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Experimental studies on the larval development of the shrimps *Crangon crangon* and *C. allmanni*

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ABSTRACT: Larvae of the shrimps *Crangon crangon* L. and *C. allmanni* Kinahan were reared in the laboratory from hatching through metamorphosis. Effects of rearing methods (larval density, application of streptomycin, food) and of salinity on larval development were tested only in *C. crangon*, influence of temperature was studied in both species. Best results were obtained when larvae were reared individually, with a mixture of *Artemia* sp. and the rotifer *Brachionus plicatilis* as food. Streptomycin had partly negative effects and was thus not adopted for standard rearing techniques. All factors tested in this study influenced not only the rates of larval survival and moulting, but also morphogenesis. In both species, in particular in *C. crangon*, a high degree of variability in larval morphology and in developmental pathways was observed. Unsuitable conditions, e.g. crowding in mass culture, application of antibiotics, unsuitable food (rotifers, phytoplankton), extreme temperatures and salinities, tend to increase the number of larval instars and of morphological forms. The frequency of moulting is controlled mainly by temperature. Regression equations describing the relations between the durations of larval instars and temperature are given for both *Crangon* species. The number of moults is a linear function of larval age and a power function of temperature. There is high variation in growth (measured as carapace length), moulting frequency, morphogenesis, and survival among hatches originating from different females. The interrelations between these different measures of larval development in shrimps and prawns are discussed.

INTRODUCTION

The common bay shrimp (or brown shrimp), *Crangon crangon*, is intensively exploited by coastal fisheries in the North Sea, and thus plays an important economic role in this region (for recent reviews on life cycle, production, and landings see e.g. Boddeke & Becker, 1979; Tiews, 1983; Kuipers & Dapper, 1984). *C. crangon* is also one of the most frequent prey items for commercially exploited fish populations such as plaice, flounder, and cod (Müller, 1968; Arntz, 1971; Summers, 1980). Its high abundance in shallow coastal areas, particularly in the Wadden Sea, makes it also one of the key predators of benthic animals (Gerlach & Schrage, 1969; Reise, 1979), possibly including O-group flat fish (Bergman et al., 1976).

The closely related species *C. allmanni* is smaller and less abundant. Due to their similarity, however, these two species might have been often confused, so that the actual

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importance of *C. allmanni* may be higher than presumed from the relatively scarce information existing on its ecology and life cycle (Allen, 1960; Creutzberg & Leeuwen, 1980).

In contrast to the extensive literature on many other shrimp species, only very little laboratory data are available on development and growth of *C. crangon* and *C. allmanni*. Descriptions of larval morphology were based mainly on material isolated from plankton samples (Du Cane, 1839; Ehrenbaum 1890; Sars, 1890; H. C. Williamson, 1901, 1915; Webb, 1921; Lebour, 1931; D. I. Williamson, 1960; Smaldon, 1979). The morphological development of laboratory-reared *C. crangon* from hatching to metamorphosis has only recently been accomplished (Gurney, 1982). Comparable studies on *C. allmanni* have not been available. In an unpublished thesis, Criales (1985) described and compared laboratory-reared larvae of both *C. crangon* and *C. allmanni* (these morphological descriptions will be published elsewhere). Influence of ecological factors on larval survival has been studied only in *C. crangon:* salinity (Broekema, 1942), temperature (Rochanaburanon & Williamson, 1976), light (Dalley, 1980), and heavy metals (Connor, 1972).

The present paper reports on effects of laboratory rearing techniques (larval density, application of antibiotics, food), and ecological variables (temperature, salinity) on larval development and survival in *C. crangon,* with preliminary results on *C. allmanni.*

After detailed morphological descriptions of the larval stages of both *Crangon* species had become available (Criales, 1985), effects of methodological and ecological factors could be measured in conjunction with qualitative (morphological) and quantitative criteria (rates of moulting and survival). It is well known from many caridean shrimp species that various environmental factors can influence the number of premetamorphic moults and thus, the rate of morphogenesis (for review of literature see Knowlton, 1974; Rochanaburanon & Williamson, 1976). Variation in larval development was found also in the study by Gurney (1982) on *C. crangon,* but the author considered "additional stages" as a laboratory artifact and did not include them in the morphological descriptions (Gurney, pers. comm.). Rochanaburanon & Williamson (1976) have also suggested that the larval development of *C. crangon,* unlike that of other caridean species may be uninfluenced by environmental factors. Criales (1985), however, found considerable morphological variation in the larval development of *C. crangon* and *C. allmanni* both in laboratory cultures and in field samples from the German Bight. This variation in development was studied in larvae reared individually under various experimental conditions.

MATERIAL AND METHODS

Obtaining and handling of larvae

Ovigerous female *Crangon crangon* were dredged from 2–8 m depth near the island of Helgoland and off the Wadden Sea coast (St. Peter-Ording). *C. allmanni* was obtained from a depth of 20–40 m southeast of Helgoland ("Tiefe Rinne"). All females were maintained separately in flow-through aquaria with filtered seawater, until larvae could be collected in sieves (mesh size: 90 µm) from the overflow. Actively swimming larvae were pipetted to rearing containers (see below) within a few hours after hatching.

All larvae were reared at constant temperature in 1 µm-filtered seawater

(30–32 ‰ S). Rearing of individual larvae was conducted in numbered vials with 20 cm^3 of water, and mass rearing experiments in bowls with 500 cm^3. Except in an experiment on the influence of larval density, these bowls were stocked with an initial number of 50 larvae. A preliminary experiment with different frequencies of water changing (daily, every 2, 3, and 4 days) showed significant negative effects only at the lowest frequency (every 4 days). Thereafter, water and food were changed regularly every second day in all experiments. Larvae were checked at daily intervals for moults and mortality. When moults occurred, larvae were grouped together according to their actual stage, so that all larvae in a bowl had the same age within a given instar.

Food

Various types of food and mixtures thereof were tested in this study: (1) freshly hatched *Artemia* sp. (San Francisco Bay Brand); (2) rotifers *(Brachionus plicatilis);* (3) phytoplankton (the diatoms *Skeletonema costatum* and *Thalassiosira rotula*).

Artemia sp. nauplii were given at an initial density of ca 10 individuals · cm^{-3}. Rotifers were cultivated in glass bottles with 10 dm^3 filtered seawater and yeast suspension. Prior to adding them as food to larval cultures (at an initial density of ca 30 individuals · cm^{-3}), they were incubated for at least 15 min in a flagellate suspension *(Dunaliella tertiolecta),* in order to enrich them with algal matter. Diatoms were cultivated at 10 °C in autoclaved seawater with F/2 medium (Guillard & Ryther, 1962) and an addition of silicate (1.47 $\mu gat \cdot dm^{-3}$). They were given to shrimp larvae at initial concentrations of 100 *(S. costatum)* and 5 *(T. rotula)* cells · mm^{-3} (densities checked by the Utermöhl method). All concentrations given for single food items were the same for food mixtures.

When no other information on larval food in a particular experiment is given (i.e. in all but food tests), a mixture of *Artemia* sp. and *B. plicatilis* was given as standard food.

Antibiotics

Three concentrations (10, 25, and 50 $mg \cdot dm^{-3}$) of streptomycin sulfate were tested at 12 °C in cultures with individually reared *C. crangon* larvae (25 individuals per concentration). The intermediate amount was added to mass cultures at three different temperatures (12°, 15°, 18 °C), with 3 replicates (50 larvae each) per experimental condition.

Nomenclature of larval stages

The instars (or stages) of larval development are generally designated as "zoea I", "zoea II", etc. Since morphological variations arise after the second moult (i.e. in the zoea III), different larval forms have to be distinguished in all instars later than zoea II. Detailed morphological descriptions of these forms were given by Criales (1985) and will be published elsewhere. In the present study, a relative scale of the degree of development is sufficient for the detection of experimental effects on shrimp larvae. The letter "a" designates the most " advanced" form found within a given instar. These forms are generally similar to those described by Gurney (1982). The subsequent letters, in

alphabetical order, refer to larval forms which are morphologically less developed. For example, a zoea IIIa has uropods with fully developed endo- and exopodites; in the zoea IIIb, the endopodites of the uropods are less developed, ca. half the length of the exopodites, and with little terminal setation (1–4 setae); in the zoea IIIc, the endopodites are rudimentary and oval shaped, and the exopodites lack a spine at the distolateral edge which is present in the two more advanced forms; the zoea IIId form has no uropods at all.

Statistical procedures

Statistical treatment of experimental data followed that of Anger & Dawirs (1981).

RESULTS

Larval density

Table 1 shows development duration of the first five larval stages in relation to initial density. Later instars are not included, because metamorphosis to the first juvenile occurred after 5–7 larval stages. There was a slight tendency toward increasing development duration with increasing rearing density. This presumed crowding effect, however, was not statistically significant. Mortality rates did not show clear trends either.

Since the technique of mass rearing is necessary for obtaining sufficient material to measure larval biomass and body composition, the highest density was considered acceptable for such purposes in later experiments with both *Crangon* species.

The tracing of developmental pathways, however, requires individual rearing. A comparison of the two standard techniques (mass rearing with 50 larvae per bowl vs. individual rearing in vials of an equal number of larvae) revealed again similar mortality and moulting rates, but differences in morphological development (Table 2). In mass culture there was a clearly higher frequency of stunted forms than in individually reared larvae. This tendency occurred from the zoea III and persisted until metamorphosis. This finding suggests that larval morphology (provided the number of moults, i.e. the instar, is known) is a more sensitive indicator of environmental conditions than mortality or moulting rates.

