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Seasonal movements and the osmotic behaviour of the shrimp *Crangon crangon* L.

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Document Version

Publisher's PDF, also known as Version of record

Publication date:

1941

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Broekema, M. M. M. (1941). *Seasonal movements and the osmotic behaviour of the shrimp Crangon crangon* L. s.n.

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TABLE 10

Salinity limits for egg development in *Ostrea* and *Crangon*.

lower salinity limit* (in ‰)	higher salinity limit* (in ‰)
26	40
20	40
6	37
8	36
18	45
12	42

the highest or the lowest salinity in which development can take place; that is to say, salinities at which development were recorded.

This discrepancy can be explained by BROEKHUYSEN (see page 37), very probable in view of the fact that all-grown shrimps point in the

whether differences in salinity affect the rate of development of the eggs. (p. 97) development of *Carcinides* is retarded by differences in salinity. and that in *Ostrea gigas* development is retarded in extremely high and low salinities. Although in my experiments with *Crangon* on the rate of development is retarded in low salinity, this influence, as shown in Table 10, is negligible.

Number of days elapsing between the beginning of the first larval stage and the beginning of the first moult. For a number of cases, each case was recorded at a certain temperature and salinity. The average was calculated for each group belonging to a certain temperature and salinity, the number of which is recorded in a table. The average rate of development is given to different parent animals in Table 11. It is slightly retarded in low salinity, although to a smaller

TABLE 11

Rate of development of shrimp eggs in relation to temperature and salinity

Series 1. Temp. 8-10° C			Series 2a. Temp. 16-18° C			Series 2b. Temp. 16-18° C		
salinity in ‰	average number of days	number of parent animals	salinity in ‰	average number of days	number of parent animals	salinity in ‰	average number of days	number of parent animals
10 -11			5-8	10	1	10 -11	12	1
15.5-16.5	23	1	10-13	11	2	15.7-17.3	9	1
20 -21	15	3	15-18	8	4	20.3-22.1	9	1
25 -26	17	1	20-23	10	3	25.5-28.8	9	2
30 -31	16	1	25-28	8	3	30.7-33.5	6.5	2
35 -36	11	3	30-33	8	2	35.5-39.4	10.5	2
40 -41	11	2	35-38	8.5	2	40.5-44.8	9	2
45 -46			40-42	10.5	2	45.3-51		

degree, is exercised by extremely high salinities. The highest rate of development was recorded in salinities of 35-41 ‰ at a temperature of 8-10° C and in salinities of 25-33 ‰ at 16-18° C. The retarding influence exercised by a too low salinity is much more distinct at a high than at a low temperature. Table 11 at the same time shows that at a temperature of 16-18° C the development proceeds $1\frac{1}{2}$ -2 times as quickly as at a temperature of 8-10° C.

The difference appears to be greatest in salinities lower than 30 ‰. The conclusions drawn from the data compiled in Table 11 must be regarded as provisional, however, the number of data being too small to permit of any well founded inference.

Summary of part I

1. The salinity optimum for shrimps of about 2 years old is ca. 33 ‰ at a temperature of 3-5° C, and 28-29 ‰ at 20-22° C. In other words: with increasing temperature the salinity optimum shifts towards the less saline water.

2. The salinity optimum for shrimps of about one year old at a temperature of 22° C is 18-19 ‰. Consequently, with increasing age the optimum shifts towards a higher salinity.

3. A combined influence of temperature and salinity in the same sense as stated sub 1 could also be demonstrated in the case of newly hatched larvae; here, too, increasing temperature caused the salinity optimum to shift in a downward direction.

4. The salinity range available for normal development of the eggs proved to depend on temperature in a similar way as described sub 1 and 2, the higher as well as the lower salinity limit shifting downward with increasing temperature.

5. The salinity range for a normal development of the eggs proved to be very wide. It includes not only the more saline part of the salinity range of full-grown shrimps in nature, but also higher salinities up to 40 ‰, i.e. 4-5 ‰ more than we find in their natural habitat.

