BIOLOGY AND DISTRIBUTION OF *GAMMARUS AEQUICAUDA* AND *G. INSENSIBILIS* (CRUSTACEA, AMPHIPODA) IN THE LAGOON SYSTEM OF BAGES-SIGEAN (FRANCE)

by

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ABSTRACT

1. *Gammarus aequicauda* (Martynov, 1931) and *Gammarus insensibilis* Stock, 1966 have been the subject of a quantitative ecological research project in the lagoon system of Bages-Sigean (France, dépt. Aude). From April 1976 till August 1977 samples have been taken at 31 different stations all over the lagoon at intervals of about 2 weeks. With the samples thus obtained we studied the biology and distribution of the two species in relation to environmental factors, the most important being chlorinity and temperature.

2. Both species reproduce throughout the year and have a regular reproductive pattern with maxima in spring and autumn. In *G. aequicauda*, as compared to the other species, this peak is earlier in spring and later in autumn. This is caused by a different influence of the temperature on the reproductive activity of each species.

3. The reproductive success of *G. insensibilis* is greater than that of *G. aequicauda* and during most of the time *G. insensibilis* has a wider distribution over the lagoon than *G. aequicauda*.

4. The tolerance spectrum of *G. aequicauda* is much broader than that of *G. insensibilis*. In stable environments *G. insensibilis* is the dominant species and *G. aequicauda* is scarcely found. In more unstable environments both species occur but *G. aequicauda* has advantage over *G. insensibilis*, especially at higher and at lower chlorinities.

5. In localities where both species coexist competition is avoided by a spatial separation based on differences in preferences for substrate and food. Moreover competition is avoided through a rapid succession of changes in the environment which intermittently work in favour of one of the two species.

I. INTRODUCTION

Gammarus insensibilis Stock, 1966 and *Gammarus aequicauda* (Martynov, 1931) are two closely related species of amphipod crustaceans. *Gammarus insensibilis* is an atlantic-mediterranean species occurring in both marine and brackish water habitats. *Gammarus aequicauda* is a mediterranean species occurring in brackish water only (Stock, 1966; Brun, 1971).

Both species occur sympatrically in the lagoon system of Bages-Sigean (France, dépt. Aude) and together they form an important part of the total biomass in the lagoon. Preliminary research carried out in 1967 and 1971 showed that the distribution of the two species changed throughout the year. The question arose if these changes in distribution could be considered as the results of biological responses to the marked environmental instability that is so characteristic of this lagoon complex (Boutière, 1974). To all appearance these factors show their impact in the first instance on the reproductive cycle of the two species. On the other hand, we may consider the possibility of interspecific competition between these two species so often coexisting in the same habitats.

These habitats can be characterized in terms of depth, bottom substrate and vegetation. In this context, it is important to point out that two gammarid species can live in the same habitat without competing, by using as a food resource the same plant material but in different stages of decomposition (Brun & Dumay, 1974).

To answer the questions raised above, a study of the reproductive cycles and the population dynamics of the two species throughout the year and throughout the lagoon complex was undertaken. In view of the possibility of interspecific

competition it seemed worthwhile to pay special attention to the egg production of both species, the various developmental stages of the eggs and the duration of these stages (Dumay, 1972).

II. STUDY AREA AND PHYSICAL FACTORS

The lagoon system of Bages-Sigean belongs to a series of brackish water lagoons along the French Mediterranean shore between Marseille and the French-Spanish border. Its origin lies in the Pleistocene. Presently it is about 14 km long and has an average width of about 2.5 km. The axis lies roughly in a N.-S. direction. It can be subdivided into three different basins with a maximum depth of about 2.5 to 3 m (see fig. 1). Basins I and II are separated by a ridge near Bages, basins II and III by a ridge between Ile des Oulous and Ile de l'Aute (Petit & Mizoule, 1962). The "Grau de Port la Nouvelle" in the southernmost basin is the only narrow connection with the sea. In principle this connection is always open, except for during gales from N.W. or S.E. direction with wind-velocities of above 54 km/h (communication Ponts et Chaussées, Port la Nouvelle) when it is closed by a sluice.

Climatical factors that are of major importance on the environment are wind, precipitation, solar irradiation and as a consequence temperature. Dominant are gales from the Northwest ("Tramontanas") which blow on average for about 200 days per year. Less frequent are the winds from SSE direction ("Marins") blowing on average for about 100 days per year (Mercier, 1973). Characteristic for the Mediterranean climate is the short, but heavy, rainfall, with maxima in spring and fall. High temperatures and strong solar irradiation cause a high evaporation, especially during summer. For almost the whole year the evaporation exceeds the freshwater influx. The water level is highly dependent on the wind. During NW winds the water is blown towards the narrow exit in the South and the lagoon is emptied. During SE winds much water is blown into the lagoon.

A chlorinity gradient exists from S to N increasing from an average of $17^0/_{00}$ Cl in the South to $8^0/_{00}$ Cl in the North. This gradient is caused by the influence of the sea on the one hand

and the flow of rain-water through small drainage streams on the other hand.

The northern basin is relatively "fresh" because of the influx of many small drainage streams north of Bages and of the rivulet Canelou, flowing through the reedlands near Station XXV, forming a connection with the Canal de la Robine. Chlorinity changes are moderate, from 7 to $12^0/_{00}$.

The middle basin is a more or less transitional zone in which chlorinity can rapidly fluctuate from 5 to $19^0/_{00}$. This is caused by the varying water supply through the most important freshwater influx of the lagoon, the river Berre, and some smaller rivulets near Station XIII (see also Mercier, 1973). The southernmost basin is relatively "salt" and shows frequent fluctuations in chlorinity from 10 to $28^0/_{00}$. Chlorinity can rise to these high values because of evaporation.

From the sedimentological point of view some distinct deposit-zones can be distinguished e.g. silt, sandy silt, sand and gravel. This sedimentary pattern is caused through water action, influenced by winds and currents. The eastern shores are more exposed than the western ones (Boutière, 1974) and as a result are sandy with gravel and cobbles; the western shores of the lagoon are mainly silty.

The distribution of the vegetation changes with the seasons and is influenced by chlorinity, temperature and wind-direction. The general aspect is determined by the Phanerogamae *Zostera marina, Z. nana* and *Ruppia* spp., the Ulvacales *Ulva* spp. and *Enteromorpha* spp., the Siphonocales *Chaetomorpha* spp. and *Cladophora* spp. and the Gigartinales *Gracilaria* spp. In the deeper parts of the lagoon, the bottom is covered with *Ulva* spp., *Gracilaria* spp. and *Chaetomorpha* spp. These species are absent in places where water currents are strong. Here they are replaced by *Zostera marina* (on silt bottom, deeper than 1 m) and *Zostera nana* (on coarse substrate, less deep). Both *Zostera* species tolerate high chlorinities; *Z. marina* is stenohaline, *Z. nana* euryhaline (Boutière, 1974; Mercier, 1973). *Enteromorpha* spp. are predominantly found along the exposed rocky shores. The shores of the lagoon are often fringed with thick layers of dead material washed ashore. They consist of *Ulva, Gracilaria, Chaetomorpha* and especially of *Zostera*, all in various stages of
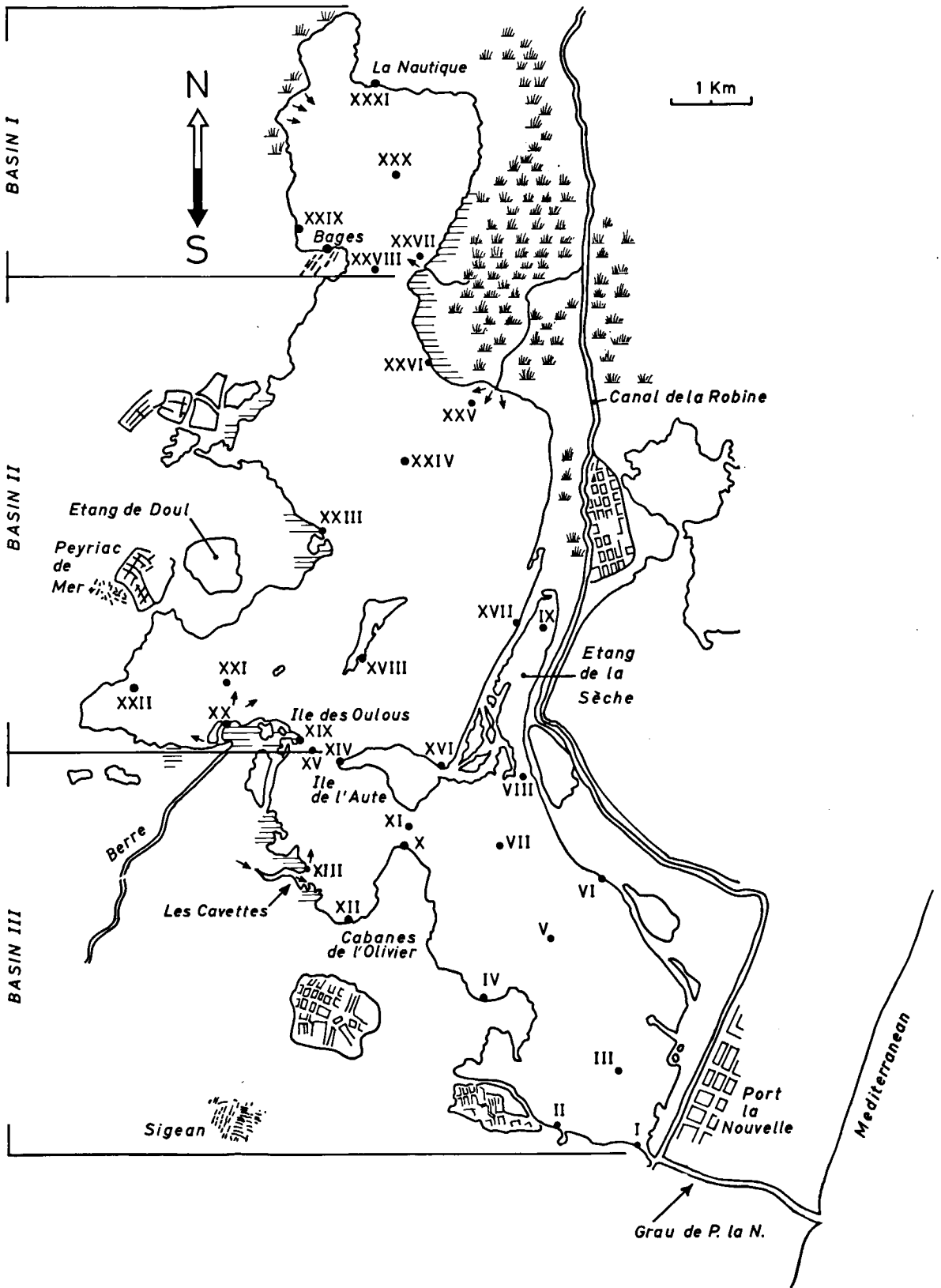
Fig. 1. Map of the Étang de Bages et Sigean and its surroundings. The Roman numerals indicate the sampling stations. Arrows indicate the influx of fresh water.

decomposition. As we will see later on, these layers are an important habitat for amphipods, especially for *G. insensibilis*.

The lagoon shows a series of divergent habitats in which the degree of stability and the occurrence of extreme conditions are of interest. Examples of more or less stable habitats can be found in the deeper parts of the lagoon near the bottom. Unstable habitats are found near the connection with the sea (salinity fluctuations) and in the very shallow parts of the lagoon (fast and frequent fluctuations in temperature). Likewise, the mouth of the river Berre is an unstable habitat because of the extremely fluctuating influx of fresh water. In the row of unstable habitats the Étang de la Sèche and the small pools around the lagoon occupy a special place. The water level in the Étang de la Sèche is very low and the exchange with the rest of the lagoon complex is very limited. It is only when the water level in the rest of the lagoon is extremely high that the pools are connected with the latter. During high summer, temperatures and chlorinities in these habitats can rise to high values. The pools may even desiccate. *G. aequicauda* was still found at chlorinities of over $50^0/_{00}$ (Étang du Doul, 25 May 1977).

III. MATERIAL AND METHODS

III.1. From April 1976 to August 1977 samples have been taken at 31 localities at intervals of about 2 weeks (fig. 1 and table VI at the end of this paper). The localities were chosen with the aid of salinity maps of the lagoon (Mercier, 1973). It was our aim to collect a sample of at least about 100 animals at every locality within the limits of one hour. The sampling was either done with a dip-net (opening 19 × 31 cm) in the shallower reaches or with a small bottom dredge in the deeper parts (semicircular opening, $r = 17$ cm). The mesh size in both types of sampling devices was 1 mm. In the field the two

species were provisionally identified. As criteria we used the presence or absence of red pigmentation in the second antenna and on the coxal and epimeral plates. In *G. aequicauda* this pigment pattern is always present, in *G. insensibilis*, on the contrary, always absent. (This is unlike the situation described by Brun, 1971). The animals were killed on the spot with a 4% formaldehyde solution and later on transferred to and stored in 70% aethanol. Samples, used for counting the eggs (see IV.5) were stored in a mixture of 70% aethanol and glycerine.

