

**The Mollusca of the estuarine region of the rivers  
Rhine, Meuse, and Scheldt in relation to the  
hydrography of the area. V. The Cardiidae<sup>1</sup>**

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**1. INTRODUCTION**

Three species of the Cardiidae have been mentioned in the southwestern part of The Netherlands where the rivers Rhine, Meuse and Scheldt form a large estuarine area, generally known as the Delta area (fig. 1). Jutting (1943) recorded *Cerastoderma edule* (L., 1758) (s.n. *Cardium edule*) as a common species, and mentioned also a var. *lamarcki* Reeve, 1843. This variety was raised to specific rank by Petersen (1958) as *Cardium lamarcki* Reeve, 1843, and is now widely known either as *Cerastoderma glaucum* (Poiret, 1789) (Bowden & Heppell, 1968) or as *Cerastoderma glaucum* (Bruguère, 1789) (Russell, 1971). The second combination is wrong (Boyden, 1971). Van Dalsum (1947) recorded the occurrence of *Cardium exiguum* Gmelin, 1791, from a canal with stagnant brackish water on the island of Walcheren. Judging from the descriptions by Van Dalsum (op. cit.) and by Petersen & Russell (1971) the animals from Walcheren belong to *Cerastobysum exiguum* (Gmelin, 1791) and not to the recently described *Cardium hauniense* Petersen & Russell, 1971. *Cerastobysum exiguum* was never found again, but *Cerastoderma edule* and *Cerastoderma glaucum* proved to be common species in the Delta area. Originally we wanted to investigate whether there existed taxonomical differences between the latter two species, but when we became convinced that we really studied two different species, more emphasis was placed on the investigation of the ecological characteristics of these

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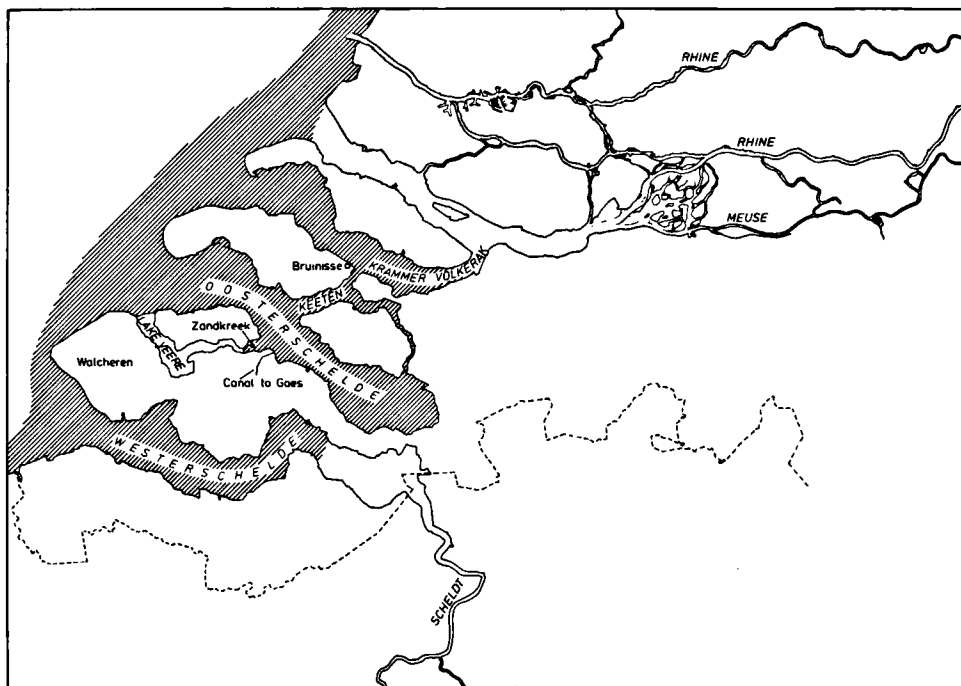


Fig. 1. Map of the estuarine area of the rivers Rhine, Meuse, and Scheldt. The distribution of *Cerastoderma edule* is indicated by cross hatching.

two cockles. Also the relation between mean rib number and salinity as formulated by Eisma (1965) was studied in detail, because Eisma did not distinguish between *C. edule* and *C. glaucum*.