6. The above-mentioned results agree with data collected by HAVINGA concerning:

- a. distribution of young and full-grown shrimps,
- b. seasonal migration,
- c. salinities in which development of the eggs takes place in nature.

Various statements in literature concerning distribution and migration in a number of Crustacea make it clear that in this respect *Crangon* is no isolated instance. For a detailed account I refer to a paper by BALSS (1930), from which the following is quoted:

"Bei den marinen Formen sind sie (die Wanderungen) besonders aus der gemässigten Zone bekannt, und erfolgen so, dass die Tiere im Sommer ins oberste Litoral gehen, wo die Temperaturen höher sind, während sie im Winter, wenn die Oberflächentemperaturen niedriger und stark wechselnd sind, sich mehr in die Tiefe (etwa 40 m) mit ihrer wärmeren und gleichmässigeren Temperatur zurückziehen." These general conclusions are based on data concerning the following species: *Leander adspersus*, *Homarus vulgaris*, *Homarus americanus*, *Cancer pagurus*, *Callinectes sapidus*, *Pandalina brevirostris*, *Galathea squamifera*, *Chionoecetes opilio*, *Maja squinado*, *Portunus puber*, *Carcinides maenas* and *Eriocheir sinensis*. In all these cases a seasonal change in distribution occurs, essentially similar to that described for *Crangon* and *Carcinides*. Possibly in these cases, too, a combined

influence of temperature and

BALSS also compiles the data on the eggs develop in nature. It only takes place in the more saline *Carcinides maenas* (see also BALSS 1930), *Pandalus montagui*, *Leander adspersus*, *Cancer pagurus*, and *Callinectes sapidus*. In some fresh water Crustacea a similar place in the sea; to this end sea in order to spawn (e.g. *Callinectes rostris*).

PART II. THE INFLUENCE OF TEMPERATURE AND SALINITY ON THE OSMOTIC BEHAVIOUR

Introduction

The experiments described in this section deal with the suitability of a given medium for the development of the shrimp under different temperature-salinity conditions. Obviously, the combination of temperature and salinity is of great importance. This brings us immediately to the question: does this combined influence have any effect on the development of the shrimp?

The most plausible suggestion is that temperature has some influence or other on the development of the shrimp. Distributional data for *Crangon* is a pre-eminently suitable example. The salinity range between appropriate and unsuitable distributional data show that only a part of the range is covered twice, while the rest as I could make out nothing of. This suggests that the internal concentration is not in equilibrium with the external concentration, but that it is regulated.

1. all changes in concentration are followed passively by the internal concentration; the animal is perfectly poikilohaline.

2. the shrimp disposes of a mechanism which enable it to maintain an internal concentration independent of the external concentration.

The object of the experiments described in this section can be summarized as follows:

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influence of temperature and salinity could be demonstrated.

BALSS also compiles the available data as to the area where the eggs develop in nature. In the following cases development only takes place in the more saline part of the area of distribution: *Carcinides maenas* (see also BROEKHUYSEN 1936), *Crangon crangon*, *Pandalus montagui*, *Leander adspersus*, *Homarus americanus*, *Cancer pagurus*, and *Callinectes sapidus*. It should be added that even in some fresh water Crustacea development of the larvae takes place in the sea; to this end the parent animals migrate to the sea in order to spawn (e.g. *Eriocheir sinensis* and *Leander longirostris*).

PART II. THE INFLUENCE OF TEMPERATURE AND SALINITY ON THE OSMOTIC BEHAVIOUR OF THE SHRIMP

Introduction

The experiments described in part I prove that for *Crangon* the suitability of a given medium depends largely upon its temperature-salinity conditions. Obviously these two factors act in combination. This brings us immediately to the next question: how does this combined influence of temperature and salinity come about?