At the same time some physicochemical factors were determined, such as air temperature with a mercury thermometer (precision 0.1°C), water temperature with a YSI oxygen/temperature meter model 54 (precision 0.1°C), dissolved oxygen with the same YSI oxygen/temperature meter model 54 (precision 0.1 ppm), conductivity with a LTH conductivity meter, model PB (precision 10 μmhO). [Later, the thus obtained values have been expressed as chlorinities in mg/l after making a gauge with an E.E.L. electrical chlorinity meter]. All data thus obtained together with the data from populations in the laboratory (III.2.) were stored in and treated with a CDC Cyber 73-28 computer of the Stichting Academische Rekencentrum, Amsterdam.

III.2. In the laboratory the gammarids were identified with the aid of a stereomicroscope (for criteria see Stock, 1967, and Brun, 1971) and subdivided into males, females, ovigerous females and juveniles (i.e. animals that have not yet developed sex-determining characters). The taxonomic distinctions described in the literature are mainly valid for males but unfortunately no such characters have been described for females. We found the following criteria to be valid for descriminating females of the two species (see fig. 2).

	G. insensibilis	*G. aequicauda*
pigment	absent	bands of red pigmentation, especially on coxal plates
dorsal humps on urosome segments	symmetrical in lateral view	asymmetrical, especially on somites I and II
setation of urosomites	setae never longer than spines	setae may be longer than spines
armature of telson	setae shorter than spines, or absent	setae present, always longer than spines

<p style="text-align:center">G. aequicauda</p>
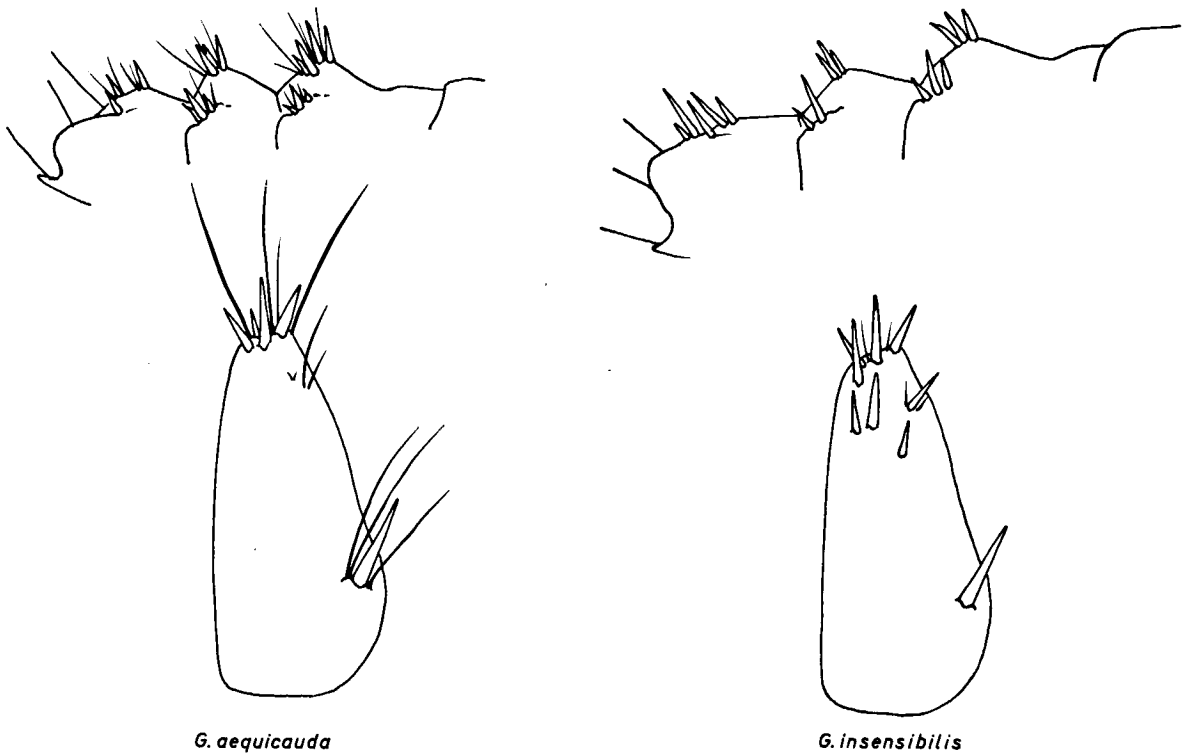<p style="text-align:center">G. insensibilis</p>

Fig. 2. Morphological differences in urosome and telson between *G. aequicauda* (left) and *G. insensibilis* (right).

III.3. To determine the composition of the population and the reproductive cycle throughout the year we took the cephalic length of the animals as a measure of the body length. This is only permissible if a linear correlation exists between the cephalic length and the total body length as demonstrated for *G. zaddachi* by Dennert et al., 1969, for *G. chevreuxi* by Girisch et al., 1974, and for *G. p. pulex* by Van den Beld, 1973. For *G. aequicauda* and *G. insensibilis* our data correspond closely with their findings, viz. the relations can be described by linear correlations (see fig. 3).

For *G. insensibilis* the regression line was calculated as

$L_c = 0.088 \ L_b + 0.26$ in which L_c is the cephalic length and L_b the total length of the body (tip cephalosomite to tip telson)
correlation coefficient: 0.98
probability: 0.00001

For *G. aequicauda* the regression line was calculated as

$L_c = 0.09 \ L_b + 0.17$
correlation coefficient: 0.98
probability: 0.00001

Because of the absence of a sufficient number of juveniles in our samples, no separate regression line was made for the juveniles.

III.4. At sampling sites XII, XIII, and XXXI all ovigerous females were preserved separately and afterwards the eggs of every single female have been counted and subdivided in one of the following developmental stages (Vloemans, unpubl.)

A_1: The stage between fertilization and a multi-cellular stage.

A_2: The multi-cellular stage as in A_1 with a primitive streak visible.

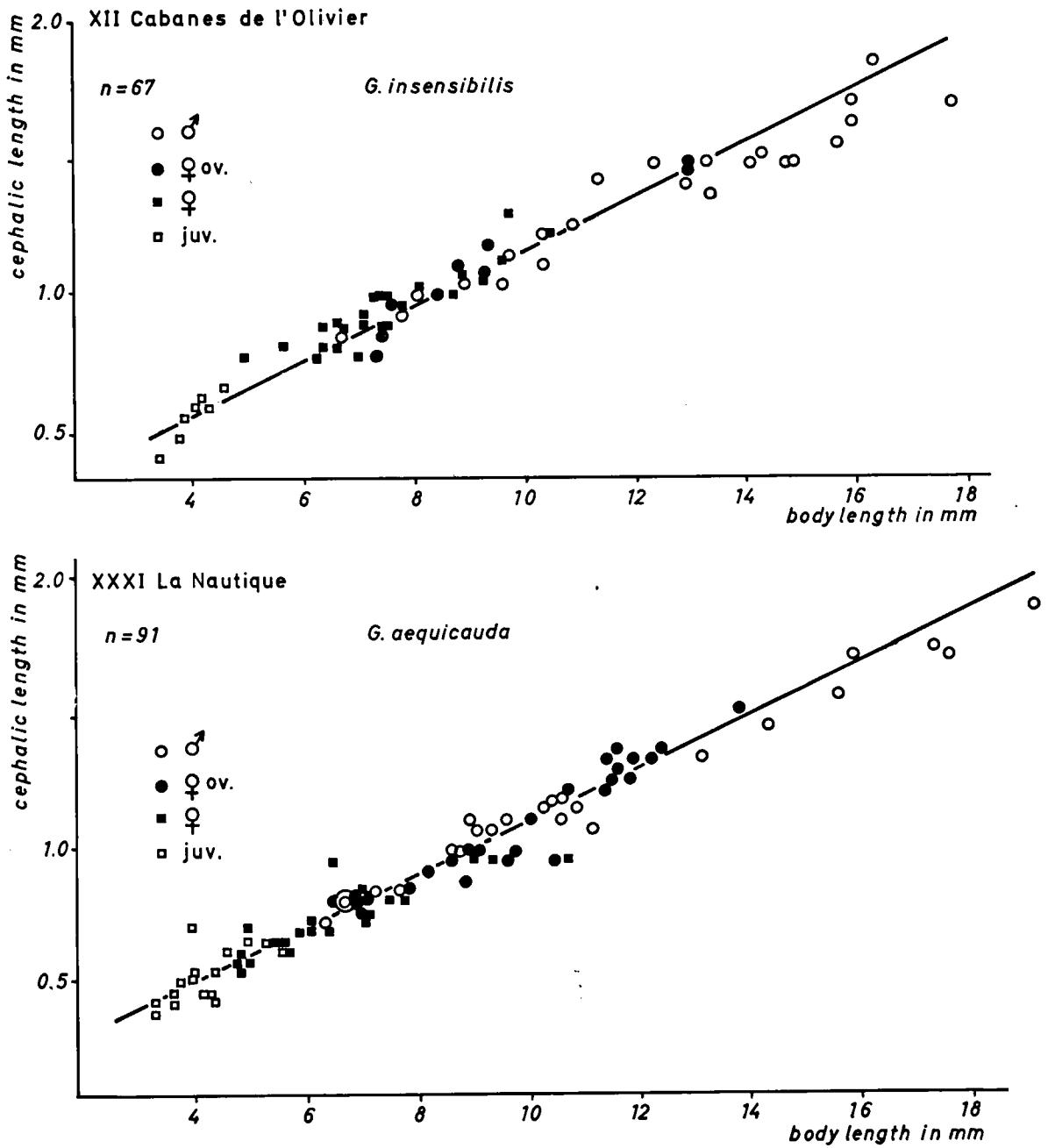B: A well developed dorsal organ visible.

Fig. 3. The relation between body length and cephalic length in *G. insensibilis* and *G. aequicauda*.

C_1: Characterized by the comma-shape and the initiation of pereiopods.

C_2: Clearly visible constriction of the comma; appendages are clearly segmented and making a slender impression.

D_1: Eyes visible, first as white later on as red spots.

D_2: Juveniles completely developed.

IV. LIFE CYCLES

IV.1.1. Reproductive cycle of *G. aequicauda* (see figs. 4-6).

Gammarus aequicauda reproduced throughout the year with a maximum in February-March. This resulted in many juveniles and relatively small animals in the early spring. As the spring passes by, reproductive activity decreased and the per-
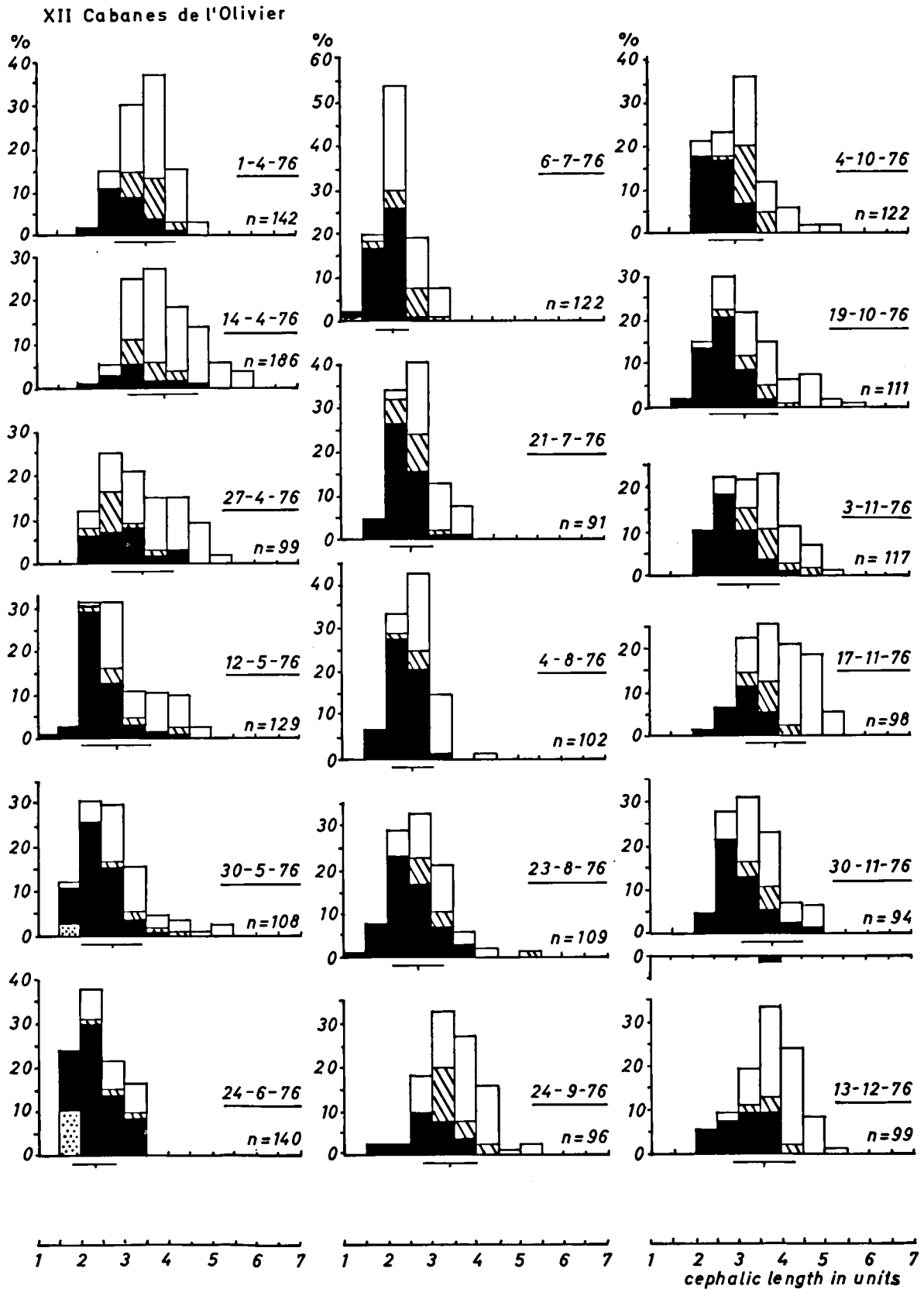
XII Cabanes de l'Olivier