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## 2. TAXONOMICAL DIFFERENCES BETWEEN *C. EDULE* AND *C. GLAUCUM*

### 2.1. Cytology

To study the cytology of *C. edule* and *C. glaucum* animals of both forms were collected at several places. In the laboratory microscopic slides of the gonads were made

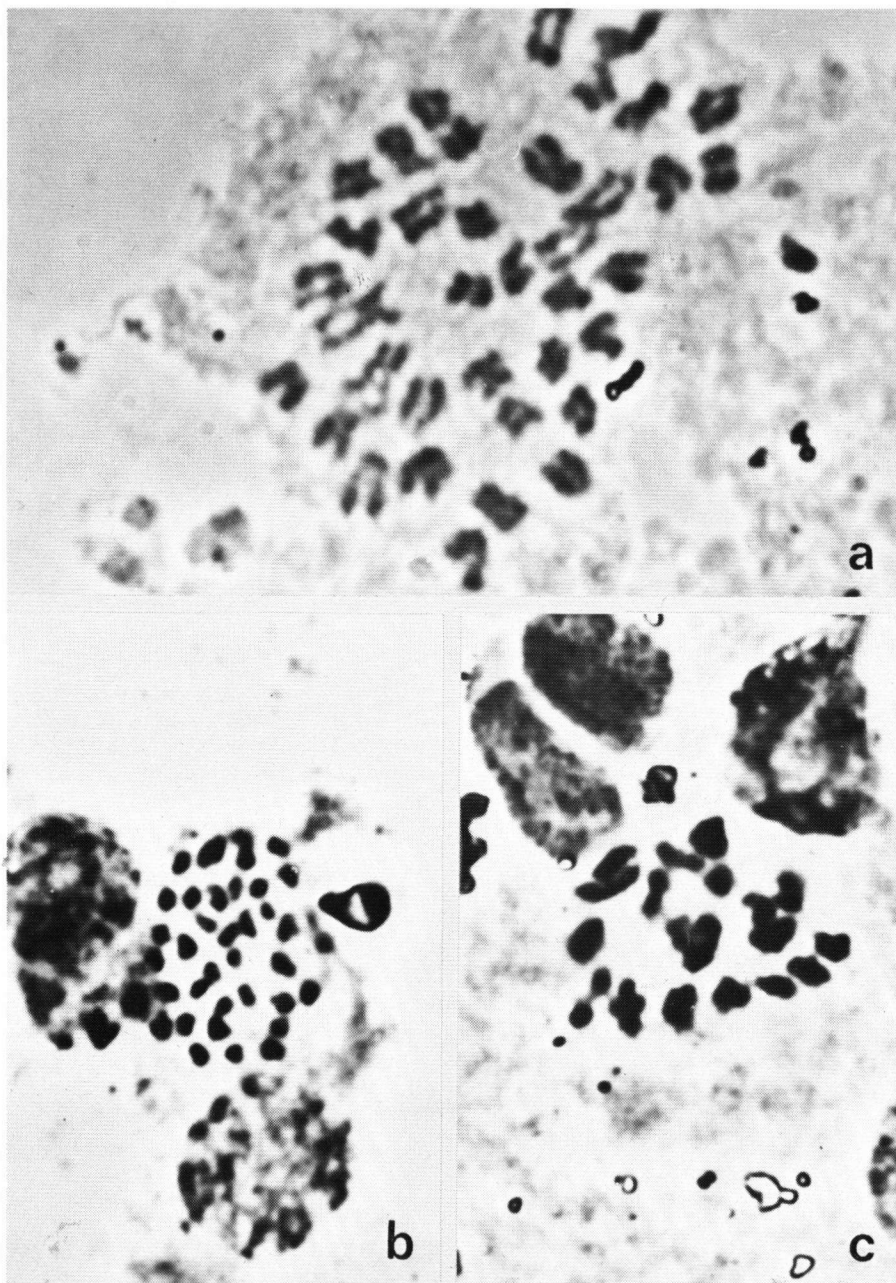


Fig. 2. a. Mitosis of *Cerastoderma edule*; b. Meiosis of *C. edule*; c. Meiosis of *C. glaucum*.

chromosome no.	position of centromere	length specimen a	length specimen b	mean length
1	submedian	3.75	4.00	3.87
2	terminal	3.50	3.25	3.37
3	terminal	3.25	3.25	3.25
4	subterminal	3.00	3.00	3.00
5	submedian	3.00	2.75	2.87
6	subterminal	2.50	2.75	2.62
7	terminal	2.50	2.75	2.62
8	subterminal	1.75	2.50	2.12
9	submedian	1.75	2.25	2.00
10	subterminal	1.50	2.25	1.87
11	submedian	1.50	2.00	1.75
12	submedian	2.00	1.75	1.87
13	subterminal	1.75	1.75	1.75
14	subterminal	1.75	1.50	1.62
15	submedian	1.50	1.75	1.62
16	subterminal	1.50	1.50	1.50
17	terminal	1.25	1.25	1.25
18	terminal	1.25	1.25	1.25
19	submedian	1.25	1.25	1.25

Table 1. Karyotype of *Cerastoderma edule*. The data refer to two different animals. Lengths in  $\mu$ .

with the lacto-acetic-orcein squash method. Selected slides were photographed and handled as described by Butot & Kiauta (1966). Although Keyl (1956) stated that in *Cardium edule* the chromosome number cannot be studied due to technical problems we did not encounter any particular problem. The difference probably may be ascribed to the different types of fixation used.

In this way up to 60 specimens of *C. edule* and 71 specimens of *C. glaucum* were studied. About 300 photographs of *C. edule* and 380 of *C. glaucum* were made. For *C. edule* three meiotic metaphases II could be studied in detail, for *C. glaucum* only two. Mitotic metaphases could be studied in detail in *C. edule* only.