Table 1. *Crangon crangon*. Duration of development (days; mean ± 95 % confidence intervals) in larval stages I–V, in relation to initial density

Larval density		Duration of development (days)				
Individuals per 500 cm^3	cm^3 per individual	Zoea I	Zoea II	Zoea III	Zoea IV	Zoea V
12	41.7	5.5 ± 0.3	5.4 ± 0.3	6.0 ± 0.8	6.0 ± 0.8	6.3 ± 0.9
15	33.3	6.1 ± 0.3	5.5 ± 0.4	5.8 ± 0.7	6.2 ± 0.8	6.3 ± 0.8
25	20.0	5.9 ± 0.4	5.6 ± 0.4	5.9 ± 0.7	6.3 ± 0.8	6.7 ± 0.9
50	10.0	6.0 ± 0.3	5.8 ± 0.4	6.1 ± 0.6	6.2 ± 1.0	6.8 ± 1.0

Table 2. *Crangon crangon*. Frequency (%) of different morphological forms in individually and mass reared larvae

Larval form	Rearing technique	
	Individual	Mass culture
III a	33	13
III b	42	40
III c	25	33
III d	–	13
IV b	60	15
IV c	30	55
IV d	10	30
V a	50	20
V b	50	60
V c	–	20
VI a	50	20
VI b	50	80

Antibiotics

The first experiment comprised sets of 25 individually reared larvae under three different streptomycin concentrations and a seawater control (without antibiotics). Survival rates and occurrence of larval moults are shown in Figure 1. It is obvious that the highest streptomycin concentration (50 mg·cm^{-3}) had toxic effects: a decrease of survival and a delay of moulting. Lower concentration had no statistically significant influence on these criteria, but did affect the developmental pathways (Fig. 2). In the

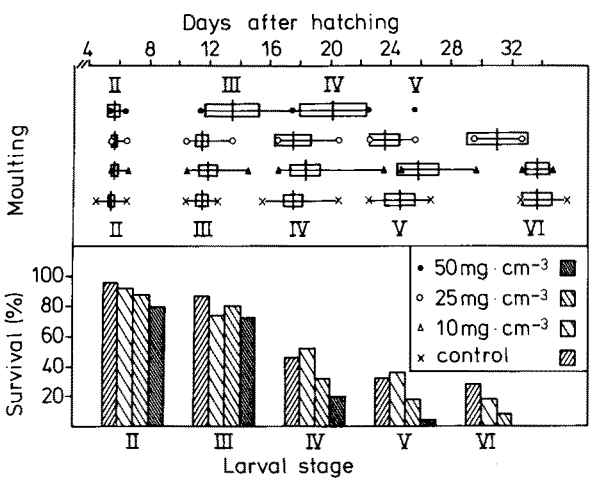

Fig. 1. *Crangon crangon*. Time of moulting (days after hatching; mean ± 95 % confidence intervals, range between minimum and maximum) and rate of survival (%) in larvae reared without (= control) and with streptomycin (three concentrations)

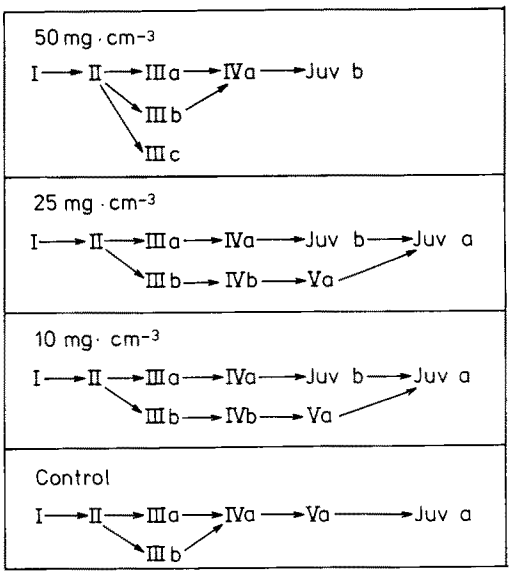

Fig. 2. *Crangon crangon*. Pathways of larval development with and without streptomycin (cf. Fig. 1)

control there were five larval stages followed by a normal juvenile (called "Juv a"), and only little morphological variation occurred (in stage III). Streptomycin caused increased variation with more stunted forms, which showed higher mortality than the more advanced ones. The zoea IIIc larvae, occurring only at the highest concentration, were unable to develop any further and died. The zoea IIIb also had a low survival rate (in all experiments; cf. Fig. 1: drop of survival before stage IV).

In all experiments with streptomycin there was also a disturbance of the metamorphic process. Some larvae moulted from the zoea IVa directly to a stunted juvenile ("Juv b"). It still had some larval characters besides its generally juvenile morphology (Criales, 1985). Most (at the highest concentration, all) of these abnormal individuals died, although some developed successfully to the normal juvenile ("Juv a") which usually originated from a zoea Va.

Another experiment was conducted to find out if streptomycin could improve the results of mass rearing, in particular at higher temperatures. Only the intermediate concentration (25 mg · cm^{-3}) was tested, since the higher concentration had clearly negative effects and the lowest one was considered ineffective. Larvae were reared communally in bowls at constant 12°, 15°, and 18 °C, with and without antibiotics.

Development (moulting) rate was, in this experiment, controlled only by temperature, not by presence or absence of antibiotics. Table 3 suggests, however, that streptomycin had a slight, positive effect on survival rate at 15° and 18 °C. Mortality was, in any case, conspicuously higher at 18 °C than at the two lower temperatures.

Since mass rearing is the principal method for growth studies, the carapace length of larval exuviae was measured in this experiment in order to detect possible improvement of growth rates by streptomycin. Table 4 shows that temperature may be an important factor influencing larval size, whereas the antibiotic had no significant effects. There

Table 3. *Crangon crangon*. Survival (%) of larvae (stages I–V) with (+) and without (–) streptomycin (25 mg·cm^{-3}), at 3 different temperatures

Stage	Survival rate (%)					
	12 °C		15 °C		18 °C	
	(+)	(–)	(+)	(–)	(+)	(–)
I	100	100	100	100	86	80
II	80	60	70	50	50	30
III	50	40	60	30	20	10
IV	30	30	30	20	0	0
V	20	24	24	16		

Table 4. *Crangon crangon*. Carapace length (mm) of exuviae in larvae (stages I–IV) reared with (+) and without (–) streptomycin (25 mg·cm^{-3}) at different temperatures. Mean ($\bar{x}$) ± 95 % confidence intervals

Temperature		Larval stage							
		I		II		III		IV	
		(+)	(–)	(+)	(–)	(+)	(–)	(+)	(–)
12 °C	$\bar{x}$	0.841	0.842	0.930	0.927	1.025	1.024	1.121	1.117
	±	0.008	0.008	0.009	0.007	0.013	0.012	0.010	0.016
15 °C	$\bar{x}$	0.839	0.840	0.935	0.928	1.021	1.023	1.100	1.095
	±	0.009	0.008	0.008	0.007	0.010	0.016	0.017	0.018
18 °C	$\bar{x}$	0.830	0.827	0.920	0.918	1.005	1.010		
	±	0.009	0.009	0.009	0.009	0.011	0.010		

was a decreasing tendency in carapace length with increasing temperature in almost all stages, regardless of presence or absence of streptomycin.

The experiments suggest that rearing of *Crangon* larvae is in general not improved by the addition of streptomycin. Therefore, all later experiments were carried out without antibiotics.

Food

A number of experiments with different types of food (all with 25 individually reared larvae in each subexperiment; at constant 12 °C) was carried out during the initial (methodological) part of this study (Criales, 1985). Most results will only be summarized in the following chapter.

The first experiment was conducted with three groups of *Crangon crangon* larvae fed brine shrimp (*Artemia* sp.) nauplii, rotifers *(Brachionus plicatilis)*, and a mixture of these organisms. The group feeding on the mixed diet showed highest survival and fastest moulting rates throughout development. In the first 3 larval stages, survival was higher in the group fed rotifers as compared to that fed *Artemia* nauplii, although in later stages the *Brachionus* group had the lowest survival of all. Development (moulting) rate was consistently slowest in larvae fed exclusively rotifers.

This experiment suggested that a mixture of brine shrimp nauplii and rotifers is a better food than either of these organisms alone, and that (presumably due to their differential size) rotifers are consumed particularly by earlier stages, whereas *Artemia* is a suitable prey for later stages of *C. crangon*. Moulting rates, however, were similar in the two groups fed the mixed diet and *Artemia* alone. Therefore, the comparison of these two types of food was repeated twice, with *C. crangon* larvae hatched from different females.

In the first repetition (Fig. 3), there was higher mortality during the zoeal stages I and II in the group fed only *Artemia*. This difference in survival rates did not further increase in later larval stages. The group feeding on the mixed diet not only showed higher survival rates but consistently also faster development (Fig. 3, upper graph).

In the second repetition of this comparison, larval size (carapace length) was measured as an additional criterion of food value. The larvae were much more viable than those in the first two experiments: survival to stage VI was 76 % in the group with mixed diet and 64 % in the *Artemia* fed group. The difference in survival rate was small but consistent throughout development. The same was true for the rate of moulting, again with faster development in larvae fed the mixture. Larval size, however, was almost identical in the two experimental groups.

