POPULATION DYNAMICS OF THREE BRACKISH WATER ISOPODS SPECIES (CRUSTACEA) IN THE LAGOON SYSTEM OF BAGES-SIGEAN (FRANCE) II. LIFE CYCLES, SEXUAL ACTIVITY AND FECUNDITY

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II. LIFE CYCLES, SEXUAL ACTIVITY AND FECUNDITY

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ISOPODES
DYNAMIQUE DES POPULATIONS
SEX RATIO
ACTIVITE SEXUELLE
ETANG SAUMATRE

RÉSUMÉ. — 1. Dans ce second article d'une série de trois sur la dynamique des populations de *Idotea baltica, I. granulosa* et *Sphaeroma hookeri,* le sex-ratio, l'activité sexuelle et la structure des populations sont pris en considération. 2. Le sex-ratio (nombre de mâles/nombre de femelles) est toujours supérieur pour *I. granulosa* que pour *I. baltica,* des valeurs maximales étant trouvées au printemps et en début de l'été. Le sex-ratio de *S. hookeri* est toujours fort bas. 3. L'activité sexuelle (femelles ovigères/femelles ovigères + non ovigères × 100 %) est globalement identique pour les trois espèces; elle n'est pas réglée par la température mais par les modifications saisonnières de la longueur de la journée. 4. L'activité sexuelle est considérablement influencée par la salinité, cette influence étant différente pour les deux espèces d'*Idotea.* 5. La distribution dans l'étang des différentes classes de taille n'est pas homogène : dans les stations à eau peu profonde on trouve beaucoup de juvéniles et d'adultes jeunes, tandis que les adultes de grande taille dominent dans les stations à eau profonde. 6. Le nombre d'œufs par femelle change pendant l'année. Pour *I. granulosa* ces changements sont plus importants que pour *I. baltica,* produisant un nombre d'embryons plus élevé pendant l'hiver. Il existe une corrélation linéaire entre le nombre d'œufs et la longueur totale de l'animal. 7. Pendant le développement, le nombre d'œufs reste constant.

ISOPODS
POPULATION DYNAMICS
SEX RATIO
SEXUAL ACTIVITY
BRACKISH LAGOON

ABSTRACT. — 1. In this second of three articles about the population dynamics of *Idotea baltica, I. granulosa* and *Sphaeroma hookeri,* the sex ratio, sexual activity, composition of the population and egg production are treated. 2. The sex ratio (no. of males/no. of females) of *I. granulosa* is higher than that of *I. baltica.* Peaks are found in spring and early summer. The sex ratio of *S. hookeri* is always low; 3. The sexual activity (no. of ovigerous females/total number of females × 100 %) of the three species has basically the same pattern. It is not regulated by temperature but by changes in the day length during the year. 4. Sexual activity is strongly influenced by salinity. The pattern is different for the two *Idotea* species. 5. The size classes are not evenly distributed throughout the lagoon system. At shallow stations many juveniles and young adults are found. At deeper stations the larger animals prevail. 6. The main numer of eggs per ovigerous female changes during the year. The pattern of *I. granulosa* is more erratic than that of *I. baltica,* resulting in a higher number of embryo's per female during the winter months. A linear correlation exists between the mean number of eggs and the total body length. 7. No loss of eggs is found during development.

INTRODUCTION

From Feb. 1982 to the end of May 1983 we studied the population dynamics of three free-swimming isopod species *Idotea baltica* (Pallas, 1772), (most probably we were dealing with the subspecies *I. baltica stagnea* Tinturier Hamelin, 1960, the most common subspecies in the brackish lagoons along the French Mediterranean coast. However, some doubt remains about its identity since the animals attain greater lengths than is common for this subspecies. Moreover, in larger animals the shape of the pleotelson, which is discriminative for the various subspecies is intermediate between the subspecies *I. b. baltica* and *I. b. stagnea* (Tinturier Hamelin, 1960). Since it was not our aim to do a taxonomical study, we thought it wise to use just the specific name *I. baltica* (Pallas, 1772), *Idotea granulosa* (Rathke, 1834) and *Sphaeroma hookeri* (Leach, 1814) in the lagoon system of Bages-Sigean, France. In part I (General aspects and Distribution) an extensive review is given of the study area and physical factors which is summarized here (Kouwenberg & Pinkster, 1985).

The lagoon system of Bages-Sigean is one of the brackish water lagoons along the French Mediterranean shores between Marseille and the French-Spanish border. It is about 14 km long, on average about 2.5 km wide and never deeper than 2.80 m. Its main freshwater influx comes from the river Berre in the S.W. and some small rivulets in the N.E. In the S.E. there is a narrow connection with the Mediterranean through the "Grau de Port-la-Nouvelle". Because of this a salinity gradient exists from the N. to the S.E. (Fig. 1). The most important climatic factors are the winds viz. the "Cers" or "Tramontane", a gale from the N.W. that blows for more than 200 days per year and the "Marin" which also blows quite powerfully from S.S.E. for about 20 % of the year. Together with solar irradiation they cause considerable and rapid changes in environmental conditions. The vegetation is dominated by *Zostera marina, Z. nana, Ulva lactuca* and *Gracilaria*

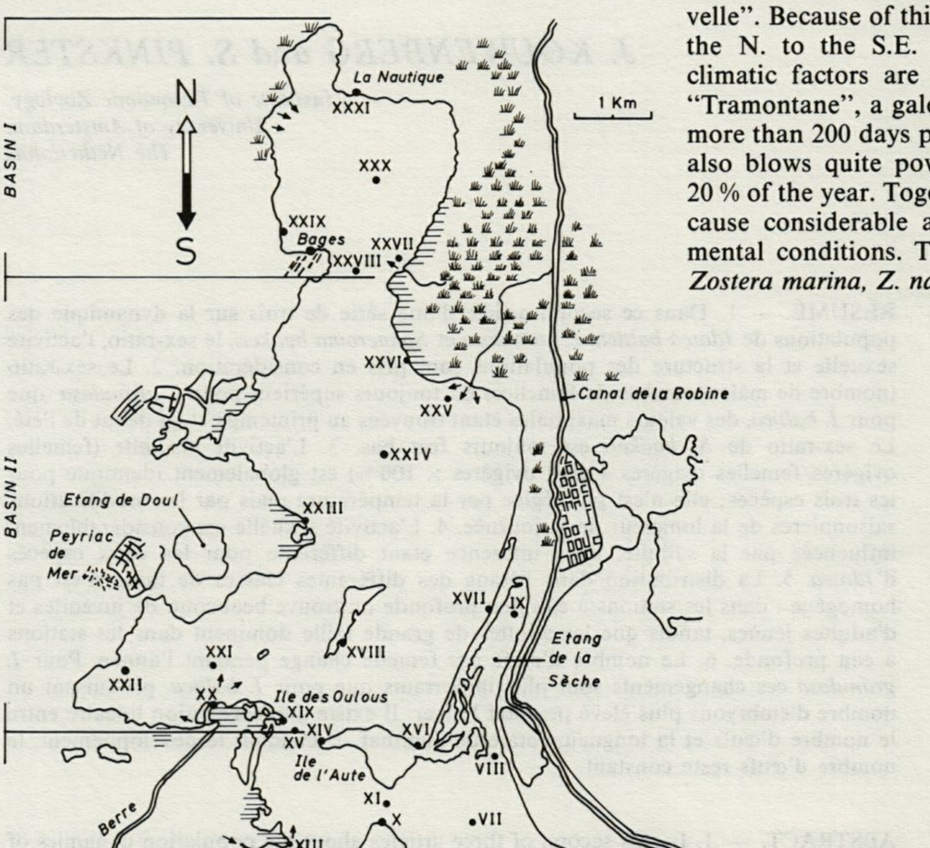


Fig. 1. — Map of the Etang de Bages-Sigean and its surroundings. The roman numerals indicate the sampling stations. Arrows indicate the influx of freshwater (From Janssen *et al.*, 1979).

species but varies with salinity, depth and substrate. In this part further factors that influence the population dynamics of the three species are presented, such as sex ratio, sexual activity, length composition and egg-production and development. Emphasis is given to the two *Idotea* species, in order to get a deeper insight into the smaller differences that exist between these closely related species. In this way we hope to answer the question posed in part I how it is possible that these two species, that apparently have the same life-cycle, use the same resources and occupy the same "niche", can coexist without clearly visible competition.