Fig. 4. The population composition, the mean cephalic length and its standard deviation of both *G. insensibilis* and *G. aequicauda* at station XII Cabanes de l'Olivier.
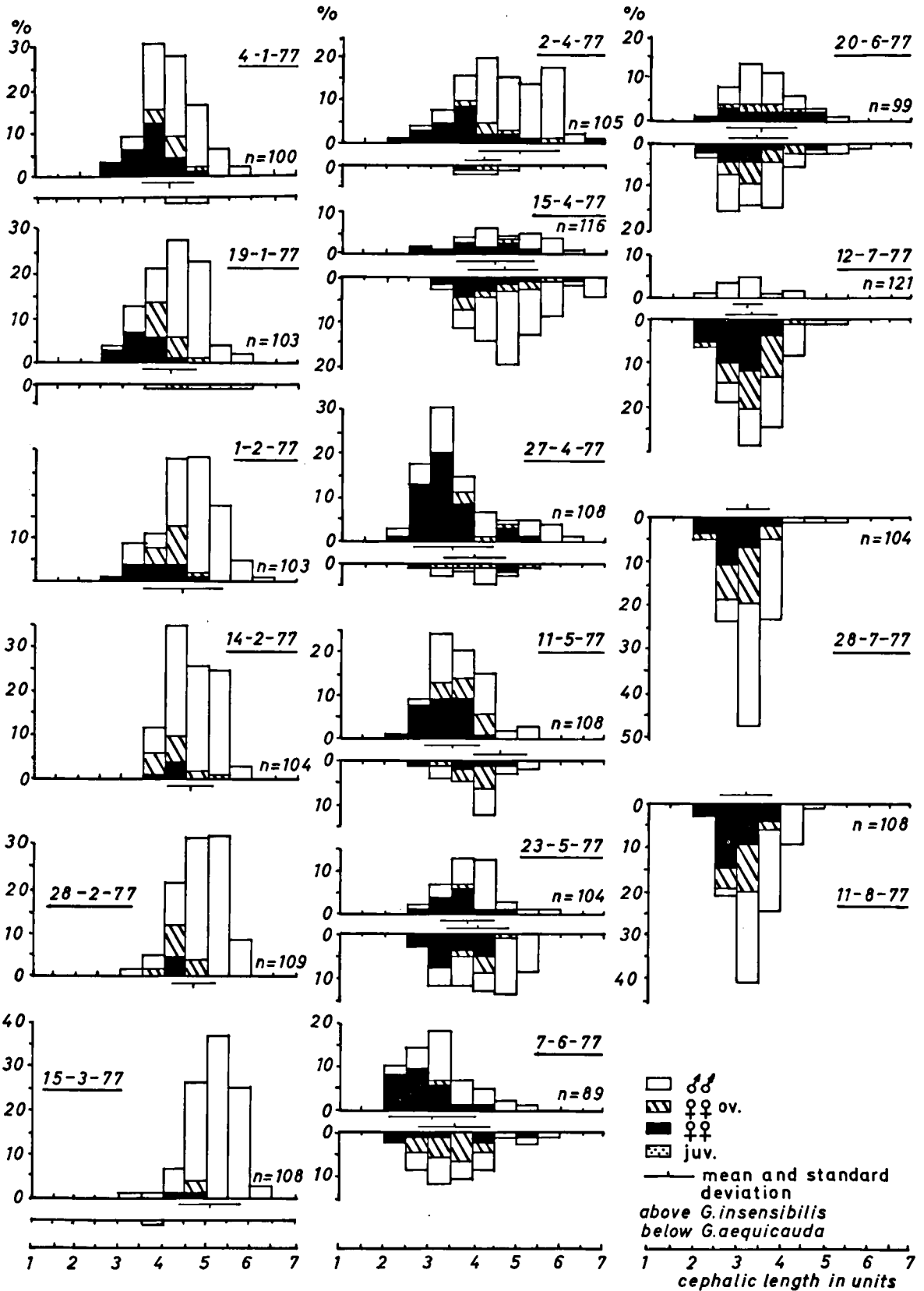
XII Cabanes de l'Olivier

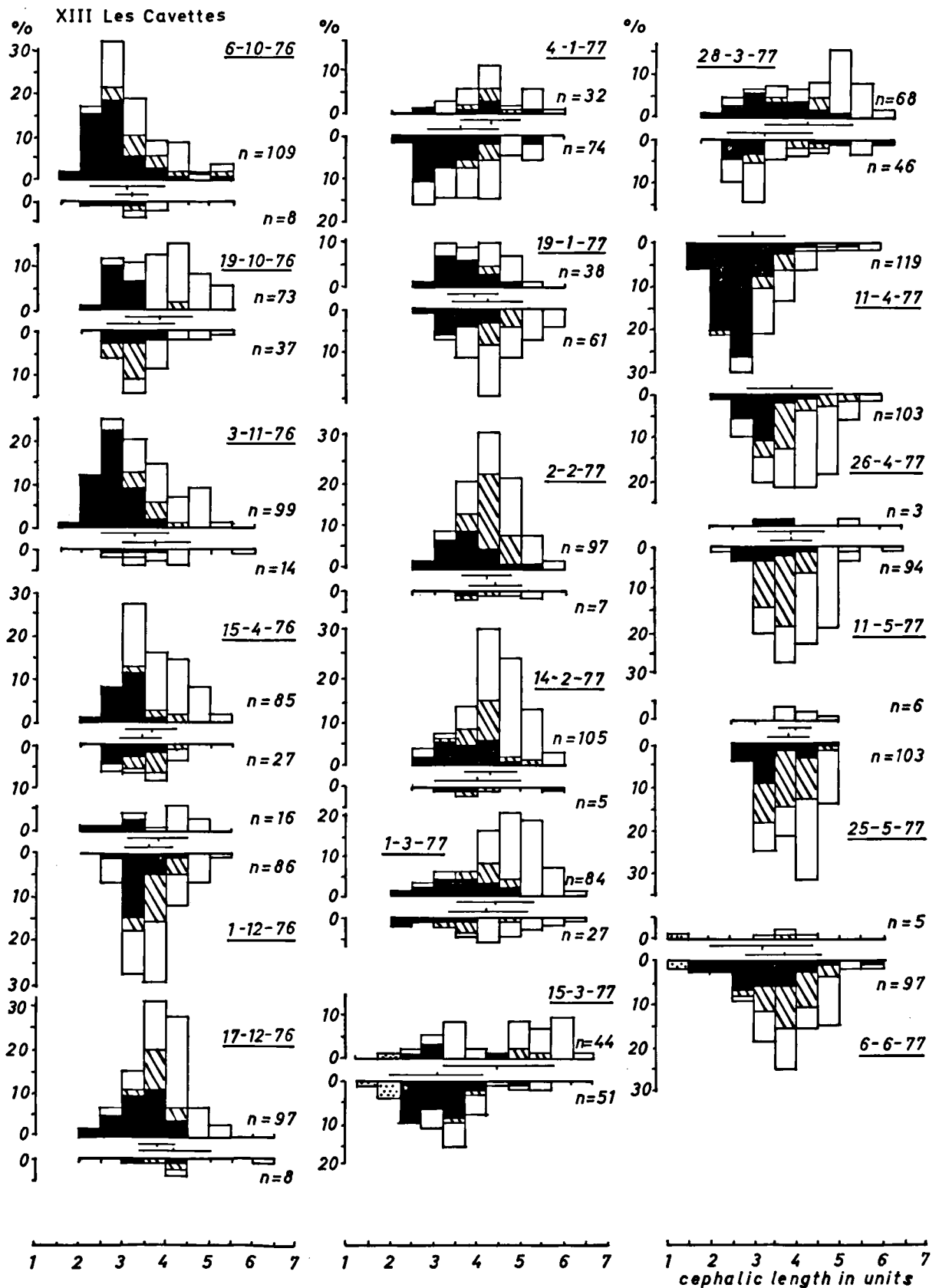Fig. 4. Continuation of previous page.

Fig. 5. The population composition, the mean cephalic length and its standard deviation of both G. *insensibilis* and G. *aequicauda* at station XIII Les Cavettes.

XIII Les Cavettes

%

n = 5

n = 107

21-6-77

n = 2

n = 129

13-7-77

n = 104

28-7-77

n = 92

11-8-77

□ ♂♂
⧄⧄ ♀♀ ov.
■ ♀♀
▥ juv.
—•— mean and standard
      deviation

above G. insensibilis
below G. aequicauda

1 2 3 4 5 6 7
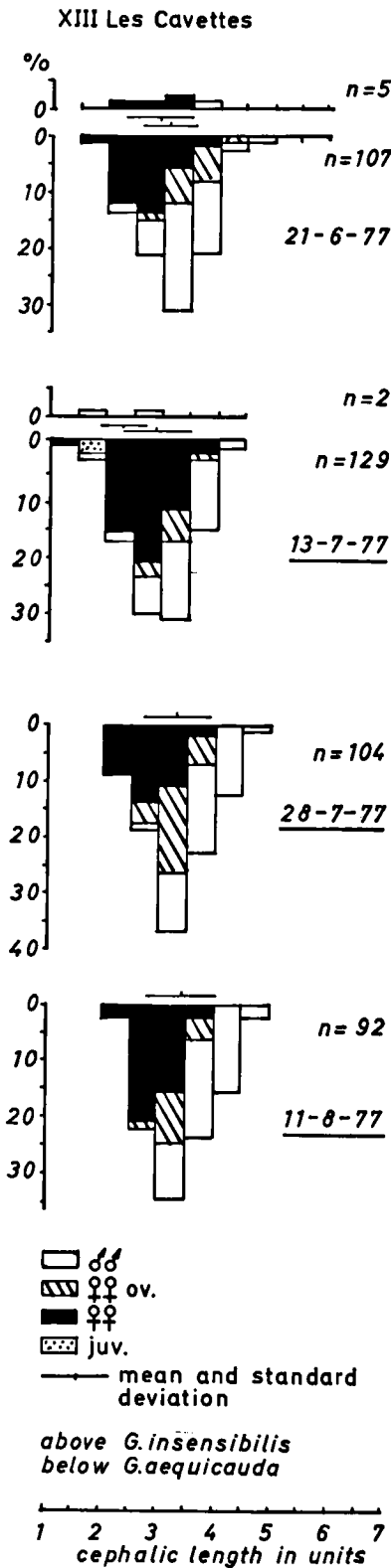cephalic length in units

Fig. 5. Continuation of previous page.

centage of males increased. In May the mean length of the population decreased. This was simultaneously caused by the death of the over-wintering generation, the increasing number of juveniles and a decrease in growth. Females died before the males. In summer the reproductive activity decreased still further, and gradually a relative increase of non-ovigerous females with respect to ovigerous females was seen. In summer there was a first succession of new batches of juveniles; the animals remained small and did not grow much. In September-October breeding activity increased again, giving birth to the over-wintering generation. In November-December reproduction dropped to a minimum. The mean body size in the population increased again be-cause of a higher growth-rate and a decreasing number of juveniles. During this period animals of the late summer generation died and a relative increase in males became visible. In January females increased in number; they all became ovigerous in February-March. In the end of January and in February no more juveniles or small animals could be found. Probably, the low winter temperatures caused a very long egg in-cubation period or even a standstill in egg devel-opment. Moreover it is possible that the death-rate of newly hatched juveniles or juveniles in the brood-pouch is rather high at these tem-peratures.