So far, these results indicated that an addition of rotifers will increase the food value of an *Artemia* diet, at least in the earlier stages of *Crangon* development. In another experiment, one group of larvae was fed this mixture throughout development, whereas the other group received the same food only during the zoeal stages I–III, and exclusively *Artemia* thereafter. Both survival and moulting rates were not influenced by this change of diet. This means that brine shrimp nauplii are sufficient for the later larval instars.

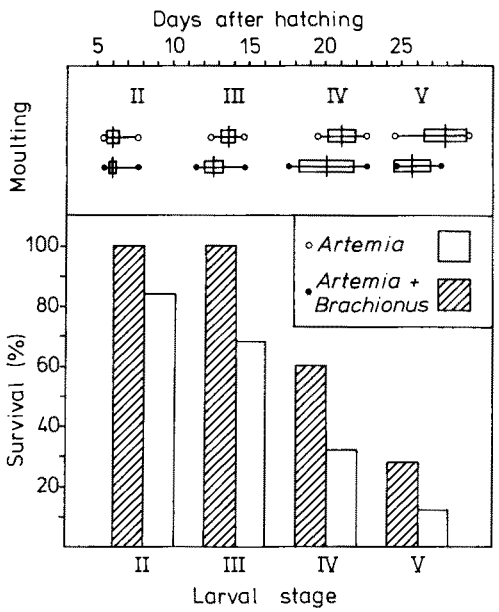

Fig. 3. *Crangon crangon*. Time of moulting and rate of survival (explanation: see Fig. 1) in larvae reared with two types of food (*Artemia* sp. with or without *Brachionus plicatilis*)

The small size of early shrimp larvae suggested that diatoms, instead of rotifers, might be a suitable alternative addition to an *Artemia* diet. In an experiment with *C. crangon* larvae, first a direct comparison of monospecific foods was conducted: (1) *B. plicatilis*, (2) *Skeletonema costatum*, and (3) *Thalassiosira rotula*. The zooplankton (rotifer) diet gave consistently best results, i.e. shortest development and highest survival. Mortality with *S. costatum* was only little higher, but development in all stages later than zoea III was significantly delayed. Larvae which were fed exclusively *T. rotula* consistently revealed highest mortality and slowest development.

The larval forms occurring in this experiment showed that all three diets tested were inferior to the mixture of brine shrimp nauplii and rotifers. All third-stage larvae belonged to type zoea IIIc. Only a few of these (a total of 17 %) developed further, again to the stunted form zoea IVc and (only with *B. plicatilis*) IVb. Still fewer reached the following instar (zoea Vb) and, eventually, metamorphosis.

Since *T. rotula* had proven to be a valuable food for a number of other zooplankton cultivated in our laboratory, its suitability as an additive was checked again in another experiment with (1) exclusively *Artemia* sp., (2) a mixture of *Artemia* sp. and *B. plicatilis*, and (3) a mixture of *Artemia* sp. and *T. rotula*. As in previous experiments, the mixed zooplankton diet yielded far better results. The addition of diatoms instead of rotifers did not improve survival of shrimp larvae as compared to those fed exclusively *Artemia* sp., but duration of development in the zoea II, III and IV was somewhat (not statistically significant) abbreviated when *T. rotula* was added. The effect of the phytoplankton addition was clearly visible only in pathways of morphological development (Fig. 4). When only *Artemia* sp. was given as food, most larvae showed reduced morphogenesis, and some particularly stunted forms (IIId, IVc) occurred but did not develop any further. The addition of *T. rotula* had a clearly positive effect on development, though it was less pronounced than the effect of rotifers. Metamorphosis was always reached after 5 larval

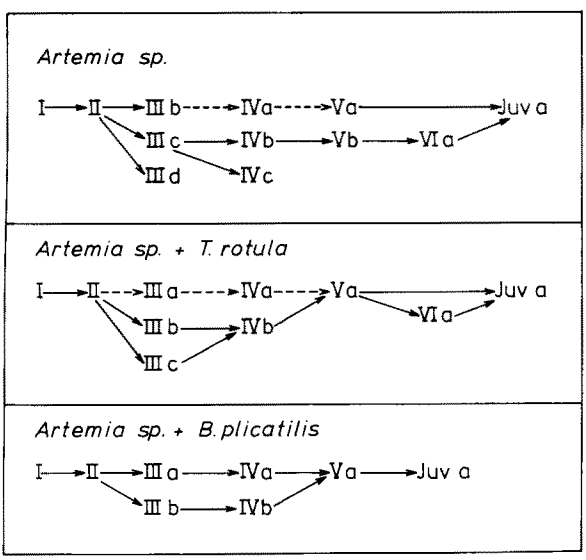

Fig. 4. *Crangon crangon*. Pathways of larval development with three types of food

instars when the mixed zooplankton diet was given, after 5 or 6 instars, however, in the other subexperiments (Fig. 4).

The food requirements of *C. allmanni* were studied in one preliminary experiment comparing (1) *Artemia* sp.; (2) *Artemia* sp. and *B. plicatilis*, and (3) *S. costatum*. Metamorphosis occurred (at 12 °C) after 36 to 54 days. Survival was highest in larvae fed diatoms, slightly lower in those fed mixed zooplankton diet, and clearly lowest in the group fed exclusively *Artemia* sp. Neither duration of development nor size (measured as carapace length) of the larval stages was significantly influenced by the type of food. The number of larval instars was 6 to 7 in the zooplankton-fed groups, and 6 to 9 in larvae fed diatoms. Morphological variability, particularly in the zoeal stages V to VII, was stronger (with more reduced forms) in the latter group. This suggests that large diatoms are suitable food for early *C. allmanni* larvae, but late premetamorphic stages develop better when zooplankton is available. This conclusion is corroborated by the fact that mortality increased in stage V larvae feeding on *S. costatum*.

Summarizing, one can say that a mixture of *Artemia* sp. and *B. plicatilis* is a suitable laboratory food for rearing of *Crangon* spp. larvae. Development and growth are, in principle, also possible with diatoms as a sole food source, or in combination with zooplankton. Since consistently acceptable results were obtained with brine shrimp nauplii and rotifers, and both food species are easily available, they were in all later experiments given as a standard diet.

Temperature

Larvae of *Crangon crangon* could be reared successfully from hatching to metamorphosis at temperatures between 9° and 18 °C. Development at 6 °C did not proceed beyond stage III. The first juvenile stage was usually reached after 5–7, or in a few exceptional cases after 4 or 8–9 moults (Fig. 5). The larvae of the hatch employed for this rearing experiment at five different constant temperatures showed in general a tendency to high variability in larval morphology and the number of premetamorphic instars. This variability was lowest at 9 °C, where all survivors (32 %) moulted to the first juvenile

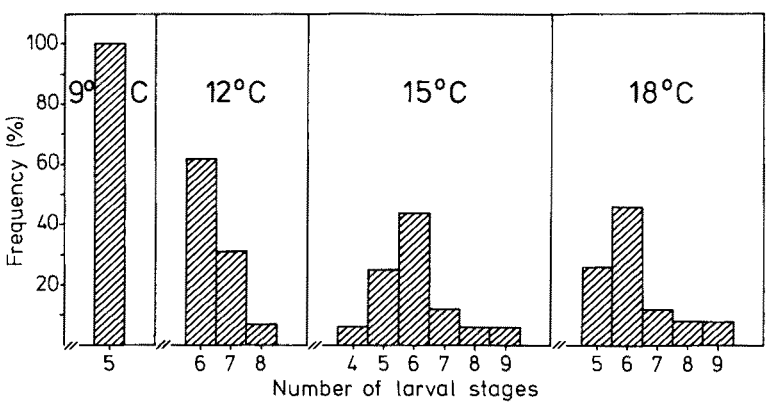

Fig. 5. *Crangon crangon*. Frequency (%) of different numbers of larval stages occurring prior to metamorphosis, in relation to temperature

after 5 larval stages. 6–8 moults were necessary at 12 °C, where 64 % survived to metamorphosis. Variability was highest at 15° and 18 °C (Fig. 5), where 70 and 60 % reached the first juvenile, respectively. One individual moulted at 15 °C directly from an advanced form IVa to the first juvenile. Some others, however, needed as much as 8 or 9 moults. In the latter case, there was no more morphological development after stage VII, i.e. moulting and growth became independent of the process or morphogenesis.

The number of larval forms also increased with temperature. At 9° and 12° there were usually two different forms in each larval instar subsequent to III. At higher temperatures, three forms per instar usually occurred with the number of developmental pathways increasing correspondingly. The metamorphic moult to the first juvenile was observed most frequently in the zoea Va, Vb, VIa, and VIIa, and less in forms IVa, VIb, VIII, and IX.

The size (carapace length) of the larval instars was not or very little influenced by temperature. There was only a weak (not statistically significant) tendency towards decreasing size with increasing temperature. The mean size values for the larval stages I–VII are given in Table 5, together with the durations of development at different temperatures. Stages VIII and IX are not included in Table 5, because only a few individuals went through these stages, and their development duration and morphology did not differ significantly from the preceding stage VII. The relationship between temperature (T; °C) and duration of development (D; days) in a given instar may be described by the power function:

$$D = b \cdot T^m, \tag{1}$$

where b and m are fitted constants. They are given for the linearized equation

$$\ln D = \ln b + m \cdot \ln T \tag{2}$$

in Table 6, as computed from single observations (individually reared larvae). Due to high individual variation, the correlation coefficients *(r)* are relatively low, although most differ significantly from zero ($P < 0.05$). When the mean values of development time are used instead of individual figures, the correlation coefficients vary between −0.9033 (stage IV) and −0.9999 (stage VI).