II. MATERIALS AND METHODS

In part I an extensive review is given which is summarized here. Samples of about 100 specimens were taken at 31 Stations distributed over the lagoon (Fig. 1) at intervals of about two weeks during the period from Feb. 1982 to May 1983 (For details about sampling techniques and micro-habitats see Kouwenberg & Pinkster, 1985 (in press)). The animals were killed with a ca 4 % formaldehyde solution and afterwards transferred to 70 % ethanol to which some drops of glycerine had been added. In the laboratory they were identified to specific level and subdivided into males, (ovigerous) females and juveniles.

At six Stations we measured the length of every individual, counted the number of eggs per ovigerous female and noted the stage of development of the eggs. We noted 5 different stages :

Stage I, a round, not differentiated globule.

Stage II, a multicellular, almost round globule, cleft in the middle.

Stage III, elongated, more or less comma-shaped form.

Stage IV, eyes visible, beginning of segmentation.

Stage V, segmentation clearly visible, most extremities are formed, but the 7th segment still not developed.

Stages I, III and V at least are real stages, stages II and IV are less clear, based on arbitrarily established external criteria (see Fig. 2).

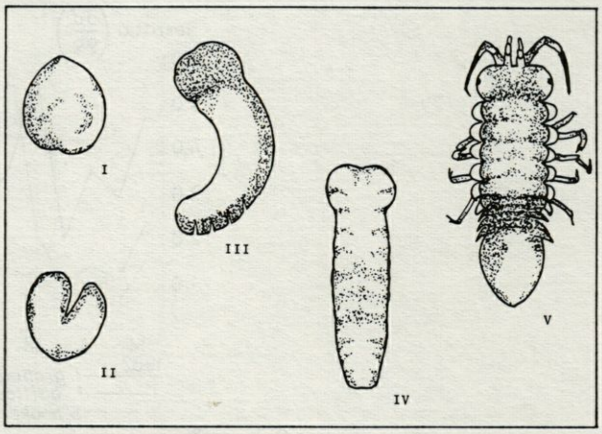


Fig. 2. — Schematic drawings of the five developmental stages of the eggs of the *Idotea* species.

III. RESULTS

III.1. Sex ratio

The sex ratio is defined as the number of males divided by the number of females. In Fig. 3A the sex ratio of *I. baltica, I. granulosa* and *S. hookeri* for the sampling period are illustrated.

When comparing the curves of the *Idotea* species it is clear that the curve of *I. granulosa* is generally higher than that of *I. baltica* showing a maximum of 5.8 in May and a second one of 5.4 at the beginning of August. At the end of August there is a sharp decline down to a minimum of ca. 1.0 in September, followed by a slight increase to values around 2 during the rest of the year.

Except for a short period in May the sex ratio of *I. baltica* is considerably lower than that of *I. granulosa.* From May onwards there is a gradual decline to values around 1 in Sept. and the rest of the year. The sharp decline in the sex ratio for both species in May/June corresponds with the disappearance of the larger males from the population before the summer (see also Fig. 4). The sex ratio of *S. hookeri* is always much lower than that of the *Idotea* species and hardly shows any peaks. In spring and summer values around 1.0 are normal; in August the values drop below 0.5 and remain so for the rest of the year.

III.2. Sexual activity

Sexual activity is defined as number of ovigerous females/total number of females × 100 %. It is meant as a measure for the reproductive activity of the three species in the course of the year and their responses to changes in abiotic factors such as temperature, salinity and day length.

Fig. 4A gives an overall view of the sexual activity of the three species throughout the sampling period in the whole lagoon system. From March to July 1982 the pattern of the three species is identical, all showing a high activity oscillating between 70 % and 90 %. In summer a decline can be observed in all three species followed by a rise at the end of the winter period. However, differences can be observed in the periods in which these changes occur.

Sexual activity of *I. baltica* gradually decreases from 90 % at the end of July to about 10 % at the

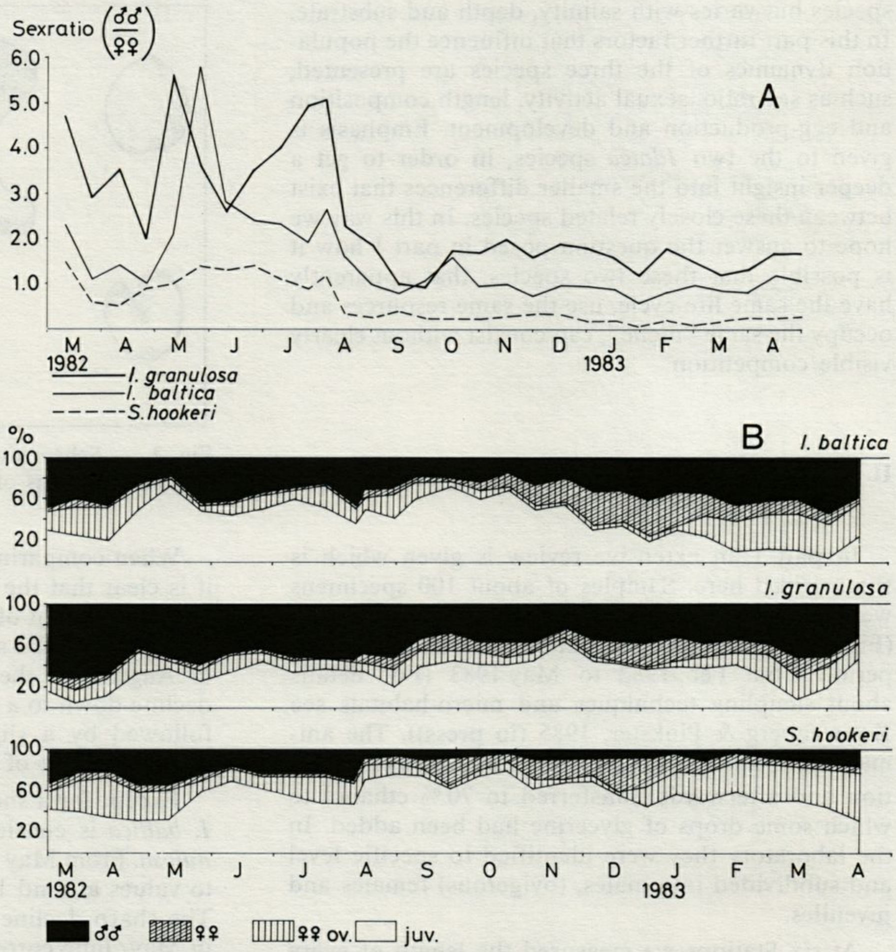


Fig. 3. — A, The sex ratio of *I. granulosa*, *I. baltica* and *S. hookeri* during the period of investigation expressed as ♂♂/♀♀. B, composition of the populations of *I. baltica*, *I. granulosa* and *S. hookeri* from March 1982 to April 1983 in the whole lagoon system.