The most plausible suggestion seemed to me that temperature has some influence or other on the osmotic behaviour of the shrimp. Distributional data make it abundantly clear that *Crangon* is a pre-eminently euryhaline species, occurring over a salinity range between approximately 10 and 35 ‰. Besides, distributional data show that the greater part, if not the whole of the range is covered twice a year by each individual. As far as I could make out nothing is known about the way in which the internal concentration is influenced by these drastic changes in external concentration, but, a priori, there are two possibilities:

1. all changes in concentration of the external medium are followed passively by the internal medium; in other words the animal is perfectly poikilosmotic;

2. the shrimp disposes of osmoregulatory mechanisms which enable it to maintain an internal concentration more or less independent of the external concentration.

The object of the experiments to be described in the following section can be summarized as follows.

determined all the same, although the result was left out of account in the calculation of average concentrations.

Summary of part II

1. *Crangon* is homoiosmotic.¹⁾ The blood concentration, however, is not independent of the concentration of the external medium; an increase (decrease) in external concentration results in an increase (decrease) in internal concentration, although in general to a much smaller degree.

2. In salinities lower than 21–23 ‰ *Crangon* is hypertonic, in those higher than 21–23 ‰ *Crangon* is hypotonic in respect to its medium.

3. The difference between in- and external concentration is greater at high than at low temperatures; this applies both to those situations where the animal is hypotonic and to those situations where the animal is hypertonic in respect to its medium.

4. The position of the point of isotonicity partly depends on temperature: at a temperature of 20° C isotonicity prevails in a salinity of about 21.5 ‰, at 4° C in a salinity of about 23 ‰.

5. Shrimps which were subjected to the seasonal increase (decrease) in temperature taking place during spring (autumn) showed a slight decrease (increase) in internal concentration. That this decrease (increase) is directly related to the change in temperature, no other seasonal influence being involved, could be proved by comparing the influence of a changing with that of a constant temperature. In the animals kept at a constant temperature no seasonal decrease or increase in blood concentration could be recorded.

6. Adaptation of the internal concentration to a change in external concentration takes place at a higher rate as temperature is higher. During adaptation to a medium of much higher (lower) concentration the blood concentration reaches a maximum (minimum) value which may considerably exceed the final blood concentration in the new medium. These

¹⁾ The term „homoiosmotic” is used here in the broader sense suggested by KROGH (1939, p. 8).

maxima (minima) are more than when it is high, indicated less checked by low tempera

7. In a constant salinity of 10° C brings about a decrease constant salinity of 25 ‰, 0 in temperature brings about It is important to note that in- and external concentrati

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7. In a constant salinity of $15/_{00}$ a decrease in temperature of 10°C brings about a decrease in blood concentration. In a constant salinity of $25/_{00}$, on the other hand, the same decrease in temperature brings about an increase in blood concentration. It is important to note that in both cases the difference between in- and external concentration becomes smaller.

8. Neither during increase nor during decrease in external concentration a change in weight could be recorded.

9. In newly moulted shrimps the difference between in- and external concentration is always smaller than in "hard" animals.

10. No difference in average blood concentration could be proved to exist in young and old animals (aged 16 months and 33 months respectively). As young animals apparently are able to stand much lower salinities than the older specimens it would seem that in the younger animals the lower admissible limit for the blood concentration is lower than for the older animals.

Nor could a difference in blood concentration be recorded in ovigerous and non-ovigerous females. The fact that ovigerous females do not occur in low salinities might possibly be caused by the parent animals losing their eggs in media of low salinity.

GENERAL SURVEY

The original object of this investigation was to try and find an explanation for the distribution of *Crangon crangon* L.

The fact that this distribution shows a marked seasonal change made it conceivable, especially in connection with former experiments (BROEKHUYSEN 1936, CAUDRI 1937), that we should have to do with a combined influence of temperature and salinity.

Briefly, the seasonal change in distribution of *Crangon* comes to the following. During winter the animals can be found in the coastal regions of the North Sea and in a small part of the adjoining shallows; that is to say, in an area of relatively high salinity. During spring a general migration takes place towards the brackish waters, where the animals remain in great numbers throughout the summer months. Towards autumn the animals