Table 5. *Crangon crangon*. Average carapace length (CL; mm) of larval stages; duration of development (days; mean ± 95 % confidence intervals) in relation to temperature (°C)

Stage	CL (mm)	Development (days)				
		6 °C	9 °C	12 °C	15 °C	18 °C
I	0.78	18.0 ± 1.1	10.0 ± 0.4	5.5 ± 0.1	4.6 ± 0.1	3.6 ± 0.3
II	0.89	13.8 ± 2.8	7.8 ± 0.3	4.7 ± 0.2	4.1 ± 0.4	3.0 ± 0.4
III	0.95		8.0 ± 1.1	4.5 ± 0.4	3.7 ± 0.5	3.2 ± 0.5
IV	1.01		8.1 ± 1.0	4.6 ± 0.4	4.5 ± 0.7	4.1 ± 1.2
V	1.07		11.7 ± 4.1	4.8 ± 0.5	4.1 ± 0.5	3.5 ± 0.8
VI	1.10			5.5 ± 0.4	4.3 ± 0.4	3.5 ± 0.4
VII	1.14			6.0 ± 1.1	4.5 ± 0.7	3.5 ± 0.6

Table 6. *Crangon crangon*. Parameters of the regression Eq. (2) for development duration in relation to temperature (ln *b*, *m*; see text) in larval stages I–VIII. *r* = correlation coefficient; *n* = number of observations; *P* = level of significance for *r* (n. s. = not significant). * = only premetamorphic individuals

Stage	ln *b*	*m*	*r*	*n*	*P* <
I	5.30	− 1.406	− 0.98	102	0.001
II	4.30	− 1.100	− 0.78	95	0.001
III	4.55	− 1.202	− 0.84	84	0.001
IV	3.70	− 0.864	− 0.71	72	0.001
V	3.50	− 0.758	− 0.56	65	0.001
VI	2.91	− 0.554	− 0.42	54	0.001
VII	1.89	− 0.153	− 0.16	42	n.s.
VIII	4.16	− 1.003	− 0.74	19	0.001
V*	5.63	− 1.482	− 0.89	16	0.001
VI*	3.64	− 0.776	− 0.59	24	0.001
VII*	3.26	− 0.632	− 0.71	10	0.05

Table 6 shows a decreasing tendency in both the *m* and *r* values, i.e. development duration is controlled increasingly by factors other than temperature. This accompanies increasing morphological variation. There are always some larvae in stages V, VI and VII which prepare themselves for metamorphosis and eventually will moult to the first juvenile. Others will not change much in their morphology and will moult to another, morphologically similar larval stage. When, in these instars, only premetamorphic individuals are considered, both *m* and *r* values become higher (*in Table 6). This separation was not necessary in stage VIII, because only very few individuals in this instar moulted to a zoea IX instead of metamorphosing.

Further analysis of developmental pathways and durations from all experiments showed that, in general, development of a larval instar was shorter when the following stage was a reduced (stunted) form, and longer when it developed to a more advanced one. This relationship was apparently not influenced by the form itself which could develop one way or the other.

When the number of larval moults *(M)* was plotted against the time of development *(D)*, linear relationships were obtained:

$$M = b + m \cdot D \tag{3}$$

where *b* and *m* are again fitted constants. Since the regression lines theoretically pass through the zero point, the intercept *(b)* should be close to zero. The regression coefficient *(m)* is clearly influenced by temperature (Fig. 6). The constants of Eq. (3) are given in Table 7.

The slope of these regression lines can be expressed as a power function of temperature *(T)*:

$$m = 0.00584 \cdot T^{1.347} \tag{4}$$

Since this relationship is rather close ($r = 0.992$) and the same is true for the relation between the number of moults and larval age (Table 7: all $r \geq 0.997$), *m* may be

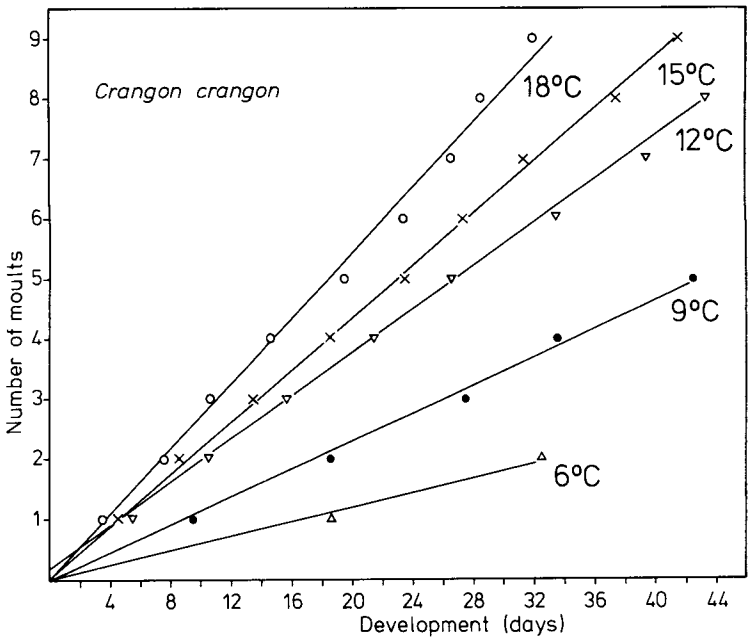

Fig. 6. *Crangon crangon*. Frequency of larval moulting (cumulative number of moults plotted against time of development) at different temperatures. Parameters of linear regression equations given in Table 7

Table 7. *Crangon crangon*. Parameters of the linear regression Eq. (3) for the number of larval moults in relation to time (days) of development, at different constant temperatures. *r, P:* see Table 6

Parameter	Temperature (°C)				
	6	9	12	15	18
b	0.04	− 0.10	0.05	0.06	0.02
m	0.061	0.119	0.183	0.215	0.272
r	0.997	0.998	0.999	0.999	0.997
P<	0.05	0.001	0.001	0.001	0.001

substituted for Eq. (4) in Eq. (3). If *b* is neglected, the number of larval moults *(M)* can be expressed as a function of both temperature *(T)* and time of development *(D)*:

$$M = 0.00584 \cdot D \cdot T^{1.347} \quad (5)$$

This multiple regression may serve as a model to predict the average number of moults (and thus, also the approximate size) in *C. crangon* larvae reared under known conditions in the laboratory. Differences among developmental pathways, however, complicate this relation and may reduce the fit of observed and predicted data. Figure 7 demonstrates the effects of shorter moult cycles in larvae developing to morphologically

reduced forms on the linear regressions, which may be obtained at a single temperature (15° taken as a rather extreme example; see above). Since, in this case, larvae with relatively abbreviated development (m = 0.166) occurred much less frequently than those developing through many reduced stages (m = 0.227), the average m was closer to the latter (m = 0.215; Table 7). In other hatches, however, where the larvae may tend to a

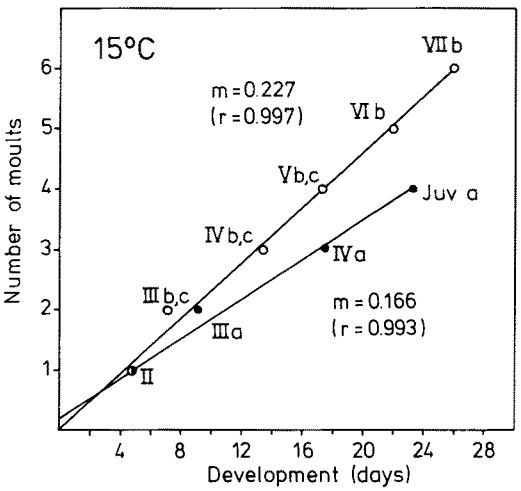

Fig. 7. *Crangon crangon*. Frequency of larval moulting (explanation: Fig. 6) at 15 °C, in larvae developing through morphologically reduced forms (b, c) and those showing abbreviated development (a); m = slope; r = correlation coefficient

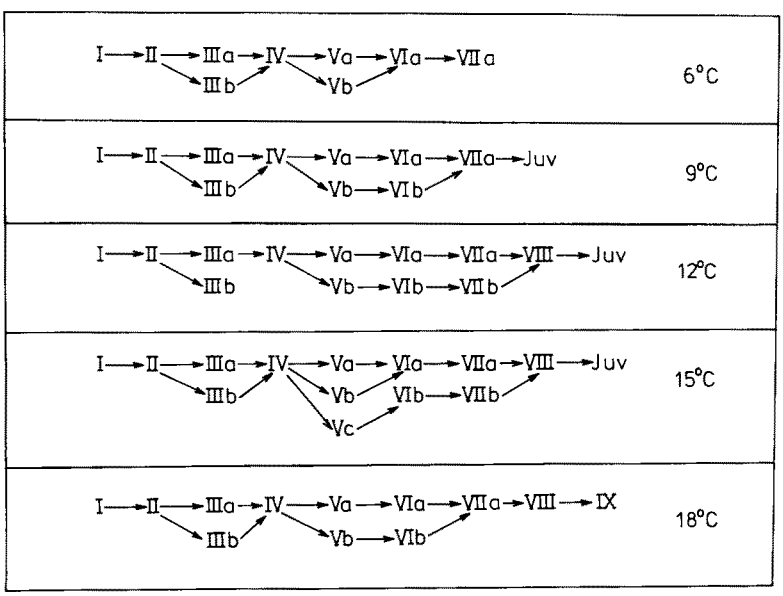

Fig. 8. *Crangon allmanni*. Pathways of larval development at different temperatures

Table 8. *Crangon allmanni.* Average carapace length (CL; mm) of larval stages; duration of development (days; mean ± 95 % conficence intervals) in relation to temperature (°C)

Stage	CL (mm)	Development (days)				
		6 °C	9 °C	12 °C	15 °C	18 °C
I	0.74	20.4 ± 0.7	11.6 ± 0.6	6.5 ± 0.2	5.4 ± 0.1	4.7 ± 0.3
II	0.81	14.5 ± 0.6	9.3 ± 0.9	5.6 ± 0.3	4.8 ± 0.2	3.6 ± 0.5
III	0.86	13.1 ± 2.4	8.8 ± 0.7	5.5 ± 1.0	4.4 ± 0.5	4.3 ± 1.0
IV	0.94	15.5 ± 2.4	9.2 ± 1.2	5.7 ± 0.3	4.3 ± 0.7	4.6 ± 2.2
V	0.99	12.5	8.8 ± 1.3	5.0 ± 0.8	4.1 ± 0.8	4.3 ± 1.6
VI	1.08	15.5	8.5	5.3 ± 0.4	3.7 ± 0.5	3.0 ± 2.4
VII	1.17		12.5	6.0 ± 2.4	4.7 ± 0.7	4.8 ± 2.4
VIII	1.25			6.5	5.5 ± 3.6	2.5

shorter development with less morphological variation, m values may be consistently lower than expected from regression Eq. (4). In such cases Eq. (5) will overestimate larval moulting rate.