After the study of this material the chromosome number of *C. edule* was determined as 38 diploid and 19 haploid. For *C. glaucum* the same numbers were found. Fig. 2a depicts a mitosis of *C. edule* from an animal collected in the Zandkreek on March 27, 1969. A meiosis of *C. edule* from an animal from the Oosterschelde is shown in fig. 2b. The karyotype of *C. edule* is presented in Table I. A meiosis of *C. glaucum* from an animal from the Kreek van Westkapelle is shown in fig. 2c. The material was insufficient for a karyotype of *C. glaucum*.

Dr. B. Kiauta (Genetical Institute, Utrecht) kindly drew our attention to the phenomenon of precocious segregation on some of the photographs of *C. glaucum* (cf. Kiauta, 1971). In *C. edule* this phenomenon was not observed.

## 2.2. Transplantation experiments

The first transplantation experiment was carried out by the second author in 1965. Many hundreds of *C. glaucum* were collected in the stagnant brackish Lake Veere and transferred to the euhaline tidal Oosterschelde estuary. At the same time many hundreds of *C. edule* were brought from the Oosterschelde estuary to Lake Veere. Of *C. glaucum* 7 specimens were recovered alive, but of *C. edule* no live specimens were observed. However, during the experiment the salinity of the brackish Lake Veere became extremely low and this probably interfered with the experiments.

The experiment was repeated early in 1969. This time 650 specimens of *C. edule* were collected in the Oosterschelde estuary near Yerseke and distributed over several places in the brackish Lake Veere. In Lake Veere 550 specimens of *C. glaucum* were collected and distributed over four places at different tidal levels in the Oosterschelde estuary.