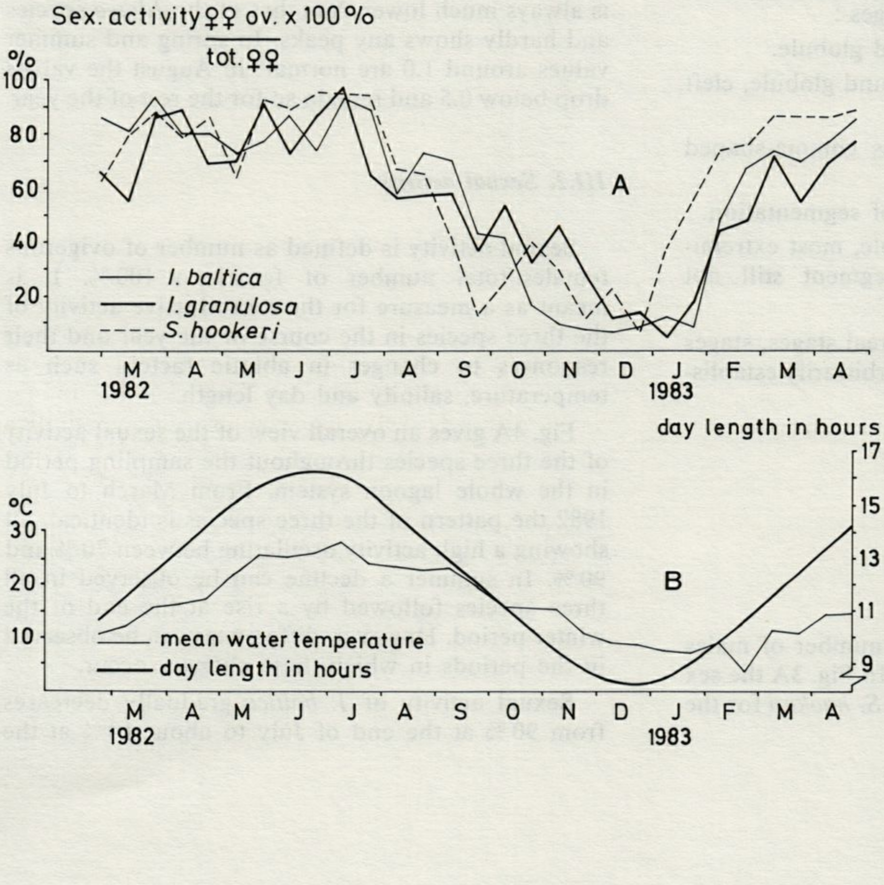


Fig. 4. — A, Sexual activity of *I. granulosa*, *I. baltica* and *S. hookeri* from March 1982 to April 1983 in the whole lagoon system. B, Changes in mean water temperature and day length during the period of investigation.

end of October. It stays at this low level until the end of January (viz. a minimum period of 3 months) followed by a steep increase until 70 % at the beginning of March.

III.3. Relation between sex ratio, composition of the population and sexual activity

The peaks in the sex ratio at the beginning of May for *I. granulosa* and at the end of May for *I. baltica* correspond with the sudden and mass disappearance of females from the population after the first sharp increase of juveniles in spring (Fig. 3B) resulting in a preponderance of males in both species. Likewise, it can be seen that from May to August the populations of both *Idotea* species consist for the greater part of males and juveniles. This period corresponds with the period of highest sexual activity (Fig. 4A) which can easily be explained; the enormous surplus of males makes (pre)copulation almost inevitable.

In August, when the sex ratio decreases we likewise see a sharp decline in the sexual activity and a strong increase in the number of non-ovigerous females. This can possibly be explained by the hypothesis that above a certain critical temperature only females are born (see also Bulnheim, 1972; Kouwenberg & Pinkster, 1985 (in press)), thus reducing the relative preponderance of the males and consequently the chance for a successful copulation. The increase of the sexual activity in the winter (simultaneously with the increase in day length) however is not coupled with an increase in the percentage of males; the sex ratio stays at a constant level from October onwards.

III.4. Influence of temperature on sex ratio

In the coldest months of the winter the sexual activity sharply increases (Fig. 4A). Females of both *I. baltica* and *I. granulosa* which become ovigerous in this period most probably keep these eggs in the marsupium until March/April when the first peak in juveniles is observed (Fig. 3B). These juveniles will be sexually mature in May/June. In this same period peaks in sex ratio occur (viz. more males than females) suggesting that the first batch of juveniles, born at low temperatures mainly consists of males (a phenomenon well known from other Crustacea, Kinne, 1952; Janssen *et al.*, 1979).

Sphaeroma hookeri does not show a pronounced peak, but a rather long period (from April to the beginning of August) when the sex ratio is relatively high. When comparing Figure 3A (sex ratio) and Figure 4B (a.o. water temperaure) it can be seen that in all species the sex ratio already drops (middle of August) before the water temperature starts to decrease (second half of September). In all three species the sex ratio stays at a more or less stable level although water temperatures continue to decrease.

III.5. Sexual activity in relation to water temperature and day length

Comparing the yearly changes in water temperature and the mean sexual activity throughout the lagoon (Figs. 4A and 4 B) it can be observed that at a maximal water temperature in the summer months all three species show maximal sexual activity. When water temperature decreases (beginning of July) sexual activity also starts to decrease.

On the other hand, however, we observe *the highest increase in sexual activity* in the months with the lowest temperature (Dec., Jan., and Feb.). In Dec. 1982, Jan. and Febr. 1983 at mean water temperatures of 9, 7 and 3.8°C, respectively, the sexual activity increases from 10 % to 48 %, 67 % and 76 % for *I. granulosa, I. baltica* and *S. hookeri* respectively. After this period the increase in sexual activity continues at relatively low water temperatures. So, in summer and autumn a positive correlation seems to exist between sexual activity and water temperature but in winter there is no correlation at all. In Figure 4B we also figured the yearly variation in day length. When comparing Figs. 4A and 4B a positive correlation can be observed throughout the year. When the day length decreases, sexual activity simultaneously decreases in all three species. Likewise, as soon as the day length increases at the end of December, the sexual activity rapidly increases as well. It seems as if the increase in day length has a triggering effect on the sexual activity in all three species. No correlation with other environmental factors or primary production of the algae (Mercier, 1973) has been observed.

III.6. Relation between sexual activity and salinity

In Figures 5 A, B and C, we figure the sexual activity of the three species in parts of the lagoon with different salinity regimes (see Part I), viz. Staions I. II, III, IV, V and VI in the southern Basin with relatively high and stable salinities; Stations XV, XVI, XVII, XVIII and XXIII in the middle Basin with relatively intermediate, stable salinities and Stations XX, XXV and XXVII with relatively low, instable salinities because of freshwater influx..

In the southern Basin with the highest salinities the sexual activity of both *I. baltica* and *S. hookeri* are minimal except during a short period in February (and March). On the contrary, the sexual activity of *I. granulosa* is usually high except for the winter period.

