAL STAGE



-24-

FIRST ADULT STAGE



ROSTRUM

ANTENNULE ANTENNA

MANDIBLES

first
MAXILLAE

second

first second third
MAXILLIPEDS

first second third fourth fifth
PEREIOPODS

PLEOPODS TELSON

Telson - somewhat narrower towards the tip than to the base. 4 pairs of lateral spines and 10 terminal spines. Both uropods of nearly the same length, densely fringed with about 37 and 45 setae respectively.

NINTH ZOEAL STAGE

Rostrum - 13 to 14 dorsal teeth, up to 7 rather indistinct ventral teeth.

Antennule - inner flagellum 4-segmented, as the outer is too. The latter bears 6 groups of aesthetes along its inner margin.

Antenna - up to 38 segments in the flagellum. About 48 setae on the scale.

Maxillula - endo and coxopodite unchanged, basipodite with 15 stout terminal spines and 13 subterminal and 3 lateral spinules.

Maxilla - Basal portion of coxopodite with 23 to 24 setae, the distal one with one additional, thus being 5 setae. Basal and distal portion of basipodite with 15 resp. 12 setae. Exopodite heavily equipped with about 55 setae.

1st maxilliped - protopodite heavily equipped with 40 to 45 setae. On the base of the exopodite on the outer margin 1 to 3 plumose setae.

Pereiopods - the claw of the second gets nearly adult, while that of the first remains as in stage VII. The endopodite of the third pereiopod has twice the length of the exopodite and is heavily setose. The fourth and fifth are of the same length and setation.

Pleopods - inner lamella with appendices internae and 14 to 18 plumose setae, outer ones with 24 setae. First pleopod with a little bud representing the inner lamella, but no appendices internae.

Telson - 5 lateral pairs of spines and 10 distal setae, the innerst as big as the other ones. Ventral and dorsal uropods bear 50 heavily plumose setae both.

LATER ZOEAL STAGES

A tenth and eleventh zoeal stage has been observed. These stages are nearly identical to the stage IX. However, a slight increase of the numbers of setae can be found on most of the extremities, especially on the antennal scale, the pleopods, the uropods, but no structural change of importance will be found.