The same experiment was conducted with *C. allmanni.* Larvae could be reared from hatching through metamorphosis only at 9°, 12° and 15 °C. The survival was generally much lower than in *C. crangon,* with only 1–2 individuals reaching the first juvenile instar. Mortality was at 18 °C very high from the beginning of the experiment. At 6 °C, it increased drastically in the second, and at the intermediate temperatures, in the third larval stage. As in *C. crangon,* there was a tendency of increasing morphological variability (more larval instars and forms) with increasing temperature (Fig. 8), but this variability was, in general, much lower than in *C. crangon* development.

Larval size was, in general, not significantly influenced by temperature, as in *C. crangon.* Only in the zoeal stages VI and VII was there a clear tendency of decreasing size with increasing temperature. The average carapace lengths of all larval instars (measured in exuviae) are given in Table 8, together with development duration at different temperatures.

The decrease of development time with increasing temperature can again be expressed by Eq. (1) or (2). The fitted parameters for *C. allmanni* larvae are given in Table 9. The m and r values vary among the larval instars without showing the same trend as *C. crangon* (cf. Table 6).

The number of moults is again a linear function of larval age (Fig. 9), and the slope of this function depends on temperature. The parameters of Eq. (3) are given in Table 10. The relation between the slope *(m)* and temperature *(T)* may again be described by a power function [cf. Eq. (4)]:

$$m = 0.00955 \cdot T^{1.128}, \tag{6}$$

with a correlation coefficient $r = 0.997$. When we insert Eq. (6) in Eq. (3), we obtain:

$$M = 0.00955 \cdot D \cdot T^{1.128}, \tag{7}$$

the equivalent of Eq. (5) linking the number of larval moults *(M)* with both their age *(D)* and water temperature *(T).*

Table 9. *Crangon allmanni*. Parameters of Eq. (2) for development duration in relation to temperature (for further explanation see Table 6)

Stage	ln b	m	r	n	$P <$
I	5.46	− 1.399	− 0.97	106	0.001
II	4.80	− 1.213	− 0.97	82	0.001
III	4.21	− 0.990	− 0.79	48	0.001
IV	4.84	− 1.234	− 0.80	39	0.001
V	4.32	− 1.064	− 0.79	29	0.001
VI	5.26	− 1.455	− 0.97	18	0.001
VII	4.96	− 1.229	− 0.74	10	0.05
VIII	7.09	− 2.073	− 0.72	4	n.s.

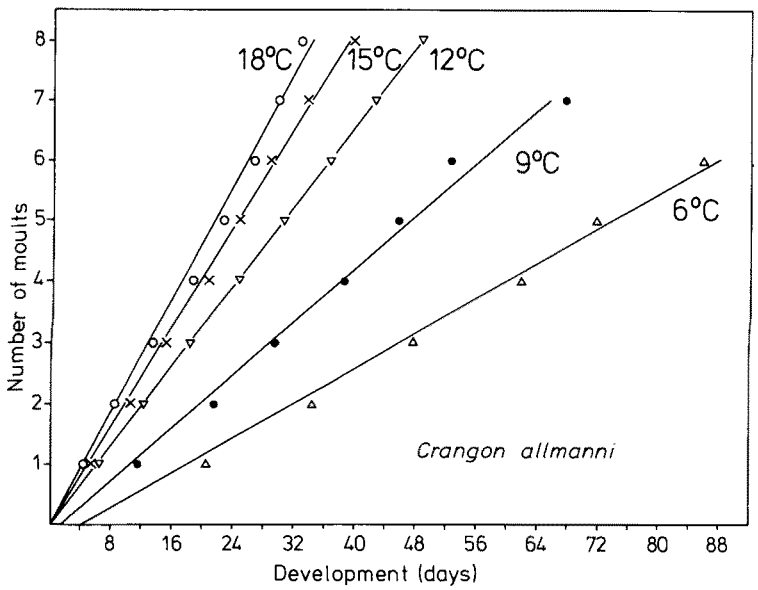

Fig. 9. *Crangon allmanni*. Frequency of larval moulting (explanation: Fig. 6) at different temperatures. Parameters of linear regression equations given in Table 10

The results of these rearing experiments carried out at different temperatures may be summarized in a brief comparison of larval characteristics in the two *Crangon* species. The growth patterns are similar, so that, in principal, similar regression models may be employed to estimate the number of larval moults in relation to temperature and time of development: Eqs. (5) and (7). The exponents in these equations suggest that temperature has a stronger effect on moulting rates in *C. crangon* than in *C. allmanni* (1.347 vs. 1.128). This increased moulting frequency at higher temperatures is, particularly in *C. crangon*, accompanied by the occurrence of more morphologically reduced larval forms, i.e. the rate of moulting is increased to a higher degree than the rate of morphological development. It appears from development and survival data (cf. Figs 6,

Table 10. *Crangon allmanni.* Parameters of the linear regression Eq. (3) for the number of larval moults in relation to time (days) of development, at different constant temperatures. *r, P:* see Table 6

Parameter	Temperature (°C)				
	6	9	12	15	18
b	0.30	0.16	− 0.05	− 0.13	− 0.13
m	0.072	0.110	0.166	0.209	0.238
r	0.996	0.996	0.9999	0.999	0.997
P<	0.001	0.001	0.001	0.001	0.001

9) that *C. allmanni* is better adapted to colder water than *C. crangon.* Larval size is only slightly or not consistently affected by temperature (Tables 4, 5, 8). The carapace length is smaller in stage I–V *C. allmanni* as compared to *C. crangon* in equal stages, but the last (premetamorphic) instars have a similar size in the two species (Tables 5, 8).

In *C. crangon* there is a particularly high degree of development variability both between and within single hatches: larval size (cf. Tables 4, 5), number of instars preceding metamorphosis (Fig. 5), and developmental pathways and larval forms (e.g. Figs 2, 4). The low number of experiments with *C. allmanni,* however, does not allow final conclusions on the actual variability in the development of this species. So far, the most frequent developmental pathways found in the two species were as follows:

C. crangon
I – II – IIIb – IVb – Va – Juv, and
I – II – IIIc – IVb, c – Vb, c – VIa – Juv

C. allmanni:
I – II – IIIa, b – IV – Va, b – VIa, b – VII – VIII – Juv

Salinity

The influence of salinity on larval development was studied only in *Crangon crangon.* Larvae hatched at ambient salinity (32 ‰) were gradually adapted in steps of 5 ‰ S per hour to the experimental salinities and reared individually with standard techniques (25 larvae per condition).

The first experiment comprised 18 combinations of 3 temperatures (6°, 12°, 18 °C) and 6 salinities (10, 15, 20, 25, 32, 37 ‰ S). The two lowest salinities caused complete mortality in the first larval stage, at all three temperatures (Fig. 10). At 20 ‰ S, very few larvae moulted successfully to the second stage, and exclusively at 12 °C. At this temperature survival was highest for the other salinities as well. Best results were obtained at a combination of 12 °C and 32 ‰ S, which represents natural conditions near Helgoland in late spring, when *C. crangon* larvae develop in the field. Slightly reduced (25 ‰) and enhanced (37 ‰) salinity caused consistently lower survival rates, with 37 ‰ figures somewhat higher than at 25 ‰ S.

Time of development in the single instars was also prolonged at salinities deviating from 32 ‰. The delay was almost equally great for enhanced (37 ‰) and lowered (25 ‰) salinity.