In the autumn of 1969 not a single live specimen of *C. edule* was recovered in Lake Veere. In the Oosterschelde estuary, however, 11 live *C. glaucum* were found among many dead specimens. The majority of the live animals occurred at the lowest tidal level with some at an intermediate level.

Hence, *C. edule* seems unable to live in the habitat of *C. glaucum* but *C. glaucum* may survive in the habitat of *C. edule*.

## 2.3. Velocity of burying

*C. edule* lives constantly buried. *C. glaucum*, however, lives in some places between plant growth (Petersen, 1958). Because Kristensen (1957) demonstrated a temperature influence on the burying velocity, this process was studied in both species. To exclude environmental conditioning the specimens for the experiments were collected at the only place where both species occur together, viz., near the locks in the canal to Goes. First experiments were carried out in the laboratory in water of nearly the same salinity (16‰ Cl<sup>-</sup>) and temperature (16-18°C) as in the canal. For animals of 15-19 mm shell length it was found that *C. edule* buried significantly (Wilcoxon test,  $p < 0.005$ ) faster than *C. glaucum*. A second series of experiments was run in Lake Veere at 18°C and 9‰ Cl<sup>-</sup>. Here *C. edule* refused to bury, but *C. glaucum* buried as fast as at a salinity of 16‰ Cl<sup>-</sup> (Wilcoxon test,  $p \gg 0.05$ ).

During the experiments it was observed that *C. edule* dug at a constant rate, but the movements of *C. glaucum* slowed down during digging.

It may be concluded that *C. edule* and *C. glaucum* differ considerably in their burying behaviour.

## 2.4. Parasites

During the cytological examination of *C. edule* a larval parasitic trematode, probably an undescribed species, was found. The cyste is about 40  $\mu$  in diameter. This worm was never met with in the slides of *C. glaucum*.

## 2.5. Discussion of the taxonomical status of *C. edule* and *C. glaucum*

The rapidly expanding literature on *C. edule* and *C. glaucum* contains many data pointing to a taxonomical difference between the two species. Petersen (1958) and Van Urk (1973) describe the morphological differences of the shells, whereas Rygg (1970) mentions a morphological difference in the spermatozoa. Jelnes, Petersen & Russell (1971) found clear differences in the electrophoretic patterns of the two species. There are also physiological differences. Rygg (1970) experimentally found an important difference in salinity tolerance, Boyden (1972) reports on differences in the survival of both species in air, and Kingston (1974) found differences in growth velocities of the larvae at higher water temperatures. Behavioural differences are mentioned by Petersen (1958), Rygg (1970), Boyden (1972) and this paper. A difference in the time of spawning has also been reported (Rygg, 1970; Boyden, 1971a). Rygg mentions that *C. glaucum* spawns before *C. edule*, but he infers this conclusion from the size of the shells of the metamorphosed larvae. Therefore, Boyden's conclusion that *C. edule* spawns before *C. glaucum* seems more reliable. Kingston (1974a), however, does not find an appreciable difference in timing. There also exist differences in the parasite fauna of the two species (Fenchel, 1966; Boyden, 1971a; Lauckner, 1971; this paper).

The taxonomical differences made probable by these data, have been tested by transplantation experiments (this paper) and by hybridization experiments (Kingston, 1973, 1974). Interspecific matings appear less viable than intraspecific ones. The cytological data (this paper) also show differences, but these appear to be slight.

When *C. edule* and *C. glaucum* are accepted as taxonomically different species, differences in distribution and ecology also become apparent.

*C. edule* has been found in tidal waters from the Arctic Ocean to Morocco. *C. glaucum* has a discontinuous distribution along the coasts of Europe up to southern Norway and also lives exclusively in the Baltic, the Mediterranean and the Black Sea (Russell, 1971). On a smaller scale *C. edule* lives in tidal waters, and *C. glaucum* mostly in non-tidal ones (Petersen, 1958; Russell, 1971, 1972; Boyden & Russell, 1972; Van Urk, 1973; this paper).