IV.1.2. Reproductive cycle of *Gammarus insen-sibilis* (see figs. 4-6).
The life cycle of *G. insensibilis* basically showed the same pattern as in *G. aequicauda*, but the sequence of events was somewhat shifted in time. In March and April a new generation was born from the overwintering generation. The large, overwintering animals died during the end of May and June. Females died before the males. In May we noticed an enormous increase of ♀♀ in the smaller size classes; there are more ♀♀ than ♂♂. In mid-summer the mean body length in the population was at its minimum. From May to August reproduction was continuous. In this period the mean length of the ovigerous ♀♀ gradually increased while the mean length of the total population remained constant; in the smaller
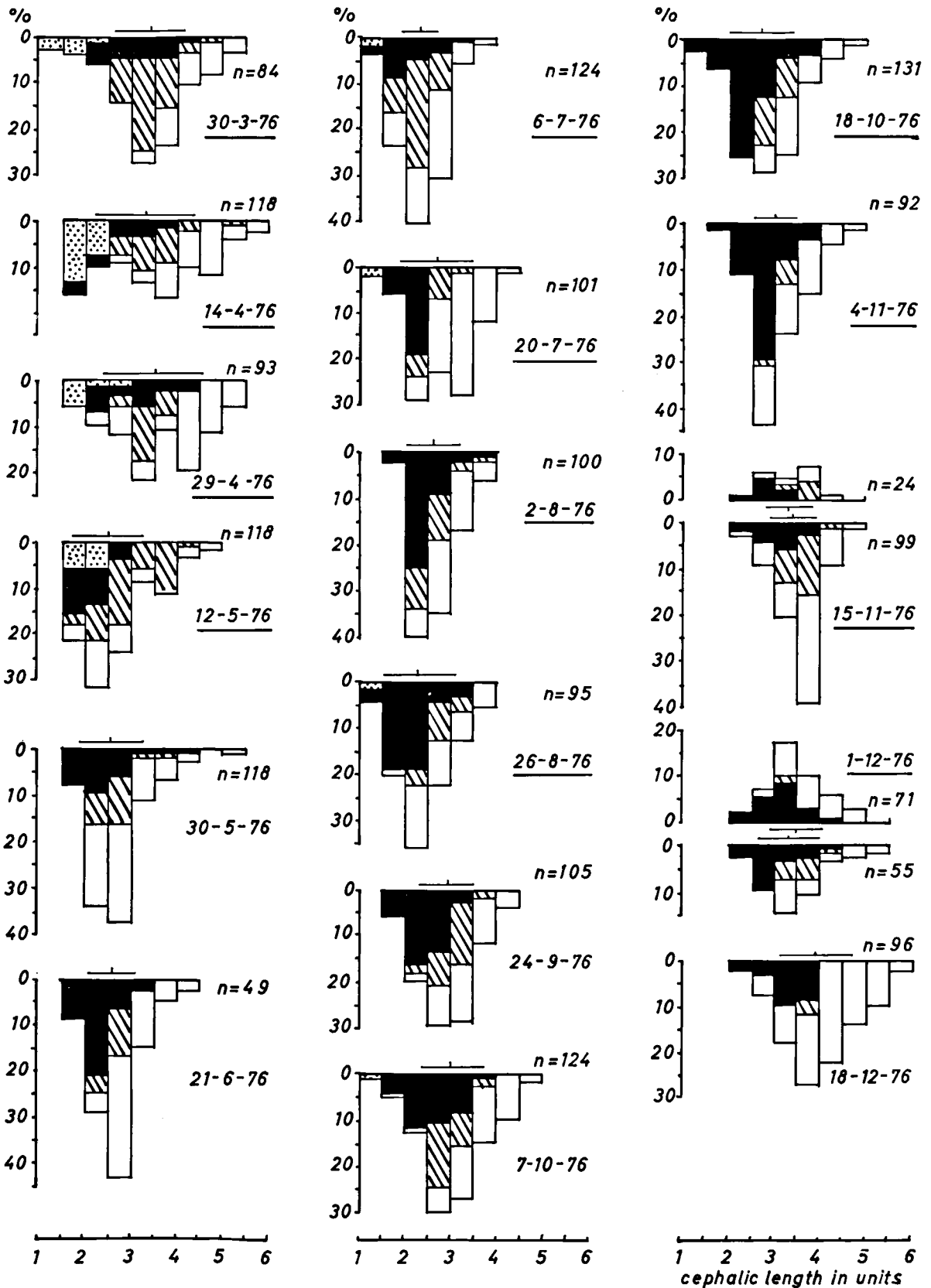
XXXI La Nautique

Fig. 6. The population composition, the mean cephalic length and its standard deviation of both *G. insensibilis* and *G. aequicauda* at station XXXI La Nautique. For meaning of the shades of the block diagrams, see fig. 5.
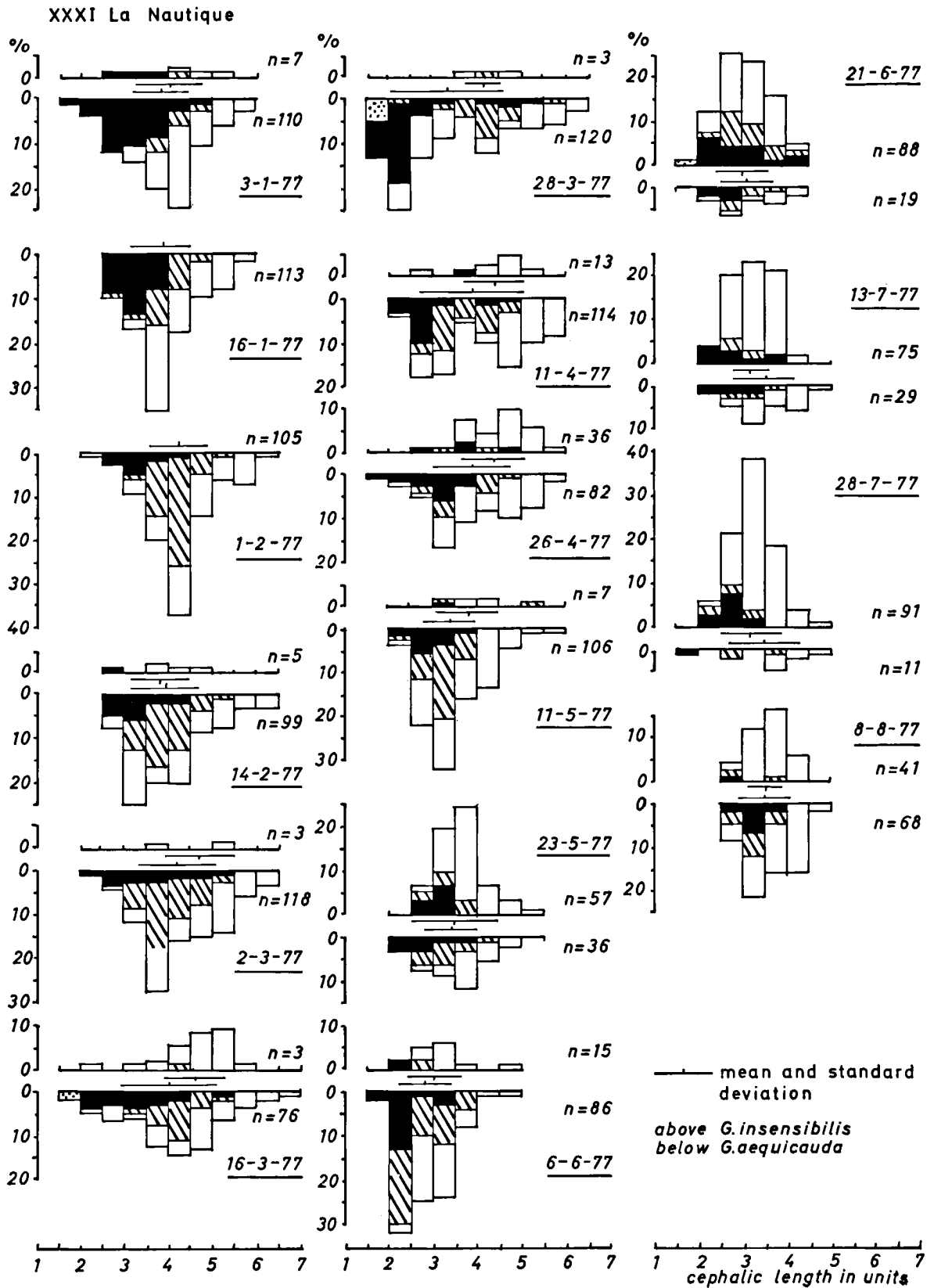
XXXI La Nautique

Fig. 6. Continuation of previous page.

size classes we found predominantly non-ovigerous females. In September the percentage of all ♀♀ decreased, but the percentage of ovigerous ♀♀ increased, giving birth to the overwintering generation. Starting in October the mean body length of the population increased and the percentage of ♀♀ decreased. Of these females one part became ovigerous, another part just disappeared. During the winter the percentage of ♂♂, as well as the mean body length of the whole population were continuously increasing.

IV.2. The mean cephalic length and its standard deviation in populations of G. aequicauda and G. insensibilis throughout the year (figs. 7a, b, c and 8a, b, c).

Since the cephalic length is correlated with the body length, increase in cephalic length can be considered as growth. During the summer months both G. aequicauda and G. insensibilis attained the age of about 50 days. They remained much smaller than animals born in colder periods of the year (Brun, 1971). Both species attained their greatest length in February-March. Males were larger than females; ovigerous females were generally larger than non-ovigerous females. The changes in mean cephalic length throughout the year were inversely proportional to temperature (see figs. 8a, 9). From October to March the mean cephalic length increased, reached its maximum in the end of March and dropped from April to June. During the summer months the mean cephalic length stayed at a constant low level.

It seems that at high temperatures the animals need so much energy for primary processes like oxygen uptake that almost nothing is left for growth. It is known that gammarids in arctic regions grow much older and attain much greater length than in temperate and warm climates. From the mean cephalic length and its standard deviation we can obtain much information about death- and birth-rates. The standard deviation is an indication of the differences in size between the juveniles and the adults. A decrease in both the mean cephalic length and its standard deviation indicates the death of part of the population in the higher size classes; an increasing standard

deviation indicates birth of juveniles. A constant or decreasing standard deviation, together with an increasing mean length, indicates a decreasing birth rate.

Reproduction continues throughout the year although not always on the same level. In March, when temperatures gradually become more favourable, the overwintering population for the first time reproduces on a large scale as can be seen from the decrease in mean cephalic length and the simultaneous increase of its standard deviation. A sharp decline in both the mean cephalic length and its standard deviation in May indicate the death of the overwintering population. During the summer months the growth rate is reduced. Animals born in early spring remain relatively small because of high temperatures and die at the end of July; this can be seen as the main cause for the minimum of the mean cephalic length in the end of July.

The population born in summer passes a period of growth in the early fall. A decline in mean cephalic length and its standard deviation in October indicates the death of this part of the population.

Apart from some variation in the curves, the pattern is basically identical for G. insensibilis and G. aequicauda. For G. insensibilis the variation throughout the year is larger than for G. aequicauda.

IV.3.1. The sex ratio of G. aequicauda and G. insensibilis throughout the year (figs. 10 and 11).

The sex ratio is defined as number of males divided by number of females. When comparing the curves of G. aequicauda (fig. 10) and G. insensibilis (fig. 11) it is clear that the curve of the latter is more erratic. Moreover, the sex ratio of G. insensibilis is in every month higher than that of G. aequicauda. Except for the period from May to August 1976, males of G. insensibilis always predominate. In G. aequicauda, on the contrary, the number of females is always higher. The curve for G. aequicauda (fig. 10) shows a sharp decline in June and from July until November the sex ratio stays at a low level; from November on, the sex ratio increases, reaching its maximum value in January 1977.

In *G. insensibilis* (fig. 11) the minimum sex ratio is found earlier in the season; it lasts a shorter period than in the other species. Starting in August 1976 the sex ratio gradually increases to a maximum in March and April 1977, reaching much higher values than in *G. aequicauda* (compare

figs. 10 and 11). In 1977 the decline in sex ratio observed in the previous year is non-existant. This is probably due to climatic conditions.

IV.3.2. The influence of temperature on the sex ratio in *G. aequicauda* (see figs. 9 and 10).

When we compare the curves of water temperature and sex ratio we can observe that a rise in temperature roughly corresponds with a decline in sex ratio and vice versa. So in summer (high T) there are many females, against many males in winter (low T). Probably we here are dealing with the influence of temperature on sex determination. Kinne (1952) found for *G. zaddachi* that at salinities of $10^o/_{oo}$ and temperatures below 5°C males are born, at temperatures above 6°C only females and in between these critical temperatures both males and females. At higher salinities these critical temperatures also rise. Bulnheim (1974) does not mention the influence of salinity or temperature on the sex determination in *G. locusta* (closely related to the two species treated here).