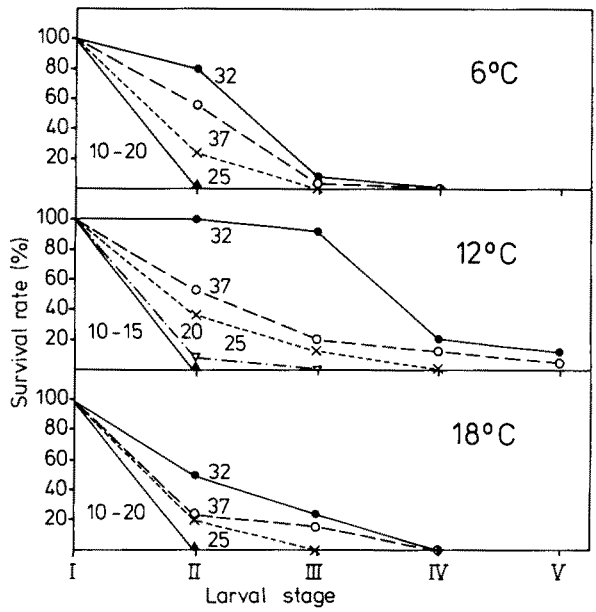

Fig. 10. *Crangon crangon*. Survival rate (%) during larval development at different combinations of salinity (designated as numbers) and temperature

Survival in this experiment was very poor in general, even at optimum conditions (Fig. 10), and, a second experiment was therefore conducted. This time, the two lowest salinities (10 and 15 ‰ S) and the lowest temperature (6 °C) were omitted. Larvae were reared at 12 combinations of 9, 12, 15 and 18 °C, and 25, 32, and 37 % S.

Survival rates in this experiment were in general much higher than in the first one. Successful development through metamorphosis occurred at 32 ‰ S at all temperatures in ca 20–30 % of the larvae. A few individuals reached the first juvenile stage (albeit the reduced form "Juv b") also at 25 ‰ S (only at 9 °C) and 37 ‰ S (at 12 and 15 °C). As in the first experiment (Fig. 10), survival rates were at all temperatures consistently higher throughout development at 32 ‰ S than at the other salinities, again with absolute lowest figures at 25 ‰ S. Rates and durations of survival at 25 and 37 ‰ S were clearly lower at 18 °C than at lower temperatures, i.e. the larvae become more stenohaline at the end of their range of temperature tolerance.

Not only mortality but also the time of development in surviving larval instars was consistently higher at 25 and 37 as opposed to 32 ‰ S. This effect was clearly visible in single stages as well as in the cumulative number of moults plotted against larval age. Again, highly significant linear regressions were obtained for this relationship (cf. Figs 6, 9). The parameters of these regressions are given in Table 11 for all temperatures and salinities tested in this experiment. Since delay in development was very similar at 25 and 37 ‰ S, the results of these two salinities were pooled. Again, the slopes of these regression lines were controlled predominantly by temperature, but also by salinity (Table 11). At both salinity regimens distinguished here (32 and 25/37 ‰ S), the slope can be described as a power function of temperature (with r = 0.993 and 0.987,

Table 11. *Crangon crangon.* Parameters of the linear regression Eq. (3) for the number of larval moults in relation to time (days) of development, at different constant temperatures (°C) and salinities (‰ S). *r, P:* see Table 6

Parameter	9 °C		12 °C		15 °C		18 °C	
	32 ‰	25/37 ‰	32 ‰	25/37 ‰	32 ‰	25/37 ‰	32 ‰	25/37 ‰
b	0.01	−0.03	0.02	0.02	0.06	−0.02	0.16	0.02
m	0.118	0.112	0.154	0.143	0.190	0.174	0.251	0.235
r	0.9998	0.9998	0.9999	0.9998	0.9998	0.9999	0.9992	0.9994
P<	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.05

respectively). This function can be inserted in Eq. (3) as above, in order to obtain a model to predict the number of larval moults *(M)* in relation to time of development *(D)* and temperature *(T)*:

$$32\ ‰\ S: \quad M = 0.011 \cdot D \cdot T^{1.069} \tag{8}$$

$$25/37\ ‰\ S: \quad M = 0.011 \cdot D \cdot T^{1.039} \tag{9}$$

The exponent in both equations is lower than in the corresponding Eqs. (5) and (7). This shows that the rate of moulting may vary more among larvae orginating from different females than between the two *Crangon* species studied.

The developmental pathways were again studied in detail (Fig. 11). Metamorphosis was reached after 4–8 larval stages. The number of different larval forms was this time not so clearly influenced by temperature as in previous experiments. Only the occurrence of reduced zoea III and IV forms was (at standard salinity, 32 ‰) more conspicuous at 18 and 9 °C than at intermediate temperatures. The influence of unsuitable salinities (25 and 37 ‰) on developmental pathways, however, was clearly visible (Fig. 11). Larval development tended to go through reduced morphological forms (no "a" forms found), but at the same time there were signs of abbreviation. When metamorphosis occurred, it was always a moult from a zoea IVb to a reduced juvenile (Juv b). This type of metamorphosis occurred only in one individual at 32 ‰ S, where the normal (Juv a) form dominated.

Another peculiar moult (dashed lines in Fig. 11) occurred only at elevated temperatures (15 and 18 °C) combined with unsuitable salinities: a direct development from stage I to a zoea II morphologically identical with a IIIc form. This "skipping" shows again that the coordination of morphogenesis with the moult cycle may be disturbed by environmental conditions.

DISCUSSION

Rearing technique and application of streptomycin

The present study has shown that there is a high degree of variability in the morphological development of *Crangon* spp. larvae, which may be influenced by genetic factors (hatches from different females), rearing techniques, and environmental variables such as temperature and salinity. Morphogenetic variability is probably

normal in the larval development of shrimps and prawns (e.g. Knowlton, 1974; Rochanaburanon & Williamson, 1976; Fincham, 1977, 1979a, b; Wienberg, 1982). In *C. crangon* it appears particularly strong, and it reflects minor differences in environmental conditions. Crowding effects, for example, often occurring in mass cultures may be observed in mortality and moulting rates (Table 1; for reviews see also Reeve, 1969; Odai et al., 1978; Emmerson & Andrews, 1981; Dawirs, 1982; Shumway et al., 1985). When

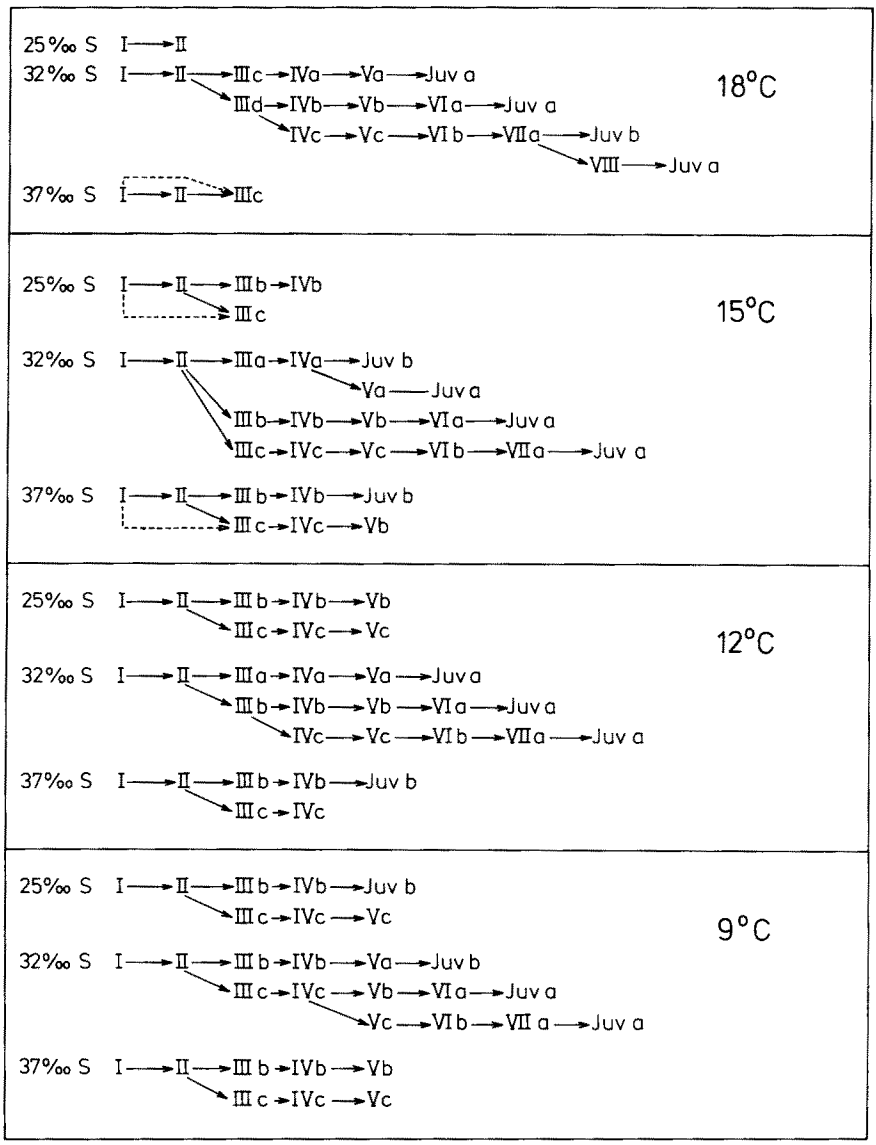

Fig. 11. *Crangon crangon*. Pathways of larval development at different combinations of salinity and temperature

these effects are weak however, they may only be found in larval morphogenesis (Table 2). This natural variability plus the possible interfering effects of methodology reduce the comparability of results obtained by different workers, in different studies, and even from different hatches.

The present results suggest that individual rearing is a suitable cultivation technique for *Crangon* spp. larvae, and allows the tracing of development pathways. If, however, great amounts of larval material are required for studies of biomass or biochemical composition, mass rearing with its disadvantages may be necessary.