In the middle Basin with intermediate salinities all three species show a rather high sexual activity

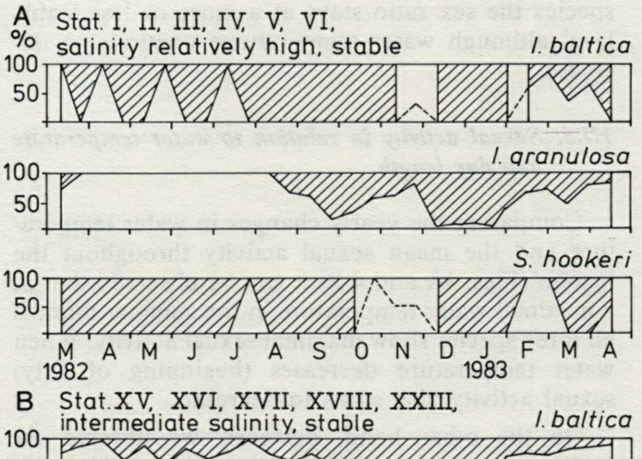


Fig. 5. — Sexual activity of *I. baltica, I. granulosa* and *S. hookeri* at different salinities : A, at Stations with relatively high, stable salinities. B, at Stations with intermediate, stable salinities. C, at Stations with relatively low, unstable salinities.

(although for *I. granulosa* it is generally a little lower than for the other two species).

At Stations with freshwater influx and consequently low and instable salinities the situation is completely contrary to that in the southern Basin; high sexual activities for *I. baltica* and *S. hookeri* and minimal sexual activity for *I. granulosa* except for the same short period in the winter months. For all three species the period with minimal activity is rather long.

At all salinities the three species show a decrease in early autumn, a minimum in the winter months and a sharp increase at the turning of the year, a pattern identical to that observed in the over all picture (Fig. 4A).

IV. POPULATION COMPOSITION OF *I. BALTICA* AND *I. GRANULOSA*

In Figures 6-8 we illustrated the population composition of *I. baltica* and *I. granulosa* expressed as size classes at 5 Stations which differ in environmental characteristics, as can also be seen in the composition of the populations. Only the most striking features will be mentioned here.

— *Station XV*, l'Aute-Oulous (Fig. 6A), a relatively deep Station with a relatively high, stable salinity. Until Sept. 1982 the pattern for both species is identical. The percentage of juveniles is low. From May to August larger males > 15 mm and females (10-15 mm) are absent. After Sept. *I. granulosa* has more males in the largest size class than *I. baltica,* whereas the latter species has more females in the 5-10 mm size class than *I. granulosa.*

— *Station XIX,* Ile des Oulous (Fig. 6B), a shallow, sheltered Station with a relatively low, instable salinity. Many juveniles are found, especially from Oct. 1982 to Apr. 1983 in *I. granulosa* and from June to Apr. for *I. baltica.* Likewise, many young adults in the 5-10 mm size class are found throughout the year. Males in the 10-15 mm size class are found in small quantities and only during the periods March/Apr. 1982 and Feb./March 1983. This Station seems to function as a nursery for the whole lagoon.

— *Station XXI,* Ile de Soulier (Fig. 7C), with a stable, intermediate salinity and largely varying depth. Peaks of juveniles are found from April to July and from Sept. to Nov. Most of the females belong to the 5-10 mm size class; in *I. baltica* the percentage of this size class is higher thant in *I. granulosa.*

— *Station XXV,* St. Louis (Fig. 7D), a shallow Station with freshwater influx and changing salinity. Many juveniles are found from Apr. to Dec. The peak in juveniles for *I. granulosa* is earlier in the year than that of *I. baltica.* Throughout the year *I. baltica* has a higher percentage of females. Most adults belong to the 5-10 mm size class. Animals of the larger size classes (10-15 mm and > 15 mm) disappear before the onset of summer.

— *Station XXXI,* la Nautique (Fig. 8E), a shallow Station with a relatively low, instable salinity. Many juveniles are found, especially from Oct. to Feb.. Throughout the sampling period juveniles and adults of the smallest size Class (5-10 mm) prevail. Larger animals are only found occasionally. (Compare Station XIX);

Conclusions : at all stations males from the largest size class (> 15 mm) are absent from early summer untill Feb./March of the next year. At shallow stations juveniles and young adults prevail; both the

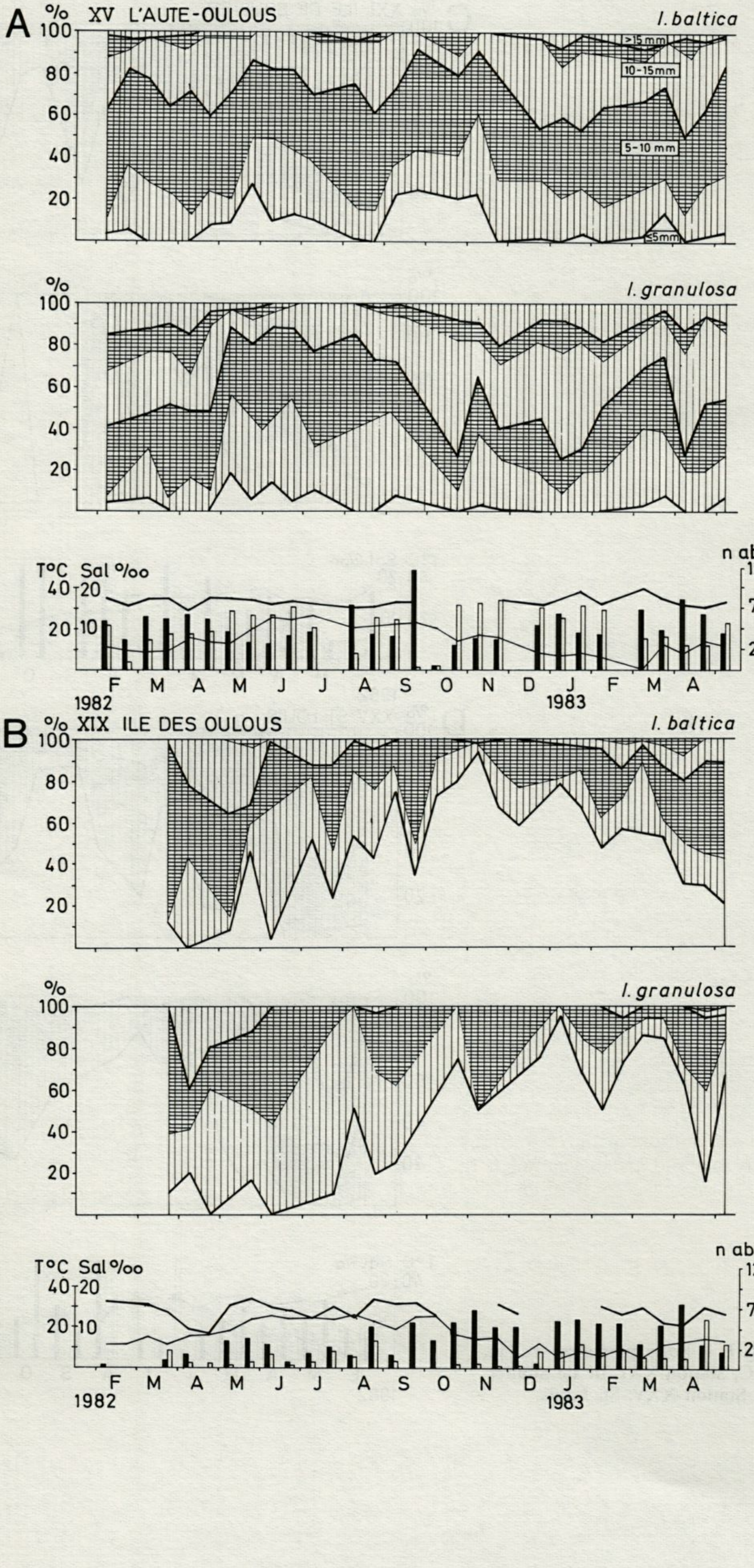


Fig. 6. — The composition of the populations of *I. baltica* and *I. granulosa* expressed as size classes at Stations with different environmental conditions. In the bottom part of the figures the numbers investigated of *I. baltica* (black bars) and *I. granulosa* (white bars), the salinity and the water temperature are illustrated for every sampling period. A, Station XV, l'Aute-Oulous. B, Station XIX, Ile des Oulous.