The final conclusion is that *C. edule* and *C. glaucum* are a pair of closely related, but nevertheless different species.

## 3. DISTRIBUTION AND ECOLOGY IN THE ESTUARINE AREA OF THE RIVERS RHINE, MEUSE AND SCHELDT

### 3.1. *Cerastoderma edule*

The distribution and ecology of *C. edule* in the estuarine area of the SW. Netherlands have already been described by Wolff (1973). Therefore, only those aspects will be discussed which are important for a comparison with *C. glaucum*.

*C. edule* may be found nearly everywhere in tidal waters with a fairly high salinity (fig. 1). In stagnant inland waters it is virtually absent, except for some specimens found living just behind the locks to the Oosterschelde estuary in the canal to Goes. In Lake Veere only one stunted specimen was found among thousands of *C. glaucum* during a

sampling program in 1964. From the growth marks it could be deduced that this specimen had settled before that estuary was changed into a lake in 1961, whereas all specimens of *C. glaucum* had settled in 1963 after the extremely severe winter 1962/63. It has to be concluded that *C. edule* is almost completely restricted to areas with tidal or other water movement, a conclusion also reached by Russell (1971), Boyden & Russell (1972), and Barnes (1973). The reason for this pattern of distribution is not yet clear, although Russell (1971) postulates a detrimental effect of a substance liberated by the living cockles themselves.

The salinity range of *C. edule* is difficult to determine from observations in the field. In the Westerschelde estuary it reaches its riverward limits about at the isohaline of  $12^{\circ}/\text{oo Cl}^{-}$  during average river discharge, but during periods of high river discharge in winter the same animals have to tolerate salinities of  $4\text{--}5^{\circ}/\text{oo Cl}^{-}$ . However, during such periods considerable numbers die. In the Keeten-Krammer-Volkerak estuary *C. edule* was found up to about the isohaline of  $10^{\circ}/\text{oo Cl}^{-}$  during average river discharge, but during periods of high river discharge in winter salinities of  $3\text{--}4^{\circ}/\text{oo Cl}^{-}$  were measured at the same locality. Here also considerable mortality was noted. It may be concluded that the lower limit of the salinity tolerance of *C. edule* lies at about  $10\text{--}12^{\circ}/\text{oo Cl}^{-}$ . This is in accordance with the conclusion of Petersen (1958) who mentions salinities of about  $11^{\circ}/\text{oo Cl}^{-}$  as the lower limit. It is not possible to infer anything from field observations about the upper salinity limit of *C. edule*. In the Delta area it was still found in salinities of  $17^{\circ}/\text{oo Cl}^{-}$ . Its absence from still higher salinities seems to be caused by other factors (Wolff, 1973). Rygg (1970) experimentally found a salinity tolerance ranging from  $5.5$  to  $25^{\circ}/\text{oo Cl}^{-}$  at  $16\text{--}17^{\circ}\text{C}$ .

### 3.2. *Cerastoderma glaucum*

In the estuarine area of the SW. Netherlands *C. glaucum* only has been found in stagnant brackish inland waters (fig. 3). Water movements in these waters are mostly minimal (below  $1\text{ cm/sec}$ ), although in some waters slightly higher current velocities may occur.

The maximal salinity to be tolerated by *C. glaucum* in these inland waters is about  $13^{\circ}/\text{oo Cl}^{-}$  but it has to be noted that higher values have only rarely been found in any stagnant brackish water. The lowest salinities *C. glaucum* had to endure, are  $4\text{--}5^{\circ}/\text{oo Cl}^{-}$ . This seems to be the lower limit of tolerance because similar inland waters with still lower salinities are abundant. Rygg (1970) experimentally found a salinity range of  $2.7\text{--}25^{\circ}/\text{oo Cl}^{-}$  at  $16\text{--}17^{\circ}\text{C}$ .