Moreover, when comparing the temperature in a given month with the changes in sex ratio in the next month we can observe a certain parallelism. This means that the sex ratio reacts to changes in temperature with a lag of about a month. In periods of extreme temperatures this pattern is obscured.
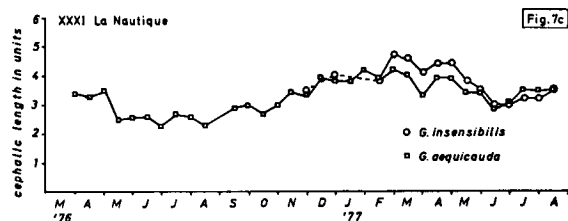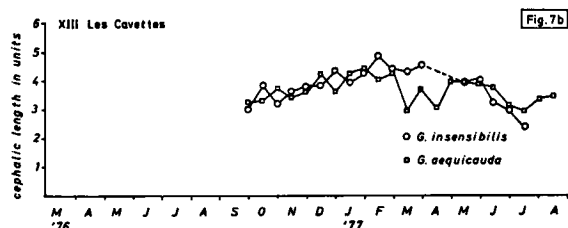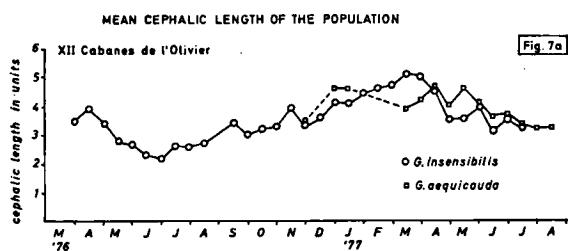

Fig. 7a, b, c. The mean cephalic length of the population at three different stations.
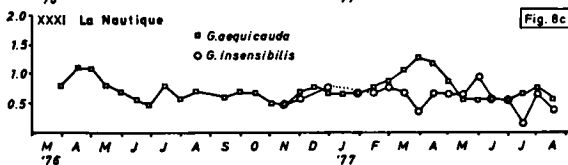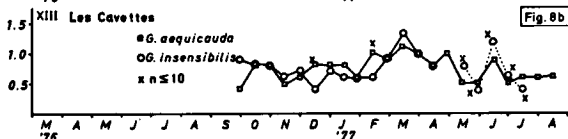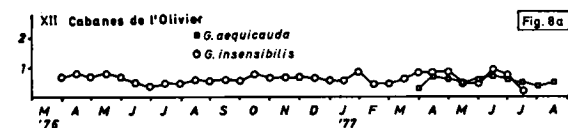

Fig. 8a, b, c. The standard deviation of the mean cephalic length of three different populations.
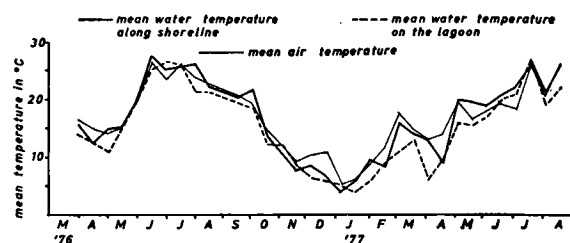

Fig. 9. Temperature fluctuations during the period of investigation measured at stations along the shoreline and on the lagoon.

Fig. 10. The sex ratio of *G. aequicauda* during the period of investigation expressed as ♂ ♂: ♀ ♀.

IV.3.3. The influence of temperature on the sex ratio in G. insensibilis (figs. 9 and 11).

The two patterns, described in IV.3.2 can also be found in G. insensibilis but minor differences exist. So the peak caused by low temperatures was somewhat retarded to March/April as compared to G. aequicauda. In summer the low minimum in the curve (many females present) lasted much shorter and from August onward the percentage of males already increased. Probably, the critical temperature for G. insensibilis is higher than for G. aequicauda. Because of the early increase in the percentage of males in August and September, the parallelism described in IV.3.2 is more vague, although basically identical to that in G. aequicauda.

IV.4. Sexual activity.

Sexual activity is defined as

$$\frac{\text{ovigerous } ♀♀ + ♀♀ \text{ in precopulation}}{\text{total number of } ♀♀} \times 100\%$$

It is meant as a measure for the reproductive activity of the population.

IV.4.1. Sexual activity of G. aequicauda.

IV.4.1.1. In fig. 12a the mean sexual activity for all sampling points throughout the year is graphically represented. It can be seen that the population was sexually active in all periods of the year but that the level of activity was fluctuating. Sexual activity oscillated between 10 and 50%, with an average of 31%. In February, March and April sexual activity was high, in summer of 1976 it was low in that of 1977 not whereas a second peak could be observed in September-October. In November-December again activity was low.

IV.4.1.2. Relation between sexual activity and temperature.

Comparing the yearly changes in water temperature (fig. 9) and the sexual activity (figs. 12a, b, c) the following correlation could be observed: At high temperatures (May, June, July) sexual activity was low; at low temperatures (November, December and January) sexual activity was also reduced. These extreme temperatures appear to be limiting for sexual activity; the latter increased with a change towards a less extreme temperature. Below a threshold temperature activity increased

with a rise in temperature and decreased with a drop in temperature. The drop in temperature in March and April 1977 caused a drop in activity, when the temperature rised again, sexual activity also increased. In spring, this threshold temperature was lower than at the end of the summer.

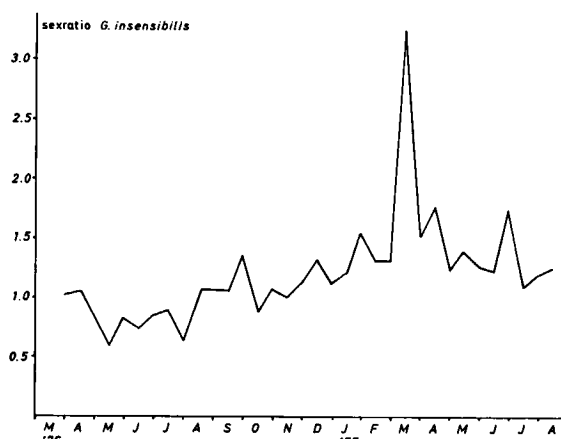IV.4.1.3. The relation between chlorinity and sexual activity of G. aequicauda, both in relation to temperature.

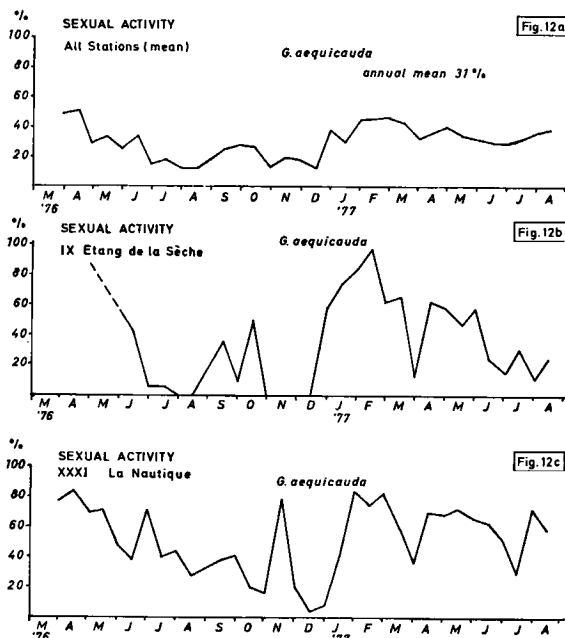Fig. 11. The sex ratio of G. insensibilis during the period of investigation expressed as ♂♂ : ♀♀.

Fig. 12. The sexual activity of G. aequicauda throughout the period of investigation: (a) as a mean value for the whole lagoon; (b) at station IX Etang de la Sèche; (c) at station XXXI La Nautique.
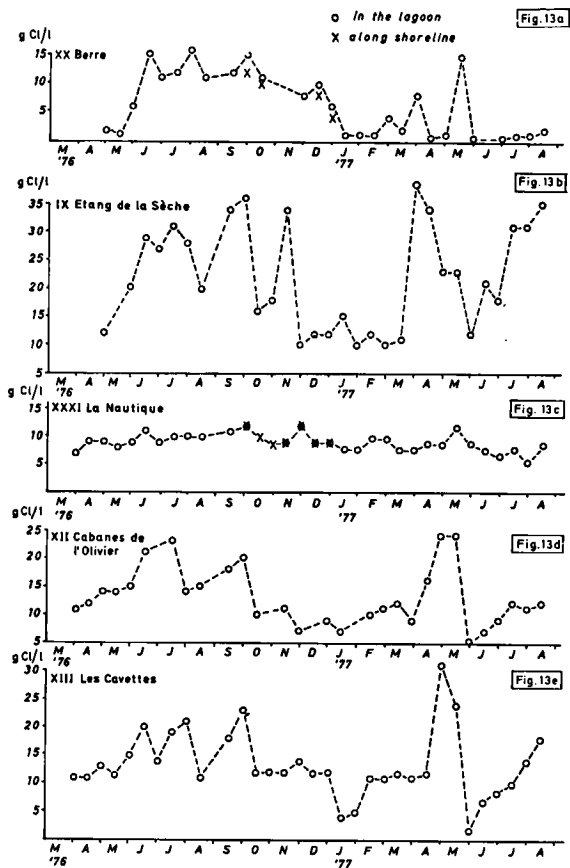
Fig. 13. Chlorinity fluctuations at five different stations throughout the period of investigation.

Fig. 14. The sexual activity of G. insensibilis throughout the period of investigation a) as a mean value for the whole lagoon b) at station XIII in a mixed population with G. aequicauda c) at station XII Cabanes de l'Olivier d) at station XX La Berre in a mixed population with G. aequicauda.

Since chlorinity is usually dependent on temperature, its direct influence could be observed at extreme situations only. This could be demonstrated on localities IX and XXXI. Sexual activity and chlorinities at these localities are shown in figs. 12b, c and 13b, c respectively. It can be seen that at extremely high temperatures and extremely high chlorinities sexual activity was declining (June-July 1976 and June, July and August 1977). From August 1976 until October 1976 a recovery in sexual activity was seen but this was negatively influenced by the high chlorinity between September and October. From medio December 1976 sexual activity rised sharply as was to be expected, chlorinities being relatively low. Between March and May 1977 chlorinities were very high. The sudden drop in temperature in March-April 1977 immediately caused a sharp decline in sexual activity. During the following

rise in temperature, sexual activity also rose. At Station XXXI it can be seen that at low chlorinities this drop in temperature caused a less sharp decline in sexual activity than at Station IX.

IV.4.2. Sexual activity of G. insensibilis.

IV.4.2.1. General.

In fig. 14a the mean sexual activity for all sampling points throughout the year is graphically represented. It oscillated between 20 and 50% (mean 34%). Sexual activity reached its peaks in August-September 1976 and February-March 1977. Lowest activity was found in May-July 1976, December 1976 and June-July 1977. Differences between the highest and lowest activity were

smaller than in *G. aequicauda*. As in *G. aequicauda* the mean values in summer 1977 were higher than in summer 1976.

IV.4.2.2. Relation between sexual activity and temperature (figs. 14a and 9).

As in *G. aequicauda* sexual activity of *G. insensibilis* was reduced in periods with the highest and with the lowest water temperatures. When temperatures changed from extreme to less extreme, sexual activity increased. Below the limiting upper temperature sexual activity increased and decreased with temperature. The minimum in activity during the summer was of relatively short duration which is an indication for a higher limiting temperature than in *G. aequicauda*.

IV.4.2.3. Relation between sexual activity of *G. insensibilis* and chlorinity.

In localities where *G. insensibilis* was found extreme chlorinities have been observed at Stations XIII and XII (see figs. 14b and c for sexual activity and figs. 13e and 13d for chlorinities). In April-May 1977 chlorinities were extremely high, $30^0/_{00}$ and $24^0/_{00}$ respectively. In both localities a negative influence on the sexual activity was observed.

IV.4.3. Comparison of the sexual activity in *G. aequicauda* and *G. insensibilis*.

In general the mean value for sexual activity in *G. insensibilis* was slightly higher than in *G. aequicauda*. More important however is that sexual activity in *G. insensibilis* was more constant than in *G. aequicauda*. The minimum in activity of *G. aequicauda* during the hot summer months was lower and lasts much longer than in the other species (figs. 12a and 14a). The decrease and increase in sexual activity at the beginning and at the end of the summer period was sharper in *G. aequicauda* than in *G. insensibilis*. The maximum values in the spring were about identical for both species (figs. 12a and 14a).

IV.4.4. Relation between sex ratio and sexual activity.

Sections IV.3. and IV.4. seemingly prove that changes in sex ratio are parallel to changes in sexual activity. Higher or lower percentages of males directly corresponded with higher or lower

sexual activity. In summer there were relatively more females. Possibly this was due to the influence of temperature on sex determination. The sexual activity of the population then decreased as can be seen from the small number of ovigerous females. In winter, when relatively more males were present, the sexual activity of the population increased as can be concluded from the high number of ovigerous females. Sexual activity not only depends on temperature but likewise on the sex ratio. The sex ratio is not dependent on sexual activity but on temperature.

IV.5. Egg-production.

IV.5.1. The relation between the average number of eggs ($\bar{x}$) and the mean cephalic length (l_c).

Following Jensen (1958) in figs. 15a, b and c, the relation between $\bar{x}$ and (l_c) is illustrated. In expressing the cephalic length we used the same length classes as were used for illustrating the population composition (figs. 4, 5 and 6). For every class the average number of eggs present in the broodpouch was determined during a period of 1 to 1.5 years. In 2 populations of *G. aequicauda* and 2 populations of *G. insensibilis* it was proved that a linear correlation exists between the number of eggs present in the marsupium and the third power of the cephalic length. The regression lines can be expressed as

for *G. aequicauda* (Stat. XXXI) $y = 9.76 + 0.68x$ $r^2 = 0,98$
G. aequicauda (Stat. XIII) $y = 0.63 + 0.69x$ $r^2 = 1.00$
G. insensibilis (Stat. XII) $y = 5.12 + 0.47x$ $r^2 = 0.97$
G. insensibilis (Stat. XIII) $y = 5.50 + 0.26x$ $r^2 = 0.97$

(see figs. 15a, 15c, 15b and 15c, respectively).