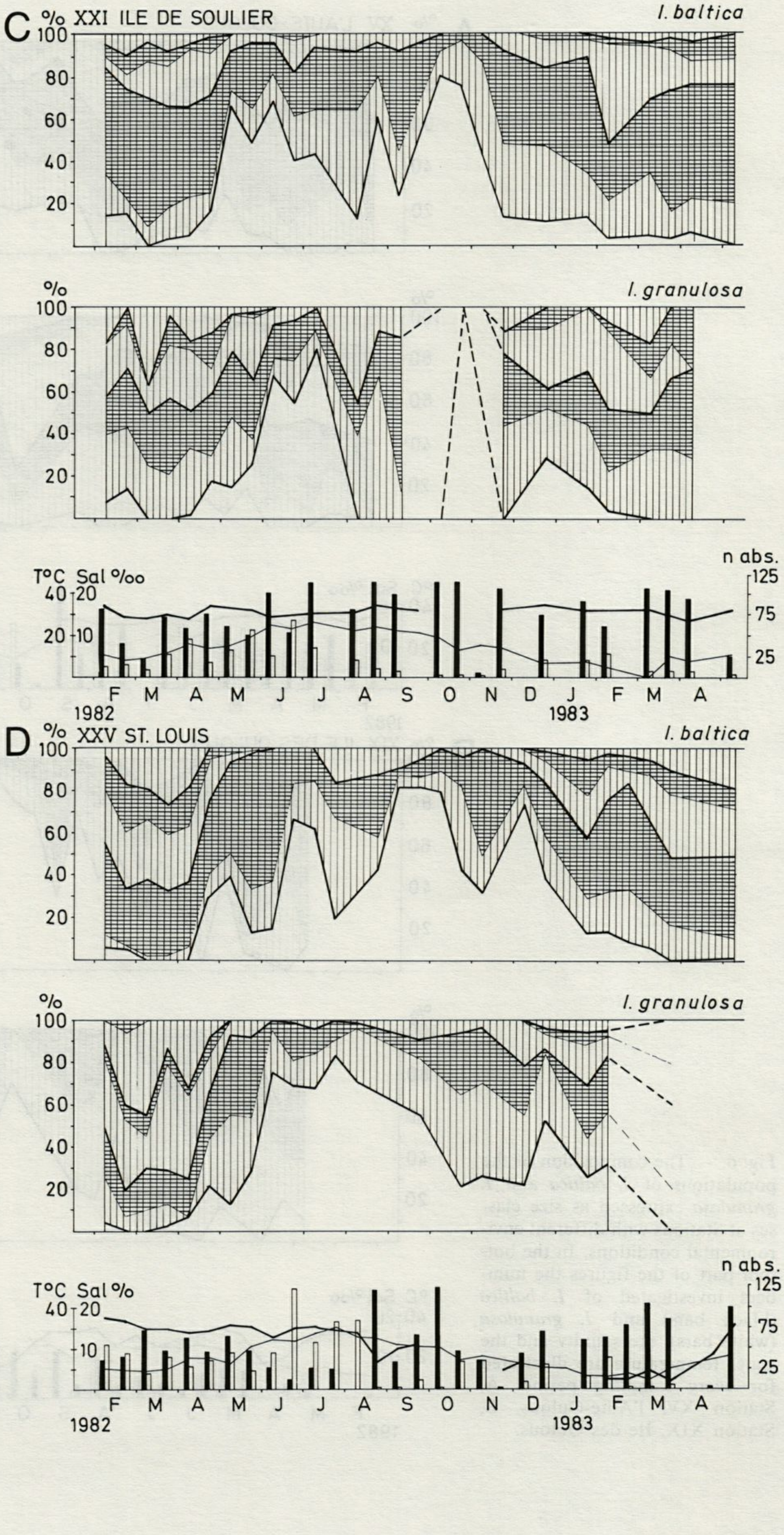


Fig. 7. — For explanation see Fig. 6. C, Station XXI, Ile de Soulier, D, Station XXV, St. Louis.

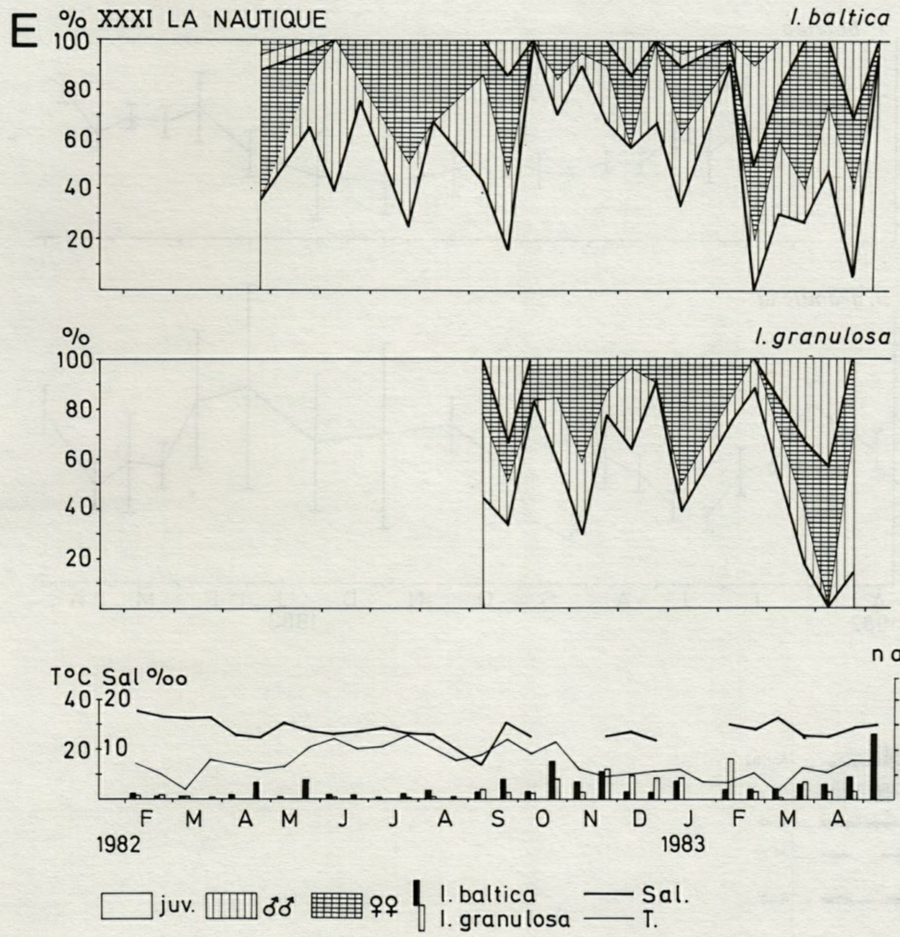


Fig. 8. — For explanation see Fig. 6. E, Station XXXI, La Nautique.

larger males and females disappear before the summer, they most probably migrate to the deeper parts of the lagoon (see also Kouwenberg & Pinkster, 1985, V and VI.3). Throughout the year females are smaller than the males. Females larger than 15 mm are never found. In *I. baltica* the percentage of females is always higher than in *I. granulosa.*

V. EGGS PRODUCTION

V.1. The mean number of eggs per female of *I. baltica* and *I. granulosa* produced during the period of investigation and taken from 6 Stations in different parts of the lagoon, is illustrated in Figure 9A. It can be seen that the mean number of eggs of *I. baltica* is more stable than that of *I. granulosa.*

V.1.1. I. baltica : in spring 1982 the mean number of eggs is relatively high (35-40) and then slowly decreases until Sept. This corresponds with the changes in population composition (see IV). It stays at about the same low level until the end of Dec. From then on, it gradually increases until Feb. 1983 whereupon it stays more or less at the same level during the following months. The 95 % confidence limit is largest in winter when mean number are low, and relatively narrow in spring and summer when mean numbers are higher. This is probably caused by the small number of ovigerous females participating in reproduction during winter. A direct influence of temperature cannot be demonstrated.