The apparent restriction of *C. glaucum* to stagnant brackish waters has been explained by an influence of temperature (Russell, 1971). *C. glaucum* should not be able to breed when summer temperatures remain below  $20^{\circ}\text{C}$ . Temperatures of over  $20^{\circ}\text{C}$  indeed do occur in all stagnant inland waters of the Delta area, but they are also a normal feature of the shallow eastern part of the Oosterschelde estuary. In 15 out of 19 summers the average water temperature for fourteen days was at least once  $20.0^{\circ}\text{C}$  or more (Korringa, 1941). Nevertheless, *C. glaucum* was never met with in this tidal area. Apparently, the hypothesis advanced by Russell needs some modification. Also Kingston's (1974) experimental data on fertilization and larval growth are not in favour of a temperature limitation of *C. glaucum*. We have the impression that the mobility of the sediments in

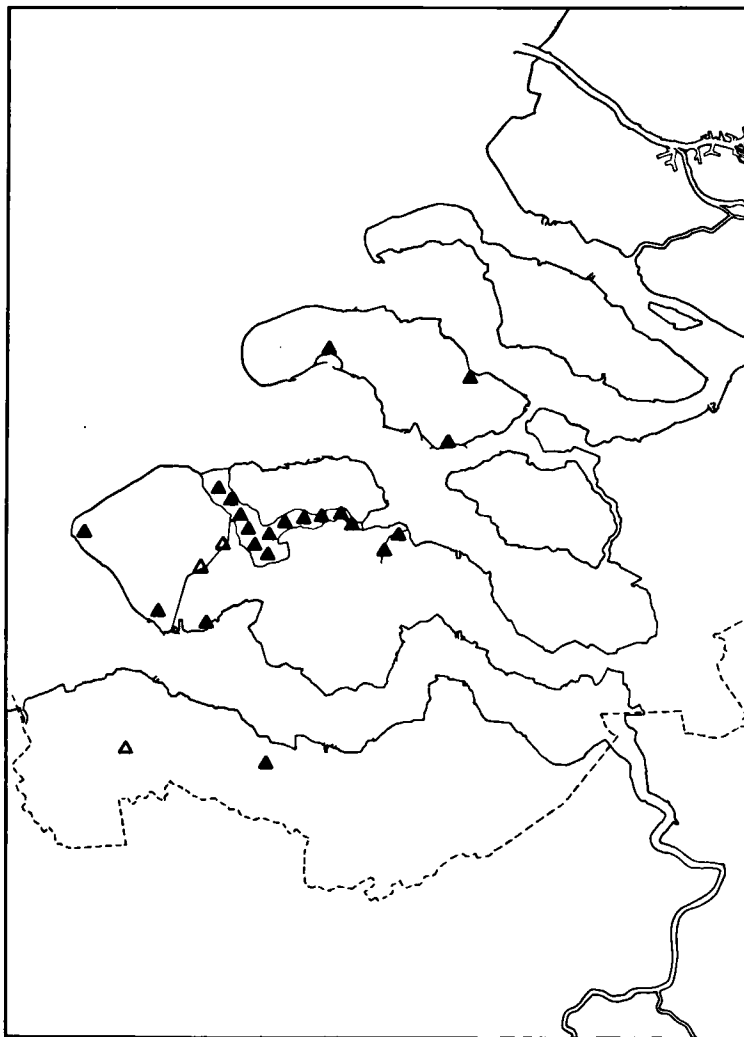


Fig. 3. Distribution of *Cerastoderma glaucum*. The open triangles denote places where the species has disappeared, probably due to water pollution.

tidal waters may also be a factor of importance in connection with the feeble burrowing capacities of the species. Russell (1972), Boyden & Russell (1972), and Barnes (1973) advance the hypothesis that *C. glaucum* neither does tolerate wave-action, nor a long