Antibiotics have often been applied to reduce negative effects of mass rearing, but with contradictory results (e.g. Wickins, 1972a, b; Brick, 1974; Fisher & Nelson, 1978; Fincham, 1979b). *C. crangon* larvae showed mostly negative responses to streptomycin in the present study, particularly in their morphogenesis (Fig. 2). Fincham (1979b) observed additional larval stages in prawn *(Palaemon longirostris)* development when antibiotics were applied. The toxicity of streptomycin may have a direct effect on the larvae (D'Agostino, 1975) or perhaps damage their symbionts (Brick, 1974).

Food

There is an immense literature on nutrition of shrimps and prawns, including their larval stages (New, 1980; Liao et al., 1983). Phytoplankton as a sole food source allows some but only rarely complete development in *Crangon* spp. larvae, which concurs with results from larvae of many other decapod species (e.g. Broad, 1957a; Regnault, 1969a; Sandifer, 1972; Roberts, 1974). These observations show that although decapod larvae are generally able to eat and convert phytoplankton, either the biochemical composition or the relatively small size of this food type make it inadequate. The rather good development in early larval stages (see above) and in small species (Broad, 1957a; Simon, 1979) suggest that algal cell (or chain) size relative to larval size, morphology (mouth parts), and behavioural traits are determinant factors for the suitability of phytoplankton as a food source. The same is probably true for small zooplankton such as rotifers (Brick, 1974; Sulkin & Norman, 1976; Sulkin, 1978; Anger & Nair, 1979; Sulkin & van Heukelem, 1980). Particularly positive rearing results with mixed diets (Regnault, 1969a; Ingle & Rice, 1971; Sandifer, 1972; Christiansen & Yang, 1976; Manzi et al., 1977) show, however, that qualitative (biochemical) aspects are also very important in larval nutrition. In the present study, a mixed diet of *Artemia* sp. and *Brachionus plicatilis* supported larval growth better than any of these items alone.

Malnutrition and other unsuitable conditions apparently affect morphogenesis more than the moulting cycle of shrimp larvae. Similar observations in many other shrimp (Broad, 1957a, b; Tesmer & Broad, 1964; Knowlton, 1974; Fincham, 1977, 1979a, b) and a few brachyuran larvae (Sulkin, 1978; McConaugha, 1982) indicate that the uncoupling of these two processes is more likely in Natantia than other decapods. The regulation of larval development (moulting, growth, morphogenesis) by genetic, hormonal, and external factors has been discussed in detail by Knowlton (1974) and Fincham (1979b).

Temperature and salinity

It is not surprising that two of the classical key factors of marine ecology, temperature and salinity, influence larval development and survival in *Crangon* spp. High

temperature (18 °C) caused increased moulting frequency, decreased survival, and an increasing morphological variation, with more larval forms and instars preceding metamorphosis. Similar effects of high temperature were found by Knowlton (1974) in *Palaemonetes vulgaris*. Sandifer (1973) also found in the same species that the lowest number of larval instars occurred at an intermediate (optimum) temperature. Fincham (1977, 1979a, b) suggested that this factor is one of the regulating forces in the development of Natantia larvae. Its effect on larval size, however, is not yet clear (cf. Tables 4, 5, 8). As in one of our experiments (Table 4), Knowlton (1974) found increasing size with decreasing temperature, whereas Regnault (1969b) and Rothlisberg (1979) observed maximum growth at an intermediate (optimum) temperature.

Salinity exerts generally a weaker influence on larval development than temperature (Regnault & Costlow, 1970; Knowlton, 1974; Sandifer, 1973; Rochanaburanon & Williamson, 1976; Rothlisberg, 1979). The present study showed, however, that not only rates of survival and development but also developmental pathways are influenced by salinity. *Crangon crangon* is generally considered a very euryhaline species (Dornheim, 1969; Heerebout, 1974), but its larvae developed only in a surprisingly narrow salinity range. This result suggests that there may be physiologically distinct populations in areas with different salinity (e.g. North Sea, Baltic Sea) and migrations of ovigerous females from estuaries may transport early larvae to polyhaline regions (Boddeke, 1976). Kühl & Mann (1963) found *C. crangon* larvae mostly in the outer part of the Elbe estuary, where salinity varies between 18 and 30 ‰S. According to the present results, development should be negatively affected in this salinity range. Our larvae, however, originated not from estuarine, but from offshore populations.

The present study has shown that various factors may influence the larval development of the brown shrimp, and it has provided a number of quantitative data on the relationships between moulting, growth, morphogenesis, age, and temperature. Our preliminary observations on *C. allmanni* development as well as literature data on *C. septemspinosa* (Tesmer & Broad, 1964; Regnault & Costlow, 1970) suggest that there is great similarity in the general features of larval development in the Crangonidae. Further experimental studies on Natantia larvae, including individual rearing with tracing of developmental pathways, should further increase our understanding of the early life stages in shrimps and prawns.

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LITERATURE CITED

Allen, J. A., 1960. On the biology of *Crangon allmanni* Kinahan in Northumberland waters. – J. mar. biol. Ass. U.K. *39*, 481–508.

Anger, K. & Nair, K. K. C., 1979. Laboratory experiments on the larval development of *Hyas araneus* (Decapoda, Majidae). – Helgoländer wiss. Meeresunters. *32*, 36–54.

Anger, K. & Dawirs, R. R., 1981. Influence of starvation on the larval development of *Hyas araneus* (Decapoda, Majidae). – Helgoländer Meeresunters. *34*, 287–311.

Arntz, W. W., 1971. Die Nahrung der Kliesche in der Kieler Bucht. – Ber. dt. wiss. Kommn Meeresforsch. *22,* 129–183.

Bergman, M., Bowe, K. & Spliethoff, P., 1976. Garnelen en Krabben als mogelijke predatoren van O – jarige schol op het balgzand. – Visserij *29,* 432–438.

Boddeke, R., 1976. The seasonal migration of the brown shrimp *Crangon crangon.* – Neth. J. Sea. Res. *10,* 103–130.

Boddeke, R. & Becker, B., 1979. A quantitative study of the fluctuations of the stock of brown shrimp *(Crangon crangon)* along the coast of the Netherlands. – Rapp. P.–v. Réun. Cons. perm. int. Explor. Mer. *175,* 253–258.

Brick, R. W., 1974. Effects of water quality, antibiotics, phytoplankton and food on survival and development of larvae of *Scylla serrata* (Crustacea, Portunidae). – Aquaculture *3,* 231–244.

Broad, A. C., 1957a. Larval development of the crustacean *Thor floridanus* Kingsley. – J. Elisha Mitchell scient. Soc. *73,* 316–328.

Broad, A. C., 1957b. The relationship between diet and larval development of *Palaemonetes.* – Biol. Bull. mar. biol. Lab., Woods Hole *112,* 162–170.

Broekema, M. M. M., 1942. Seasonal movements and the osmotic behaviour of the shrimp *Crangon crangon.* L. – Archs neerl. Zool. *6,* 1–100.

Christiansen, M. E. & Yang, W. T, 1976. Feeding experiments on the larvae of the fiddler crab *Uca pugilator* (Brachyura, Ocypodidae) reared in the laboratory. – Aquaculture *8,* 91–98.

Connor, P. N., 1972. Acute toxicity of heavy metals to some marine larvae. – Mar. Pollut. Bull. *3,* 190–193.

Creutzberg, F. & Leeuwen van F., 1980. The life cycle of *Crangon allmanni* Kinahan, in the Southern North Sea. – C. M./ICES *L 71,* 1–11.

Criales, M. M., 1985. Untersuchungen zur Larvalentwicklung von *Crangon crangon* L. and *Crangon allmanni* Kinahan (Decapoda, Natantia, Caridea). Diss., Univ. Kiel, 223 pp.

D'Agostino, A., 1975. Antibiotics in culture of invertebrates. In: Culture of marine invertebrate animals. Ed. by W. L. Smith & M. H. Chanley. Plenum Press, New York, 109–133.

Dalley, R., 1980. The survival and development of the shrimp *Crangon crangon* (L.) reared in the laboratory under non-circadian light-dark cycles. – J. exp. mar. Biol. Ecol. *47,* 101–112.

Dawirs, R. R., 1982. Methodical aspects of rearing decapod larvae, *Pagurus bernhardus* (Paguridae) and *Carcinus maenas* (Portunidae). – Helgoländer Meeresunters. *35,* 439–464.

Dornheim, H., 1969. Beiträge zur Biologie der Garnele *Crangon crangon* (L.) in der Kieler Bucht. – Ber. dt. wiss. Kommn Meeresforsch. *20,* 179–215.

Du Cane, R. N., 1839. On the metamorphosis of the crustacea. – Ann. Mag. nat. Hist. *3,* 438–440.

Ehrenbaum, E., 1890. Zur Naturgeschichte von *Crangon vulgaris.* Fabr. – Mitt. dt. SeefischVer. *Sonderbeil.* 9–124.

Emmerson, W. D. & Andrews, B., 1981. The effect of stocking density on the growth, development and survival of *Penaeus indicus* Milne Edwards larvae. – Aquaculture *23,* 45–57.

Fincham, A. A., 1977. Larval development of British prawns and shrimps (Crustacea, Decapoda, Natantia). 1. Laboratory methods and a review of *Palaemon (Paleander) elegans* Rathke, 1837. – Bull. Br. Mus. nat. Hist. (Zool.) *32,* 1–28.

Fincham, A. A., 1979a. Larval development of British prawns and shrimps (Crustacea, Decapoda, Natantia). 2. *Palaemonetes (Palaemon) varians* (Leach, 1814) and morphological variation. – Bull. Br. Mus. nat. Hist. (Zool.) *35,* 163–182.