V.1.2. I. granulosa : The mean number of eggs per female shows a more erratic pattern than in *I. baltica.* It seems as if a temperature influence is present. In April and May a high mean number of eggs is present. When temperatures rise at the end of May the mean number of eggs decreases (under 20) whereas in Oct., when temperatures drop, the number of eggs increases to around 50 in Jan./Feb.. Janssen *et al.,* 1979 found the same relationship in *Gammarus aequicauda* and *G. insensibilis.* The 95 % confidence limits are highest when the mean values are high (in winter) and low at low mean values. This is most probably caused by the higher number of size classes, participating in reproduction, during the winter. The annual mean is higher than in *I. baltica.*

V.2. The relationship between the number of eggs (n) and the length of the ovigerous females of both

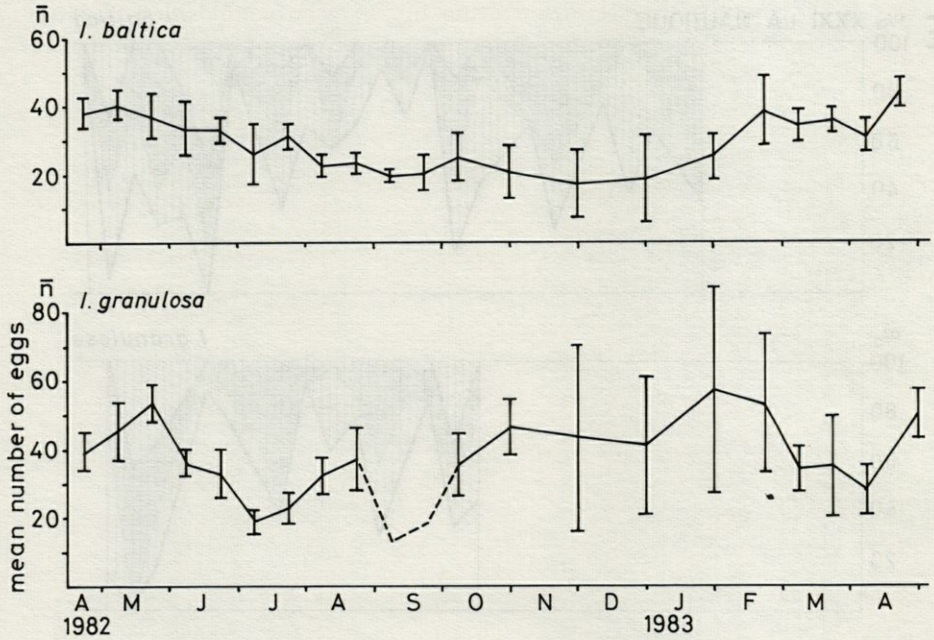
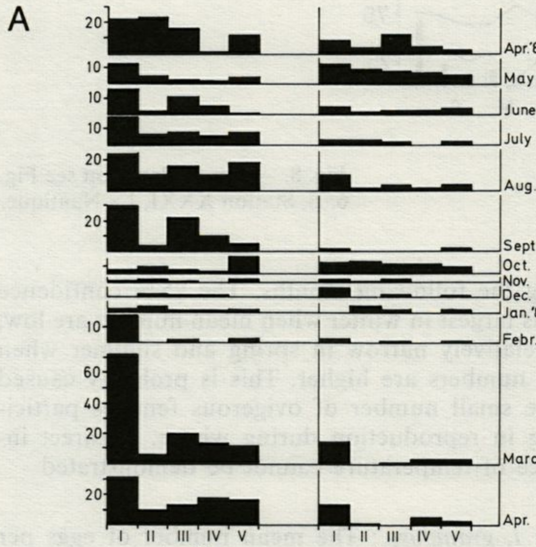


Fig. 9. — The mean number of eggs per ovigerous female per sampling period of *I. baltica* and *I. granulosa* at six Stations. The vertical bars indicate the — 95 % confidence limits. The's indicate the annual mean.



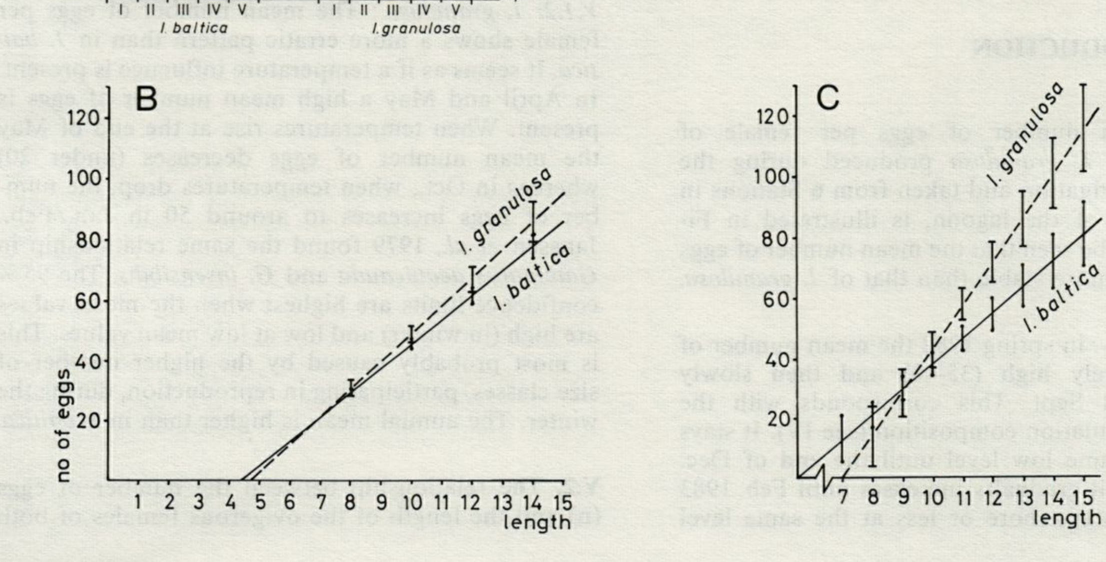


Fig. 10. — A, Proportional distribution of the five developmental stages during the period of investigation for *I. baltica* (left) and *I. granulosa* (right). B, correlation between the mean number of eggs per ovigerous female (n) and the mean body length (l) of *I. baltica* and *I. granulosa* at six Stations. Overall (yearly) situation C, do.— Situation during the winter months.

species is presented in Figure 10B. During the 15 months we measured the total length and counted the number of eggs of all ovigerous females at the 6 Stations. It is seen that a linear correlation exists between the length of the ovigerous females and the number of eggs. The number of eggs increases with length. The regression lines can be expressed as y = 8.09 x — 35.18 r = 0.69 (n = 605) for *I. baltica* and y = 9.22 x — 43.33 r = 0.7 (n = 209) for *I. granulosa*. As can be seen from the 95 % confidence limits (see Sokal & Rohlf, 1981), these figures do not differ significantly. However, when we look at the winter situation (Fig. 10C), the figures are quite different. At lengths up to about 9 mm *I. baltica* bears more eggs than *I. granulosa* but at greater lengths the number of eggs is much higher in *I. granulosa*. The regression lines can be expressed as y = 8.54 x — 46.76 r = 0.68 (n = 37) for *I. baltica* and y = 14.32 x — 100.75 r = 0.89 (n = 26) for *I. granulosa*. A linear relationship between the animal size and the mean number of eggs has already been described for *I. baltica* by Salemaa, 1979. It is also known in many other Crustacea (see Janssen *et al.*, 1979).