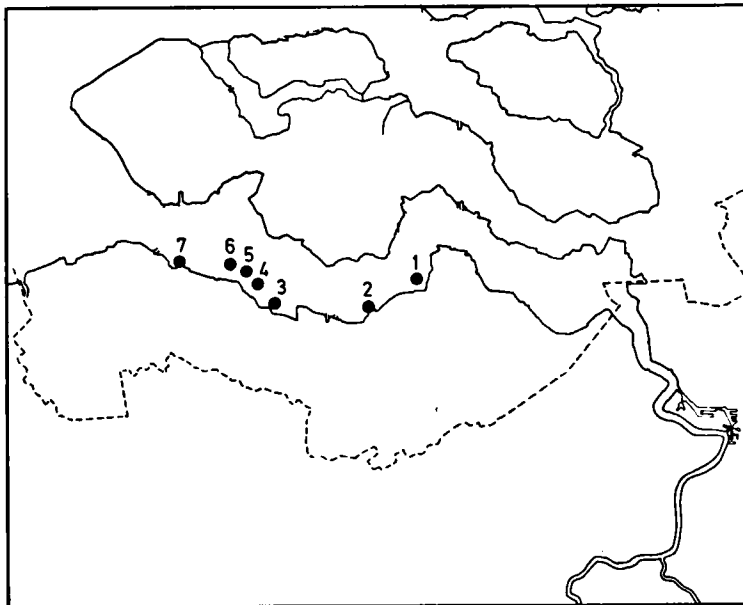


Fig. 4. Localities where *Cerastoderma edule* was collected for an investigation of the relationship between rib number and salinity.

period of emersion. The pattern of distribution in the Delta area agrees with this hypothesis.

#### 4. RELATIONS BETWEEN SALINITY AND MEAN RIB NUMBER

Using data of the work of earlier authors Eisma (1965) established a correlation between average salinity and mean rib number of *Cerastoderma* shells. However, he did not consider *C. glaucum* to be specifically different and his relationship between rib number and salinity is based on mixed data from both species. So it is not astonishing to see that the regression lines he calculated change direction at a salinity of about  $10^{\circ}/\text{oo Cl}^-$ , close to the lower limit of tolerance of *C. edule*. Apparently, the relation between mean rib number and salinity is different for both species. This conclusion has also been reached in a later paper by Eisma et al. (1976) and by Boyden (1973).

We have considered this problem in more detail. The relation between average salinity and mean rib number for *C. edule* was investigated with the aid of samples from tidal flats along the Westerschelde estuary (fig. 4). This resulted in a significant correlation between salinity at high tide during average river discharge, and mean rib number (fig. 5). The

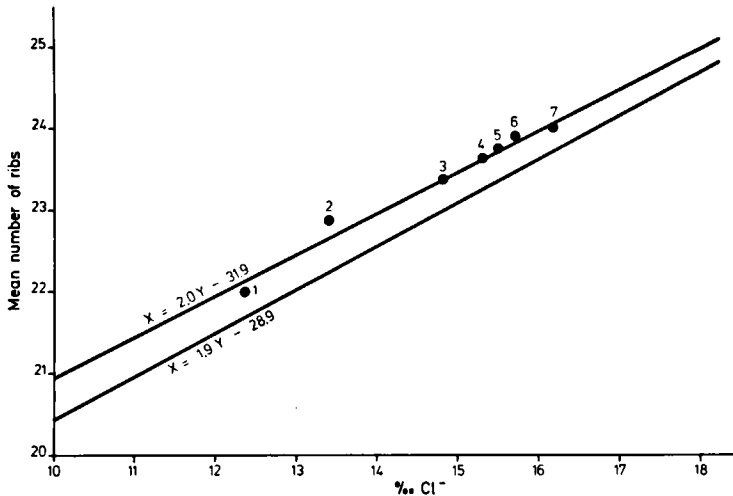


Fig. 5. Regression lines for the relationship between mean rib number of *Cerastoderma edule* and salinity. The upper line represents our data, the lower one Eisma's (1965) data.