Such a relation between animal size and the mean number of eggs was already described by Sexton (1928) for *G. chevreuxi* and *G. pulex*; by Cheng (1942) for *Chaetogammarus* spp., *G. duebeni* and *G. chevreuxi*; by Vlasblom (1969) for *Chaetogammarus marinus*; by Brun (1971) for *G. insensibilis* and *G. aequicauda* and by Dumay (1972) for *G. subtypicus* and *G. crinicornis*.
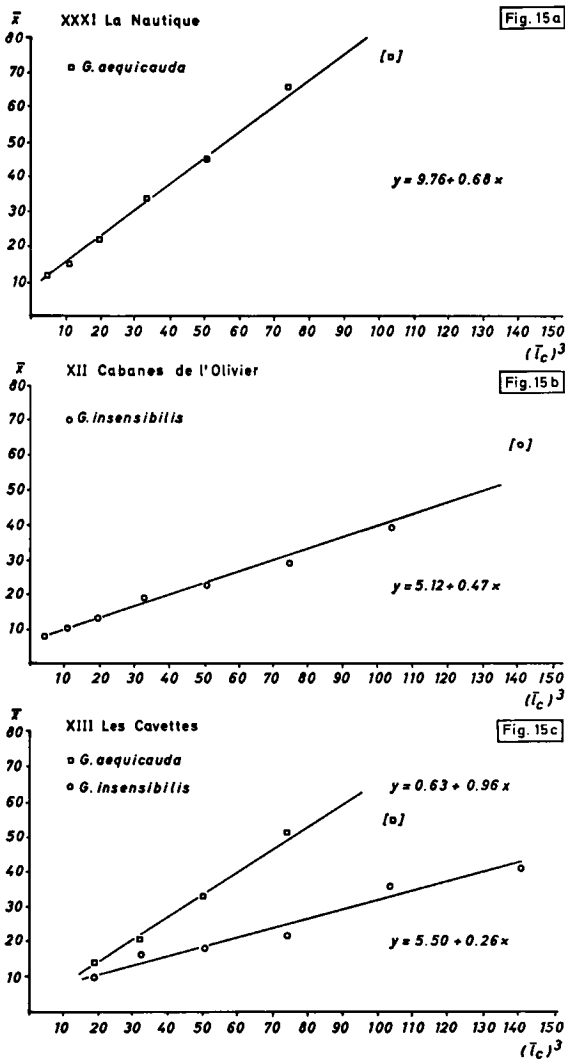
Fig. 15. Correlation between the mean number of eggs per ovigerous female and the cephalic length a) in *G. aequicauda* at station XXXI La Nautique b) in *G. insensibilis* at station XII Cabanes de l'Olivier c) in a mixed population of *G. aequicauda* and *G. insensibilis* at station XIII Les Cavettes.

Fig. 16. Histogram showing the proportional distribution of the various developmental stages of the eggs in ovigerous females at three different stations. The graph shows the mean number of eggs found in every stage $(\bar{x})$.

IV.5.2. The mean number of eggs per female of *G. aequicauda* and *G. insensibilis* during the period of investigation (fig. 18).

In April 1976 the mean number of eggs was relatively high in both species. For *G. aequicauda* at Stat. XXXI this was about 60, for *G. insensibilis* at Station XII about 30. In early summer this number decreased to an average of 15 eggs for *G. aequicauda* and 10 for *G. insensibilis*. In September 1976 the mean values in *G. insensibilis* increased and stayed at a more or less constant higher level until January 1977. From this time on the values increased to a maximum in March 1977. The situation for *G. aequicauda* is somewhat different from that in *G. insensibilis*. From June until November the mean number of eggs stayed at a rather constant low level, but in the beginning of December (at Stat. XXXI) or even in November (at Station XIII) these values increased sharply. Maximum values for both species were found from January, (December) to April. Maxima in *G. aequicauda* can be as high as 70 against 40 in *G. insensibilis*. Starting in April 1977 the values decreased to low summer values in both species. It can be seen from these figures that the total egg production of *G. aequicauda* was considerably higher than that of *G. insensibilis*.

IV.5.3. Relation between the mean number of eggs and the mean cephalic length (figs. 18 and 19).

In section IV.5.1 we demonstrated that the num-

Fig. 17. See fig. 16. Only females with a cephalic length between 1.25 and 1.45 have been used.

Fig. 18. Mean number of eggs per ovigerous female per month of *G. aequicauda* and *G. insensibilis* at three stations.

ber of eggs is linearly correlated with the third power of the cephalic length. By comparing figs. 18 and 19 we can see that indeed in *G. aequicauda* this correlation holds seasonally. However, in *G. insensibilis* (e.g. from les Cavettes) this does not always hold true. From September 1976 to March 1977 increasing cephalic length did not seem to be directly correlated with increasing numbers of eggs. Probably, this was caused by reaching a limiting fac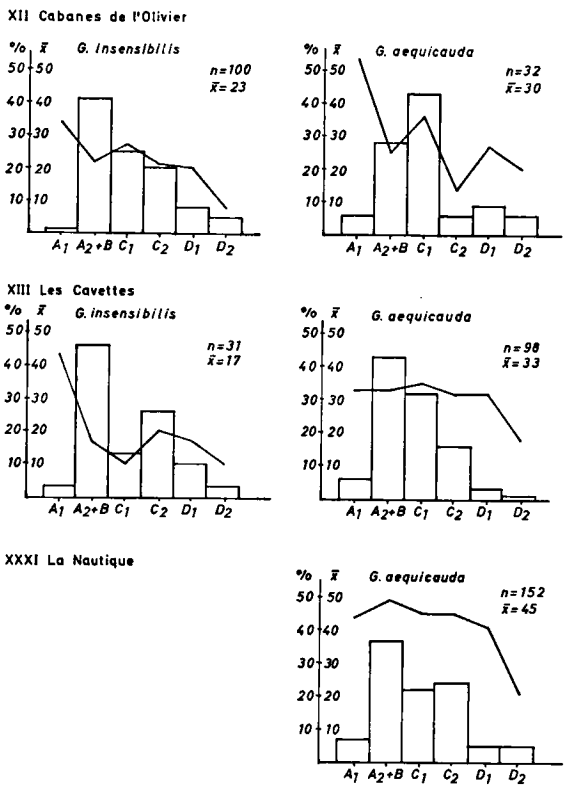tor (temperature?) that controls growth and ovoposition. Thus it can be seen that the relation between ($\bar{x}$) and (l_c) as described in IV.5.1. is not always constant throughout the year as has been demonstrated also by Dumay (1972).

IV.5.4. Influence of temperature on the mean number of eggs (figs. 9 and 18).

As can be seen in figs. 9 and 18 an increase in temperature usually corresponds with a decrease in mean number of eggs. After a period of low temperatures a rise in temperature can stimulate the production of eggs until a critical temperature of about 15°C is exceeded.

IV.5.5. The influence of chlorinity on the mean number of eggs (figs. 18, 13c, 13d and 13e).
The influence of chlorinity is less pronounced. In localities such as Station XXXI the chlorinity did not show important fluctuations so its influence could not be studied. At the other hand at Station XII strong chlorinity fluctuations occurred. It can be seen that below a certain threshold value chlorinity has no influence on the mean number of eggs, which is dependent on temperature (IV.5.3). Above this value (and probably also at extremely low values) a negative influence can be observed.

It is difficult to trace the influence of chlorinity on changes observed since this factor is usually closely correlated with temperature. Temperature not only directly but also indirectly influences the
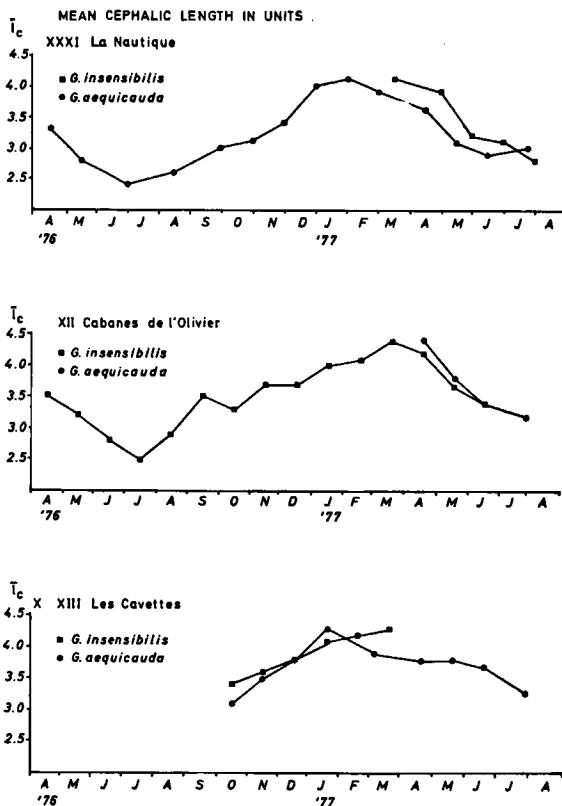
Fig. 19. Mean cephalic length of populations of *G. aequicauda* and *G. insensibilis* at three stations.

mean number of eggs by its influence on chlorinity. Therefore it is difficult to contribute certain changes to one or other of the two factors.

After the extremely high rainfall in May 1977 and the subsequent drop in chlorinity it was possible to study the influence of chlorinity apart from temperature. This influence was clearly visible at Station XIII. Usually, during this time of the year temperature is rising and consequently also the chlorinity. This rise in both temperature and chlorinity usually continues until June-July as can be seen in 1976. Indeed, temperature continued to rise but due to heavy rainfall, the chlorinity sharply dropped to extremely low values. Until that moment, the mean number of eggs of *G. aequicauda* (at Sta. XIII) was gradually decreasing as could be expected from the course of the temperature curve. However, this time the mean number of eggs suddenly increased, most probably as a reaction upon the sudden change in chlorinity. Too high a chlorinity does not seem beneficial to egg production. This has already

been observed by Kinne (1960, 1961) in his laboratory experiments with *G. zaddachi* and *G. salinus*. Grèze, 1976b, in comparing populations of *G. insensibilis* from the Black and Adriatic Seas found that females produced more eggs at higher salinities.

IV.5.6. Developmental stages of the eggs, relative abundance of these stages and mean number of eggs per stage.

During their development in the marsupium eggs pass through different stages as explained in section III.4. In figs. 16 and 17 we illustrate the frequency of the various stages during the period of investigation. As a rule, all eggs in the broodpouch of a single female are in the same developmental stage. Some stages are frequently found, other are rare. When we assume that the chance to come 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.

In figs. 16 and 17 we also illustrate the mean number of eggs per stage. It can be seen that the number of eggs decreases during development. This decrease is most obvious between D_1 and D_2. In *G. aequicauda* it is somewhat steeper than in *G. insensibilis*. However, since the initial number of eggs is also higher in *G. aequicauda*, the ultimate number of eggs in stage D_2 is still considerably higher than in *G. insensibilis*.

Some authors (Cheng, 1942; Dumay, 1972) use the mean number of eggs as a measure for the "fecundity" of a population. However, they did not take into account the developmental stage of the eggs. Therefore it would not be correct to consider this "fecundity" as reproductive capacity. When coming upon a high mean number of eggs in a certain period we have to consider the developmental stage of the eggs in the majority of the ovigerous females before drawing conclusions about the reproductive capacity.

It was found that the percentage of D-stages is not constant during the year. So we hardly found any D-stages in *G. insensibilis* in December 1976 but many D-stages in March and April of the following year. Therefore, in December 1976 the reproductive capacity is much lower than should

be expected from the observed number of eggs whereas in March and April 1977 it is almost identical to the mean number of eggs. Brun (1971) and Dumay (1972) found that the eggs in the marsupium grow during development. During the present study a reduction in number during development was observed, especially in times of a high initial number of eggs. Combining these data we must assume that this reduction in number is caused by growth of the eggs. If, during the C-stages all available space in the marsupium is filled up with eggs, then, to secure the further growth and development of the eggs, expulsion of eggs is inevitable. This reduction in number of eggs is most probably fluctuating with the mean initial number of eggs throughout the year (fig. 18).

Kinne (1952) also observed this decrease in mean number of eggs during development in *G. duebeni*. This phenomenon, which he ascribed to the death of the eggs was found to vary from 5% in April to 50% in December. Vlasblom (1969) in his experiments with *Chaetogammarus marinus* found that at 15°C about 75% of the eggs really hatched whereas at 9°C this percentage was as low as 17. Roux (1970) attributes this decrease in number of eggs and juveniles to be due to fixation methods; because of the violent movements, ovigerous females would expel some of the eggs and juveniles. During our work, ovigerous females were always stored separately in small vials. However, we never found "loose" eggs, although occasionally, some fully developed juveniles (end of D_2 stage) have been found.

IV.6.1. Theoretical approximation of the length of some life-processes.

Temperature coefficients (Q_{10}) of various life processes in Crustacea vary between 2 and 3 (see Wolvekamp & Waterman, in Waterman, 1960). Based on this knowledge and on additional data of Kinne (1952) about *G. zaddachi* and Pinkster et al. (1977) about *G. tigrinus*, *G. duebeni*, *G. zaddachi* and *G. p. pulex*, we have chosen a temperature coefficient (Q_{10}) of 2.8 for *G. insensibilis* and *G. aequicauda* to make calculations about the duration of certain life processes.

Brun (1971) found that in laboratory experiments at temperatures varying from 18 to 20°C the mean life span of both species was about 95 days. Sexual maturity is reached after 30 to 40 days, the interval between two batches being 7 to 15 (usually 9) days. The time of precopulation varies from 1 to 3 days. For our calculations we used the following figures:

at 21°C   mean life span   95 days
            sexually mature after   35 days
            egg incubation time   9 days
            duration of precopulation   2 days

These figures have been adjusted according to the mean water temperatures as observed during the period of investigation (table I).