V.3. Developmental stages of the eggs, relative abundance of these stages and mean number of eggs per stage.

V.3.1. During the development in the marsupium eggs pass through different stages as explained in Section II. As a rule, all eggs in the brood-pouch of a single female are in the same developmental stage. Some stages are frequently found, others are rare. In Figure 10A we figured the total number of females (from the 6 stations) with embryos, separeted in the various stages throughout the period of investigation for *I. baltica* (left) and *I. granulosa* (right). It can be seen that stage I is most frequently found in both species, except from Oct. to Jan., (viz. the period with minimal sexual activity, compare Figure 4A. Stages II and IV are rarely found. When we assume that the chance of coming across a certain stage increases with the duration of this stage, it is obvious that those stages that are often found last longer than those that are rarely met with, so we may assume that stages I, III, and V last longer than stages II and IV (see also Discussion).

At the six stations we found fewer females of *I. granulosa* than of *I. baltica* and consequently fewer ovigerous females (see Fig. 3A, sex ratio), but still the same tendency can be observed. In spite of the smaller number of ovigerous females of *I. granulosa* the annual mean number of eggs per female is higher than in *I. baltica* (see Fig. 9A).

In Oct., Nov. and Dec. stage I is more frequently found in *I. granulosa* than in *I. baltica* suggesting that the minimum in sexual activity in the former is not as low as in the latter. When looking at the composition of the population throughout the year and the percentage of juveniles (Fig. 3B) the same tendency can be observed.

V.3.2. In Figure 11 the mean number of eggs per stage is illustrated. For this figure we only used females from the size class 8.0-9.0 mm, in order to avoid eventual differences between the size classes. It can be seen that in both species there is only a very slight decrease in the number of eggs during development. This means that the loss of embryos during the whole development is limited, and there is consequently a limited waste of reproductive energy.

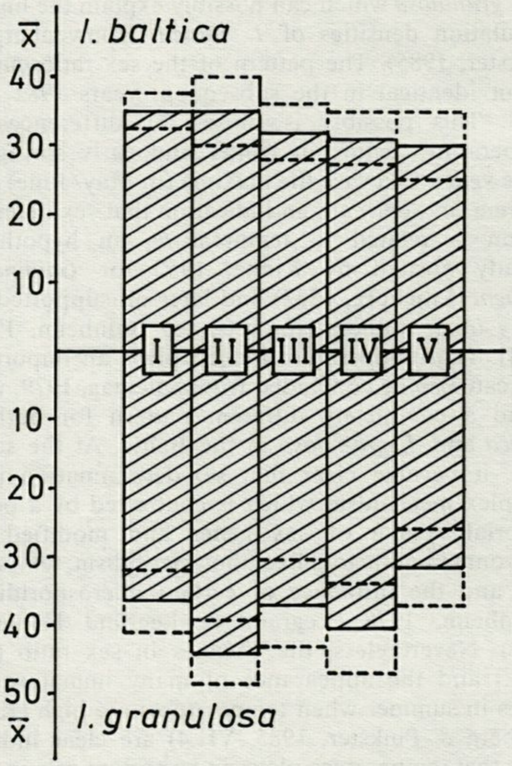


Fig. 11. — Mean number of eggs of the five developmental stages as found in ovigerous females of size class 8.0 mm for *I. baltica* (top) and *I. granulosa*. The — 95 % confidence limits are indicated by dotted lines.

Janssen *et al.*, 1979 found an important decrease in the mean number of eggs during the development in *Gammarus aequicauda* and *G. insensibilis*. A high mean number of eggs for *Gammarus* therefore cannot be considered a reliable measure for the fecundity (reproductive capacity) without taking into account the developmental stage of the eggs. For the *Idotea* species the situation is different. The annual mean number of eggs per ovigerous female of *I. granulosa* is higher than that of *I. baltica* (Fig. 9). Since there is a neglegible loss of eggs during development we may conclude that the fecundity of females of *I. granulosa* is higher than those of *I. baltica*.

VI. DISCUSSION

VI.1. In sections IV and V we only investigated the details for *I. baltica* and *I. granulosa*. This was done since it already appeared from the previous investigations (Kouwenberg & Pinkster, 1985) that *S. hookeri* does not have much in common with the *Idotea* species and clearly occupies another niche.

VI.2. Throughout the year *I. granulosa* has a higher sex ratio than *I. baltica*, viz. populations with more males than females. The populations of *I. baltica* usually have more females than males as compared to *I. granulosa* which can possibly explain the higher population densities of *I. baltica* (Kouwenberg & Pinkster, 1985). The pattern of the sex ratio curves is not identical in the subsequent years 1982 and 1983. This possibly is caused by differences in temperature regime in winter and early spring of these years. Likewise the maxima (in May/June) and minima (in Sept.) are an indication that sex determination is related to temperature, an hypothesis already posited by Kinne, 1952 for *Gammarus duebeni* (Liljeborg, 1852) and later on supported by many other authors (for refs. see Bulnheim, 1972, 1978). That temperature indeed plays an important role can also be concluded from Salemaa, 1979, who found a completely different pattern for both *I. baltica* and *I. granulosa* in the Baltic. At the same time, it became clear that sex-determination is a complex mechanism which is controlled by a polyfactorial system of sex genes and modified by environmental factors like photoperiodism, temperature and the influence of certain microsporidians (Bulnheim, 1978; Legrand & Legrand Hamelin, 1975). Nevertheless, the changes in sex ratio (see III.1.) and the appearance of many immature females in summer when temperatures are high (Kouwenberg & Pinkster, 1985, VII.4) are clear indications that temperature plays an important role in sex determination. From the yearly temperature curves it seems probable that the critical temperature lies around 15 °C.

VI.3. When temperatures drop in autumn and early winter the sexual activity of *I. granulosa* remains at a higher level than that of *I. baltica* and *S. hookeri* for a long period, thus supporting one of the conclusions from Kouwenberg & Pinkster, 1985 that *I. granulosa* is better equipped to cope with long term declines in temperatures than the other two isopods. (see also VI.6.)

VI.4. The most important factor regulating the sexual activity is the (increase in) day length. As soon as the days are lengthening, the sexual activity increases, even when temperatures are still decreasing and the productivity of the algae is going to its minimum (Mercier, 1973). It seems a logical adaptation to this instable environment where important differences can be found in the climatological conditions from year to year. The only stable factor is the yearly change in day length. In using these changes as a « Zeitgeber », the species can be assured that the first batch of juveniles will be released (March/April) when primary production of the algae is increasing to a maximum and plenty of food will be available for the juveniles. Temperature is a modifying factor since it influences the development of the eggs and the algae. So after a cold winter, the first batch of juveniles will be released in a later period (In laboratory experiments we determined the development-time of the eggs of both *I. baltica* and *I. granulosa* at 7, 15 and 25 °C. The eggs of *I. granulosa* developed a little faster than those of *I. baltica*. (8 and 25 days versus 10 and 30 days at 7 and 25 °C respectively). The results of these experiments will be treated in a third article about the Isopods in the lagoon of Bages-Sigean).