computed regression line lies very close to the regression line computed by Eisma (1965) for salinities of over  $10^{\circ}/\text{oo Cl}^{-}$  and to another very similar line by Eisma et al. (1976) for *C. edule* from all Dutch coastal waters. Whether it differs from the curved line determined by Boyden (1973) cannot be told, since we do not have data from salinities of over  $16.5^{\circ}/\text{oo Cl}^{-}$ . However, the relationship found does not exclude the possibility mentioned by Russell (1972a) that there exists a relationship between mean rib number and exposure to wave action, although this does not seem very probable in view of the localities sampled. This relationship, however, may explain the difference between our regression line and that of Boyden (1973). Eisma et al. (1976) list uncertainties in the salinity determination as another possible source of differences.

The same relationship for *C. glaucum* was investigated with the aid of samples from the inland waters shown in fig. 3. No significant correlation between mean rib number and average salinity, minimal salinity, maximal salinity, or median salinity (see Heerebout, 1970, for definition) could be found. Apparently no simple relationship exists between rib number and salinity for *C. glaucum* in the Delta area. Also Russell (1972a) was not able to correlate rib number with environmental conditions. The influence of the presence of *C. edule* on the rib number of *C. glaucum* Russell assumes, does not exclude completely the possibility that this influence can be ascribed to some abiotic factor. Boyden (1973), however, assumes a relationship with low rib numbers at low as well as high salinities and high rib numbers at intermediate values. Although this may be true, we consider his data inconclusive. For the time being we want to conclude that there is no correlation between mean rib number and any environmental factor in *C. glaucum*.

Instead we propose the hypothesis that in the case of *C. glaucum* we are dealing with many isolated populations, each with its own genetically fixed mean rib number. From Eisma's (1965) data we conclude that all Zuiderzee samples belong to one and the same population living in a salinity range of 3.0-10.0‰  $\text{Cl}^-$  and having a mean rib number between 19.7 and 20.5 (samples with less than 50 specimens have not been considered, nor has a sample from the Makkumerwaard consisting of empty valves). This is in contrast with the situation in *C. edule* where mean rib number seems to be determined primarily ecologically.

This hypothesis is at variance with the conclusion of Palenzona et al. (1971). However, their *C. edule* most probably is *C. glaucum*, because their specimens originate from the Mediterranean region (Russell, 1971). Moreover, we believe that they base their conclusion on a false assumption concerning the genetic relationship between number of ribs and shell length.

Finally we want to adjust the method developed by Eisma (1965) for the estimation of the salinity of fossil seas from the mean rib number of *Cerastoderma* shells, as follows: (1) only shells of *C. edule* present: tidal sea; salinity may be determined from mean rib number; (2) shells of *C. edule* and *C. glaucum* present: sea with feeble tidal movements; salinity may be estimated from mean rib numbers of *C. edule*; (3) only shells of *C. glaucum* present: non-tidal brackish water; information on salinity cannot be gained from mean rib numbers.

## 5. SUMMARY

Based on literature data and personal investigations it is concluded that *Cerastoderma edule* (L.) and *C. glaucum* (Poirét) are closely related, but distinct species. The haploid chromosome number of both species is 19. The distribution and ecology of the two species in the estuarine area of the rivers Rhine, Meuse and Scheldt are described in relation to environmental factors. *C. edule* lives nearly exclusively in tidal environments, *C. glaucum* in areas with stagnant water. This is in accordance with the hypotheses that *C. edule* cannot live in stagnant water, owing to a detrimental substance liberated by the living animals themselves, and that *C. glaucum* does not tolerate wave-action or a long period of emersion.

It is concluded that *C. edule* shows a correlation between mean rib number and mean salinity, whereas *C. glaucum* does not. Therefore Eisma's (1965) method for determining the salinity of fossil seas is modified.

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