TABLE I

Calculated length of some life-processes of *G. aequicauda* and *G. insensibilis* throughout the year. $(T_{10} =$ water temperature).

	T_{w}	theoretical mean lifespan in days	sexually mature after days	egg incubation time in days	duration of precopulation in days
January	5	408	175	50	9
February	11	228	88	26	5
March	13	196	70	22	4
April	14	176	65	20	3
May	17	132	59	15	3
June	27	48	21	6	1
July	25	60	25	7	1
August	25	60	25	7	1
September	20	100	35	11	2
October	17	132	59	15	3
November	9	280	105	33	6
December	7	340	140	40	7

It is possible, with the aid of table I, to calculate the life cycle of animals born at every given point of the year. Since we are interested in the number of batches per year we made our calculations for females. Time to reach sexual maturity in males and females is identical. In general females live a little shorter than males (IV.1.1), although Brun did not indicate differences between the two sexes. For the time between the exclosure of the first and following batches of eggs we added the duration of the precopulation to the egg incubation time, although it is known (Brun, 1971) that often females enter into precopulation before the juveniles of the previous batch have been released.

TABLE II

Life history of 6 females, born on different times of the year.

		date of birth		sexually mature on		after n days	release of juvenile on		date of death		life span in days
♀	1	March	1	May	7	67	May	25	June	22	112
							June	5			
							June	12			
							June	19			
♀	2	June	1	June	21	21	June	28	July	22	52
							July	5			
							July	13			
							July	21			
♀	3	August	1	August	25	25	Sept.	4	Oct.	26	86
							Sept.	15			
							Sept.	28			
							Oct.	10			
							Oct.	25			
♀	4	Sept.	1	Oct.	8	38	Oct.	26	March	20	171
							Dec.	4			
							Jan.	16			
							Febr.	21			
							March	20			
♀	5	Oct.	15	Febr.	8	113	March	9	May	31	202
							March	31			
							April	23			
							May	14			
							May	30			
♀	6	Dec.	1	March	2	122	March	26	June	12	188
							April	23			
							May	13			
							May	31			
							June	7			

IV.6.2. The examples in table II clearly underline the importance of the effect of temperature on life processes. During the summer months animals develop and reproduce 4 to 5 times as fast as during the winter months. Knowing that both species reproduce throughout the year it can be calculated that theoretically as much as 22 batches of offspring can be produced during one year. However, the question arises if all these batches are actually born. As can be seen from figs. 4, 5 and 6 and from figs. 7 and 8 there is no indication that renewal of the population takes place between December and February (see also IV.1.1, IV.1.2 and IV.2). This stop in juvenile production during extremely cold periods was also observed in G. tigrinus (cf. Pinkster et al., 1977). Vlasblom (1969) found dying brood in the brood pouches of female Chaetogammarus marinus after periods with low temperature. In warmer periods the majority of juveniles are born and the reproductive success is much greater than in colder periods. In winter, the mean age of the population

is determined by animals born in a warmer period. The majority of the animals have about the same age. So the animals born in October determine the general aspect of the winter population. The contribution of animals born in later periods is negligible since the birth-rate is very low in periods of low temperatures.

V. DISTRIBUTION AND RELATIVE ABUNDANCE of *G. aequicauda* and *G. insensibilis* throughout the lagoon and its dependance of biotic and abiotic factors (figs. 1 and 20).

V.1. Distribution and relative abundance in the different basins.

Both *G. aequicauda* and *G. insensibilis* are distributed throughout the lagoon. In the past various authors (Petit & Mizoule, 1962; Fiala, 1974; Mercier, 1973; Boutière, 1974) have subdivided the lagoon into separate sub-basins based on physico-chemical characteristics (see fig. 1).

During this study, the distribution of the two species over the lagoon appeared to be far from constant. Therefore we also subdivided the lagoon in 3 basins on the basis of the changes in chlorinity and their deviations. However, the Etang de la Sèche was considered separately because of its extremely unstable character. For characteristics of the different basins and relative abundance of the species see table III and fig. 20.

TABLE III

Mean chlorinities, annual changes in chlorinity expressed as $\sigma \mathrm{Chl}/\overline{\mathrm{Chl}}$ and mean annual percentage of *G. aequicauda* (*G.a.*) and *G. insensibilis* (*G.i.*).

	mean chlorinity in g/l per year	$\sigma \mathrm{Chl}/\overline{\mathrm{Chl}}$	mean percentage of *G.a.*	mean percentage *G.i.*
Basin I	8.5	0.18	57	43
Basin II	9.5	0.26	31	69
Basin III	14.0	0.32	9	91
E. de la Sèche	22.0	0.43	95	5
All Stations			31	69

When we follow the relative abundance of the two species throughout the year (fig. 20) we can see a great resemblance between the pattern in the whole lagoon and those in the separate basins.
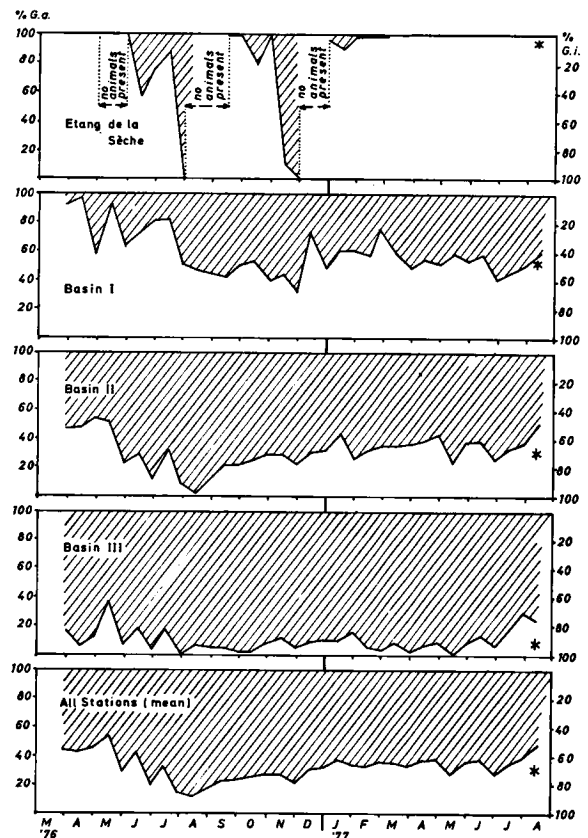

Fig. 20. Relative abundance of *G. aequicauda* and *G. insensibilis* in the Étang de la Sèche, the three different basins and the whole lagoon system. Upper parts *G. insensibilis*, lower parts *G. aequicauda*. The asterisks indicate the annual mean.

Changes in the ratio *G. aequicauda/G. insensibilis* go parallel. A relative increase of any of the species is visible in all parts of the lagoon and not in a single basin only. Therefore we must conclude that changes in the ratio *aequicauda/insensibilis* are of a higher order than the differences in stability observed between the various Stations. The only exception is the Etang de la Sèche.

V.2. Distribution, temperature and chlorinity (figs. 20, 9 and 13).

Studying figs. 20, 9 and 13 it becomes clear that changes in the distribution pattern can be seen as a function of both temperature and chlorinity. In periods of high temperature and increasing salinity a simultaneous increase of *G. aequicauda* could be observed. If the chlorinity dropped during such a period, the ratio rapidly changed in favour of *G. insensibilis*, as could be seen in

August 1976. In periods of low temperatures *G. insensibilis* can maintain itself at higher chlorinities as could be seen in March-April 1977. Very low chlorinities appeared to be unfavourable for *G. insensibilis* even when temperatures were rising, as could be observed after heavy rainfall in May 1977. In some localities the species completely disappeared after this event. The pattern is schematically illustrated in table IV.

TABLE IV

Distribution of *G. aequicauda* (*G.a.*) and *G. insensibilis* (*G.i.*) in relation to temperature and chlorinity.

	T high (24-30°C)	T moderate (10-24°C)	T low (0-10°C)
chlorinity high (>20%)	*G.a.*	*G.a.*	*G.a.+G.i.*
chlorinity moderate (20%>chl.>10%)	*G.a.+G.i.*	*G.i.*	*G.a.+G.i.*
chlorinity low (<10%)	*G.a.*	*G.a.*	*G.a.*

V.3. Distribution and relative abundance of *G. aequicauda* and *G. insensibilis* in relation to depth. In table V we summarized the distribution and relative abundance of both species against depth. *G. aequicauda* was predominantly found at depths between 2 and 11 dm and (although less frequent) in the upper layer of 0-1 dm. At greater depths than 11 dm *G. aequicauda* had almost disappeared. *G. insensibilis* was most frequently found in the upper 1 dm and below 11 dm. It was less frequent between 2 and 11 dm. The same pattern was found in the ratio *G. aequicauda/ G. insensibilis*.

TABLE V

Frequency of *G. aequicauda* (*G.a.*) and *G. insensibilis* (*G.i.*) at various depths. (*n* = number of specimens found).

depth class in dm	frequency *G.a.*	frequency *G.i.*	ratio *G.a./G.i.*	*n*
0-1	21.1	25.1	24.0-76.0	27,685
2-4	39.3	19.1	44.1-55.9	37,405
5-11	33.6	13.8	51.9-48.1	10,135
12-20	3.0	21.6	6.8-93.2	11,165
21-28	3.0	20.5	3.0-97.0	6,185
all stations	100.0%	100.0%	31.0-68.0	92,575

G. insensibilis dominated in the upper layer as well as in the lower layers. In between the numbers of both species were more or less in equilibrium. If depth may be used as a measure for stability, it may be concluded from these data that *G. insensibilis* was predominantly found in the more stable parts of the lagoon, viz. the deeper parts. At first sight, its occurrence in the upper layer may seem in contradiction with this conclusion. However, as was already mentioned in section II, *G. insensibilis* at the surface inhabits the layers of dead herbal material that fringe the lagoon. Especially in summer, when the water temperature is high and the oxygen saturation level is relatively low, the animals move into the upper layer of the vegetation, a zone with a high relative humidity, a high oxygen saturation level and relatively low temperatures because of evaporation (own observations). *G. aequicauda* was predominantly found in the more unstable parts, at depths from 1 to 11 dm. In the upper dm of the lagoon the two species were spatially separated: *G. insensibilis* in the (stable) upper layer of the herbal material and *G. aequicauda* in the less favourable deeper zone of herbal deposits or in the water with a high temperature and low oxygen saturation level.

V.4. Influence of substrate and vegetation on distribution and relative abundance of *G. aequicauda* and *G. insensibilis*.

G. aequicauda and *G. insensibilis* are spatially separated among others because of a difference in preference for vegetation and substrate. Substrate appeared to be more important for *G. aequicauda* than for *G. insensibilis*; the latter was mainly staying in the vegetation. *G. aequicauda* was more often seen while swimming over long distances from one shelter to another. *G. aequicauda* was frequently found between gravel and especially between dead shells on a bottom of sand or sandy silt, at varying depths with or without vegetation. If a vegetation was present, *G. aequicauda* preferred the fields with *Zostera nana* and *Ruppia* sp. On silty bottoms, as found in the reedlands, *G. aequicauda* was found in the sometimes decaying *Ulva* sp. and, although less frequently, in *Gracilaria* sp. It could also be found

in the thin layers of material washed ashore below and in front of the overhanging shore vegetation. Usually, thick layers of herbal material in various stages of decay fringe the borders of the lagoon. In these layers *Zostera marina, Z. nana* and *Ruppia* sp. are dominant but *Ulva* and *Gracilaria* are found also. *G. insensibilis* was concentrating there in often very dense populations. If such a zone was absent *G. insensibilis* was found in between the *Ulva* and *Gracilaria* vegetation and on rocky substrates between *Enteromorpha*. It was rarely found in beds of *Zostera nana* or *Ruppia* sp.

If both *G. aequicauda* and *G. insensibilis* occur at a given locality, a spatial separation is established on ground of these preferences. Possibly food preferences play an important role (Brun & Dumay, 1974). If a zone of herbal material is present along the shoreline, *G. insensibilis* is predominantly found within it whereas *G. aequicauda* is rather found on the substratum and in the vegetation. If such a zone is absent the density of *G. insensibilis* decreases. In such a situation *G. insensibilis* is more often found in the vegetation (especially in *Ulva* sp.) and *G. aequicauda* between dead shells and gravel.

In some parts of the year the diversity of the environment decreases and conditions gradually become uniform, making this spatial separation almost imperceptible.

V.5. Relative abundance of *G. aequicauda* and *G. insensibilis* in relation to their sexual activity (figs. 20, 12 and 14).

From figs. 12 and 14 it appears that the sexual activity can be an important mechanism in determining the relative abundance of *G. aequicauda* and *G. insensibilis*. In the end of July and in the beginning of August 1976 a sharp decrease in chlorinity took place simultaneously with decreasing temperature (V.2). In this period sexual activity was at its minimum in *G. aequicauda* but had sharply increased in *G. insensibilis* (VI.4.3). In fig. 20 it can be seen that during this period *G. aequicauda* is replaced by *G. insensibilis* in many parts of the lagoon. The curves of the relative abundance of the two species in the whole lagoon but especially in Basin II to a great extent correspond with the curve of the sexual activity of

G. aequicauda in the whole lagoon. Every important alteration in the sexual activity can be found again as an important event in the curve of the relative abundance. The curve of the relative abundance is the reverse of the sexual activity curve of *G. insensibilis*.