This same increase in sexual activity, before the sea-temperature reaches its minimum is reported by Healy & O'Neill, 1984, for populations from South-East Ireland.

VI.5. At all stations the largest size class (> 15 mm) disappears from the population before the summer, indicating that the overwintering generation from the previous year has died. From this time on, we found a reverse relationship between size and temperature : high temperatures correspond with relatively smaller animals and vice versa, which is similar to the findings of Naylor, 1955 for *I. emarginata*. In summer the larger (reproducing) males and females are only found at the deeper stations. At the shallow stations juveniles and non-reproducing males and females prevail. We therefore assume a migration from the adults to the deeper, and more stable zones of the lagoon. This agrees with the findings of Salemaa, 1979, who found a vertical zonation of the various size classes of *Idotea* species in the northern Baltic. As we already pointed out (Kouwenberg & Pinkster, 1985) *I. granulosa* is more often found in the deeper, more saline parts than *I. baltica*, nevertheless in both species a vertical zonation of the size classes can be observed.

VI.6. When looking at the relationship between body size and number of eggs important differences can be observed between the *Idotea* species. When we compare the yearly pattern (Fig. 10 B), no (statistical) differences can be observed. However, when looking at the winter situation (Fig. 10 C) important differences are found; females of *I. granulosa* (from 9 mm on) produce more eggs than females of

I. baltica, resulting in a higher percentage of juveniles in early spring. This is in agreement with the observation in V.1. (Fig. 9), that the mean number of eggs per female is more erratic in *I. granulosa* than in *I. baltica,* resulting in a higher number of eggs per female during the winter months. This again is an indication that *I. granulosa* is better equipped with long term declines in temperature than *I. baltica.* (see also VI.3.)

VI.7. In summer the mean number of eggs per female is lower than in winter; the confidence limits are relatively small. In winter the mean number of eggs is high, and the confidence limits large. Because of the high energy requirements during a short period in the summer (especially for the high oxygen uptake at higher temperatures) females consequently have less energy left for producing a high number of eggs. In winter more size classes occur together, resulting in a higher mean number of eggs and large confidence limits. Larger females produce more eggs than smaller ones, but likewise females in winter produce more eggs than females of the same size in summer. This is probably because the energy requirements are lower than in summer (lower swimming activity, high oxygen saturation level, lower O_2-uptake at low temperatures and longer egg-development time), so more energy can be used for the egg production, resulting in a higher number of eggs. This also explains the differences between the populations from the Baltic (Salemaa, 1979) and those from the lagoon (see VI.8.).

VI.8. In both *Idotea* species a linear relation can be observed between the number of eggs and the body length. The same was found by Salemaa for *Idotea baltica* in the Baltic, although the number of eggs at a given body length was much higher in the population from the Baltic than in those from the populations investigated here. This can possibly be explained by the differences in temperature regime between the Baltic and the shallow lagoons along the Mediterranean coast (see also VI.7.)

VI.9. In summer females are generally smaller than in winter as well as the number of eggs per female. However in summer the development time of the eggs is very short (see VI.4.). Likewise we observed that in spring and early summer a high percentage of females is carrying eggs (Fig. 3 B) and that the population-densities reach their maximum in summer (Kouwenberg & Pinkster, 1985, IV.1.). We therefore must conclude that a great number of cohorts is produced in spring and summer although the number of eggs per cohort is lower than in winter.

VI.10. The differences observed in the duration of the various developmental stages of the eggs can be explained by differences in the number of cleavages per stage. In stages I, III and V more cleavages will be necessary than in the arbitrarily established stages II and IV. Most probably, more stages exist than the ones which can be seen with a simple stereo-microscope.

VI.11. Howes, 1939 found a reduction of the number of eggs during development in *I. viridis (= I. chelipes).* The same was observed by Salemaa, 1979 for *I. baltica* in the Baltic and by Janssen *et al.*, 1979 for *Gammarus* species in the lagoon system of Bages-Sigean. Naylor, 1955 however, did not observe such a loss of eggs for *I. neglecta,* a situation comparable to that in *I. baltica* and *I. granulosa* as was found in this study. From stages I to IV hardly any loss is observed. (Fig. 11)

VI.12. Especially in winter, quite a few females were found with eggs in stage V, but also with large numbers of round globules under the marsupium which resembled stage I. Howes, 1939 found some females with eggs in different stages of development, but Naylor, 1955 never found females except with eggs in only one stage of development. We think that the globules we found under the marsupium are unfertilized eggs that come to development in winter when copulation (mating) is at a minimum. However, in order to draw further conclusions more research is necessary into the reproductive cycle and embryology of these Isopod species.

REFERENCES

BULNHEIM H.P., 1972. On sex-determining factors in some euryhaline Gammarus species. *In* 5th European Marine Biology Symposium. Ed. B. Battaglia. Piccin, Padova, 115-130.

BULNHEIM H.P., 1978. Interaction between genetic, external and parasitic factors in sex determination of the crustacean amphipod *Gammarus duebeni. Helgoländer wiss. Meeresunters,* **31** : 1-33.

HEALY B. & M. O'NEILL, 1984. The life cycle and population dynamics of *Idotea pelagica* and *I. granulosa* (Isopoda : Valvifera) in South-East Ireland. *J. mar. biol. Ass. U.K.,* **64** : 21-33.

HOWES N.H., 1939. Observations on the biology and postembryonic development of *Idotea viridis* (Slabber) (Isopoda, Valvifera), from New England Creek, South-East Essex. *J. mar. biol. Ass. U.K.,* **23** : 279-310.

JANSSEN H., M. SCHEEPMAKER, M. VAN COUWELAAR & S. PINKSTER, 1979. Biology and distribution of *Gammarus aequicauda* and *G. insensibilis* (Crustacea, Amphipoda) in the lagoon system of Bages-Sigean (France). *Bijdr. Dierk.,* **49** (1) : 42-70.

KINNE O., 1952. Zum Lebenszyklus van *Gammarus duebeni* Lilj. nebst einigen Bemerkungen zur Biologie von *Gammarus zaddachi* Sexton subsp. *zaddachi* Spooner. *Veröff. Inst. Meeresforsh. Bremerh.*, 1 : 187-203.

KOUWENBERG J. & S. PINKSTER, 1985. Population dynamics of three brackish water isopod species (Crustacea) in the lagoon system of Bages-Sigean (France). *Vie Milieu* **34** (4) : 229-240.

LEGRAND J.J. & E. LEGRAND-HAMELIN, 1975. Déterminisme de l'intersexualité et de la monogénie chez les Crustacés Isopodes. *Pubbl. Staz. Zool.* Napoli, **39**, Suppl., 443-461.

MERCIER A., 1973. Etude écologique de la végétation du complexe lagunaire de Bages-Sigean. Biomasse et production primaire des Macrophytes. Thèse 3e cycle, Univ. Paris VI, Biologie végétale.

NAYLOR E., 1955. The life cycle of the isopod *Idotea emarginata* (Fabricius). *J. anim. Ecol.*, **24** (2) : 270-281.

SALEMAA H., 1979. Ecology of Idotea species (Isopoda) in the northern Baltic. *Ophelia*, **18** (1) : 133-150.

SOKAL R.R. & F.J. ROHLF, 1981. Biometry. The principles and practice of statistics in Biological research. W.H. Freeman & Comp., San Francisco.

TINTURIER-HAMELIN E., 1963. Polychromatisme et détermination génétique du sexe chez l'espèce polytypique Idotea Balthica (Isopode Valvifère). *Cah. Biol. Mar.*, **4** : 473-591.

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