Fincham, A. A., 1979b. Larval development of British prawns and shrimps (Crustacea, Decapoda, Natantia). 3. *Palaemonetes (Palaemon) longirostris* H. Milne Edwards, 1837, and the effect of antibiotics on morphogenesis. – Bull. Br. Mus. nat. Hist. (Zool.) *37,* 17–46.

Fischer, W. S. & Nelson, R. T., 1978. Application of antibiotics in the cultivation of Dungeness Crab, *Cancer magister.* – J. Fish. Res. Bd Can. *34,* 432–436.

Gerlach, S. A. & Schrage, M., 1969. Freilebende Nematoden als Nahrung der Strandgarnele *Crangon crangon* L. (Experimentelle Untersuchung über die Bedeutung der Meiofauna als Nahrung für das marine Makrobenthos). – Oecologia *2,* 362–375.

Guillard, R. R. L. & Ryther, J. H., 1962. Studies of marine planktonic diatoms. I. *Cyclotella nana* Hustedt and *Detonula confervaceae* Cleve. – Can. J. Microbiol. *8,* 229–239.

Gurney, A. R., 1982. The larval development of *Crangon crangon* (Fabr. 1795) (Crustacea, Decapoda). – Bull. Br. Mus. nat. Hist. (Zool.) *42,* 247–262.

Heerebout, G. G., 1974. Distribution and ecology of the Decapoda Natantia of the estuarine region of the rivers Rhine, Meuse and Scheldt. – Neth. J. Sea Res. *8,* 73–93.

Ingle, R. W. & Rice, A. L., 1971. The larval development of the masked crab *Corystes cassivelaunus* (Pennant), reared in the laboratory. – Crustaceana *20,* 271–284.

Knowlton, R. E., 1974. Larval developmental processes and controlling factors in decapod crustacea, with emphasis on Caridea. – Thalassia jugosl. *10,* 139–158.

Kühl, H. & Mann, H., 1963. Das Vorkommen von Garnelenlarven (*Crangon crangon* L.) in der Elbmündung. – Arch. FischWiss. *14,* 1–7.

Kuipers, B. R. & Dapper, R., 1984. Nursery function of Wadden Sea tidal flats for the brown shrimp *Crangon crangon.* – Mar. Ecol. Prog. Ser. *17,* 171–181.

Lebour, M., 1931. The larvae of the Plymouth Caridea. – I. The larvae of the Crangonidae. II. The larvae of the Hippolytidae. – Proc. zool. Soc. Lond. *1931,* 1–9.

Liao, I.-C., Su, H.-M. & Lin, J.-H., 1983. Larval foods for penaeid prawns. In: Handbook of mariculture. Vol. I: Crustacean aquaculture. Ed. by J. P. McVey. CRC Press, Boca Raton, Fla, 43–69.

Manzi, J. J., Maddox, M. B. & Sandifer, P. A., 1977. Algal supplement enhancement of *Macrobrachium rosenbergii* (De Man) larviculture. – Proc. a. Meet. Wld Maricult. Soc. *8,* 207–223.

McConaugha, J. R., 1982. Regulation of crustacean morphogenesis in larvae of the mud crab, *Rhithropanopeus harrisii.* – J. exp. Zool. *223,* 155–163.

Müller, A., 1968. Die Nahrung junger Plattfische in der Nord- und Ostsee. – Kieler Meeresforsch. *24,* 124–143.

New, M. B., 1980. A bibliography of shrimp and prawn nutrition. – Aquaculture *21,* 101–128.

Odai, M., Ikegami, T., Ros, A. O., Alcazar, A. G., Arnal, J. I., Santaella, E., Segarra, J. G., Sandino, S. & Peñalver, L., 1978. Experiencias sobre cultivos de larvas de *Palaemon serratus, Penaeus kerathurus* y *Sparus auratus,* realizadas en el Laboratorio del Mar Menor del Instituto Español de Oceanografía. – Boln Inst. esp. Oceanogr. *4,* 3–54.

Reeve, M. R., 1969. Growth, metamorphosis and energy conversion in the larvae of the prawn *Palaemon serratus.* – J. mar. biol. Ass. U.K. *49,* 77–96.

Regnault, M., 1969a. Étude expérimentale de la nutrition d'*Hippolyte inermis* Leach (Décapode, Natantia) au cours de son développement larvaire, au laboratoire. – Int. Revue ges. Hydrobiol. *54,* 749–764.

Regnault, M., 1969b. Influence de la température et de l'origine de l'eau de mer sur le développement larvaire au laboratoire d'*Hippolyte inermis* Leach. – Vie Milieu (A) *20,* 137–152.

Regnault, M. & Costlow, J. D., 1970. Influence de la température et de la salinité sur le développement larvaire de *Crangon septemspinosa* Say (Decapoda, Caridea). – Vie Milieu (A) *21,* 453–466.

Reise, K., 1979. Moderate predation on meiofauna by the macrobenthos of the Wadden Sea. – Helgoländer wiss. Meeresunters. *32,* 453–465.

Roberts, M. H., 1974. Larval development of *Pagurus longicarpus* Say reared in the laboratory. V. Effect of diet on survival and molting. – Biol. Bull. mar. biol. Lab., Woods Hole *146,* 67–77.

Rochanaburanon, T. & Williamson, D. I., 1976. Laboratory survival of larvae of *Palaemon elegans* Rathke and other Caridean shrimps in relation to their distribution and ecology. – Estuar. coast. mar. Sci. *4,* 83–91.

Rothlisberg, P. C., 1979. Combined effects of temperature and salinity on the survival and growth of the larvae of *Pandalus jordani* (Decapoda, Pandalidae). – Mar. Biol. *54,* 125–134.

Sandifer, P. A., 1972. Effects of diet on larval development of *Thor floridanus* (Decapoda, Caridea) in the laboratory. – Va J. Sci. *23,* 5–8.

Sars, G. O., 1890. Bidrag til kundskaben om Decapodernes Forvandlinger. III. Crangonidae. – Arch. Math. Naturv. *1890,* 139–195.

Shumway, S. E., Perkins, H. C., Schick, D. F. & Stickney, A. P., 1985. Synopsis of biological data on the pink shrimp, *Pandalus borealis* Krøyer, 1838. – NOAA techn. Rep. (NMFS) *30,* 1–57.

Simon, M., 1979. Primeros estadios larvarios de *Pontocaris lacazei* (Gourret) (Decapoda, Macrura, Crangonidae) obtenidos en laboratorio. – Investigación pesq. *43,* 565–580.

Smaldon, G., 1979. British coastal shrimps and prawns. Acad. Press, London, 126 pp. (Synopses of the British Fauna. 15).

Sulkin, S. D. & Norman, K., 1976. A comparison of two diets in the laboratory culture of the zoeal

stages of the brachyuran crabs *Rhithropanopeus harrisii* and *Neopanope* sp. – Helgoländer wiss. Meeresunters. *28,* 183–190.

Sulkin, S. D., 1978. Nutritional requirements during larval development of the portunid crab, *Callinectes sapidus* Rathbun. – J. exp. mar. Biol. Ecol. *34,* 29–41.

Sulkin, S. D. & Heukelem, W. F. van, 1980. Ecological and evolutionary significance of nutritional flexibility in planktotrophic larvae of the deep sea red crab *Geryon quinquedens* and the stone crab *Menippe mercenaria.* – Mar. Ecol. Prog. Ser. *2,* 91–95.

Summers, R. W., 1980. The diet and feeding behaviour of the flounder *Platichthys flesus* (L.) in the Ythan estuary, Aberdeenshire, Scotland. – Estuar. coast. mar. Sci. *11,* 217–232.

Tesmer, Ch. A. & Broad, A. C., 1964. The larval development of *Crangon septemspinosa* (Say). – Ohio J. Sci. *4,* 239–250.

Tiews, K., 1983. Über die Veränderungen im Auftreten von Fischen und Krebsen im Beifang der deutschen Garnelenfischerei während der Jahre 1954–1981. Ein Beitrag zur Ökologie des deutschen Wattenmeeres und zum biologischen Monitoring von Ökosystemen im Meer. – Arch. FischWiss. *34,* 1–156.

Webb, G. E., 1921. The larvae of the Decapoda Macrura and Anomura of Plymouth. – J. mar. biol. Ass. U.K. *12,* 1–385.

Wickins, J. F., 1972a. Developments in the laboratory culture of the common prawn, *Palaemon serratus.* – Fishery Invest., Lond. (Ser. 2) *27*(4), 1–23.

Wickins, J. F., 1972b. Experiments in the culture of the spot prawn *Pandalus platyceros* Brandt and the giant freshwater prawn *Macrobrachium rosenbergii* (de Man). – Fishery Invest., Lond. (Ser. 2) *27*(5), 1–23.

Wienberg, R., 1982. Larvalentwicklung im Labor erbrüteter Tiefseegarnelen, *Pandalus borealis* (Crustacea, Decapoda). – Verh. naturwiss. Ver. Hamburg *25,* 185–205.

Williamson, D. I., 1960. Crustacea, Decapoda, Larvae. VII. Caridea, Familiy Crangonidae. Stenopodidae. – Fich. Ident. Zooplankton *90,* 1–5.

Williamson, H. C., 1901. On the larval stages of decapod Crustacea. The shrimp (*Crangon vulgaris* Fabr.). – Rep. Fishery Bd Scotl. *19,* 92–120.

Williamson, H. C., 1915. Crustacea Decapoda. Larven. – Nord. Plankt. (Zool.) *6,* 315–588.