V.6. The distribution of *G. aequicauda* and *G. insensibilis* in relation to the instability of the environment.

To judge the stability of the environment we took as criteria the depth and the chlorinity. Of all abiotic factors these factors (together with temperature) seem to be the most influential. So the disturbance through wave action and the daily temperature fluctuations are directly linked with depth (shallow parts are more sensitive to temperature changes than deep parts). Changes in chlorinity depend on temperature and depth (through evaporation), but above all chlorinity depends on the position in the lagoon.

The instability (I) of a certain Station can be defined as $I = ln \left(\dfrac{\sigma \, Chl: \overline{Chl}}{depth} \times 100 \right)$, in which ln = the natural logarithm, Chl = the standard deviation of the measured chlorinities at one Station, $\overline{Chl}$ = mean annual chlorinity; the depths are expressed in m. The factor $\sigma \, Chl / \overline{Chl}$ brings about that changes in chlorinity at a low average chlorinity are weighing more than the same changes at a high average chlorinity. For every Station this factor is constant throughout the year.

The question arises as to how far *G. insensibilis* and *G. aequicauda* can be separated on basis of the instability of the environment. It appeared to be impossible to separate the two species simply by using the presence or absence of individuals of one of the species. Since extreme conditions are especially acting upon reproductive stages, we took the presence or absence of ovigerous females and females in precopulation as a criterion. In fig. 21 are plotted the distribution and abundance of ♀♀ ov. and ♀♀ in precopulation of both species against instability and chlorinity. For the sake of clarity localities in which both species were found are omitted in this figure. At low instabilities we find exclusively *G. insensibilis* although within a limited chlorinity range. The majority of these
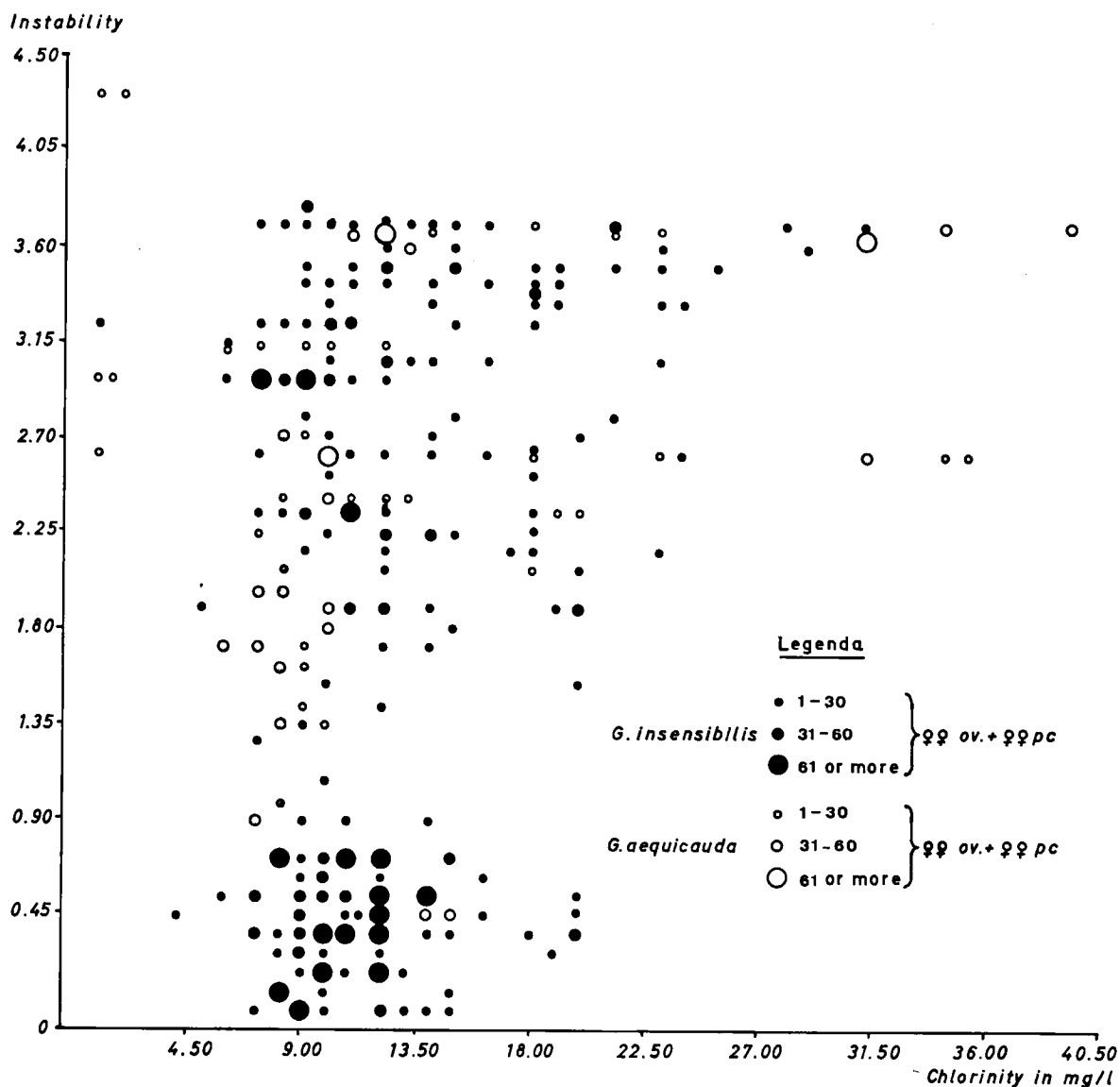
Fig. 21. Scatter diagram showing the distribution and abundance of *G. aequicauda* and *G. insensibilis* in relation to chlorinity and instability of the habitat. The size of the (open and closed) circles is an indication for the number of sexually active females found at a given habitat.

localities are found in the deeper parts of the lagoon with stable conditions. At higher instability values the two species occur together, likewise within a rather limited chlorinity range. At low chlorinities (left side of diagram) *G. aequicauda* is dominant. These conditions prevail in Basin I where the average chlorinity is low but rather stable. At increasing instability values we still find both species but *G. aequicauda* shows a much higher tolerance for extreme chlorinities than *G.*

insensibilis (upper right side of diagram). Reproductive females of *G. aequicauda* can be found from very low to very high chlorinity values, whilst *G. insensibilis* is clearly limited to the less extreme values.

VI. CONCLUSIONS

VI.1. *G. aequicauda* and *G. insensibilis* both have a regular reproductive cycle characterized by

maxima in autumn and spring. For each species the maximum in the spring is most pronounced. The maximum for *G. aequicauda* occurs in February-March, for *G. insensibilis* in March-April. The autumn-maximum for *G. aequicauda* is found in September and October; for *G. insensibilis* it lasts from August till October. During the summer months reproductive activity of *G. aequicauda* is at a much lower level than that of *G. insensibilis*.

VI.2. The sex ratio in *G. insensibilis* is always higher than in *G. aequicauda*. A positive correlation seems to exist between the sex ratio and sexual activity. Sexual activity likewise depends on temperature and chlorinity. High temperature and high chlorinity seem unfavourable for both species but especially for *G. insensibilis*. At low chlorinities reproductive activity was still observed in *G. aequicauda* but in these circumstances the populations of *G. insensibilis* usually decline sharply or even disappear.

VI.3. The mean number of eggs per ovigerous female is higher in *G. aequicauda* than in *G. insensibilis*. Nevertheless the reproductive success in *G. insensibilis* seems to be greater than in *G. aequicauda* as can be seen from the much wider distribution of *G. insensibilis* in those parts of the lagoon where the environmental conditions are favourable during most of the year.

VI.4. At very high chlorinities (e.g. the Etang de la Sèche, the Etang du Doul, various small pools) as well as at very low chlorinities (Stations XX and XIII, where the most important freshwater influx takes place) *G. aequicauda* is the only species to be found. In the other parts of the lagoon where both species are found, they are spatially separated because of differences in tolerance-limits. If an overlap takes place between these limits, e.g. because of changes in temperature and chlorinity, then a spatial separation will appear according to different preferences for vegetation and substrate and to factors like instability and depth. So the overlap is continuously decreasing.

VI.5. Only if such a spatial separation becomes impossible through too great a uniformity in habitats can there be a question of competition. Therefore it does not seem likely that one species will completely replace the other because of the constant and great changes to which the environment is liable. So climatological factors like wind (supply of herbal material) or precipitation (drop in chlorinity) can rapidly change the environmental conditions temporarily in favour of one of the two species.

Often *G. aequicauda* and *G. insensibilis* react differently in their distribution to ruling environmental factors. The changes in distribution can often be translated as changes in sexual activity. So sexual activity must be considered an important mechanism in determining distribution.

VII. DISCUSSION

VII.1. The reproductive cycles of *G. insensibilis* and *G. aequicauda* are fundamentally regular in so far that they are in agreement with the facts established by Grèze (1972, 1976b) for *G. insensibilis* in the Black Sea. Indeed there is a question of an ability to adapt rapidly to changes occurring in this brackish water environment (see also Grèze, 1976a). These changes are far from regular and this ability for fast adaptations is the origin of disturbances in the regularity of the reproductive cycle.

VII.2. Brun (1971, 1975), however, has the opinion that there is no question of a clearly defined regular reproductive cycle. About the peaks in spring and autumn he states "ces deux maximums saisonniers, bien que m'étant apparu fréquents, ne suffisent pas à définir un cycle régulier" (these two seasonal peaks, although I frequently came upon them, are not sufficient to define a regular cycle). The reproductive cycle found by Grèze (in a marine to brackish environment) which corresponds with the cycle found by us for both *G. insensibilis* and *G. aequicauda* (in a brackish environment) is cited by Brun (1975) as "well defined". Moreover, he described how in the Étang de Citis he came upon very dense populations of *G. aequicauda* in one year which appeared to be decimated the next year. But these "demo-

graphic variations" do not influence the regularity of the pattern (Brun, 1975), they are part of it and inherent to this type of life cycle. Grèze, 1976b concluded that differences in life cycles between populations of *G. insensibilis* were mainly caused by differences in temperature regime.

VII.3. Brun (1975) is of the opinion that it is of no use to do a comparative quantitative investigation into populations of *G. insensibilis* and *G. aequicauda*, considering the great heterogeneity of the populations on the one hand and, for *G. insensibilis*, a difference in behaviour between males and females on the other. Moreover, he states that localities in which sampling at regular intervals is possible, do not exist, because of fluctuations in population-density. In the Étang de Bages-Sigean it appeared to be quite possible to do such an investigation without being bothered by these aspects.

VII.4. Sexual activity as a concept cannot without further knowledge be considered a measure for the reproductive activity of a population. So the sexual activity observed during the winter months gives a false impression of the reality. Because of the low temperatures, development of the eggs takes very long and therefore as a rule the same group of ovigerous females show a virtually high sexual activity while in reality almost nothing is happening.

In summer the opposite is true; because of the fast development of the eggs the reproduction of the population is high, while the observed sexual activity seems to be low.

Likewise the concept "fecundity" (French: fécondité) as sometimes found in literature is largely confusing. As a measure for the fecundity the average number of eggs is taken and this fecundity is used as a measure for the reproductive capacity. As we demonstrated in IV.5.6 this is incorrect.

VII.5. It therefore would be better to drop the term "fecundity" and to introduce some other well defined concepts such as:

potential reproductive capacity:	The average number of eggs in the marsupium multiplied by the number of ovigerous females
reproductive success:	The percentage of the average number of eggs in the marsupium that survive, as juveniles, after the first moult
egg production:	The mean number of eggs in Stage D2
production:	Potential reproductive capacity multiplied with the reproductive success.

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TABLE VI (unfold)

Numbers of *G. aequicauda* and *G. insensibilis* collected per sampling period per station. Numbers in italics = *G. aequicauda*: numbers in romans = *G. insensibilis*; x = not sampled; — = species absent. In some stations (e.g. I, XVII) during part of the year, the samples have been subdivided in a sample from the shore (S) and one from the lagoon (L).

List of sampling periods:

1 = 25 to 28 March 1976	13 = 18 to 22 Oct. 1976
2 = 10 to 14 April 1976	14 = 1 to 4 Nov. 1976
3 = 26 to 29 April 1976	15 = 15 to 19 Nov. 1976
4 = 11 to 14 May 1976	16 = 28 Nov. to 1 Dec. 1976
5 = 27 to 30 May 1976	17 = 13 to 18 Dec. 1976
6 = 21 to 24 June 1976	18 = 3 to 7 Jan. 1977
7 = 5 to 8 July 1976	19 = 16 to 19 Jan. 1977
8 = 19 to 22 July 1976	20 = 31 Jan. to 2 Febr. 1977
9 = 2 to 4 Aug. 1976	21 = 14 to 17 Febr. 1977
10 = 23 to 26 Aug. 1976	22 = 28 Febr. to 2 March 1977
11 = 21 to 24 Sept. 1976	23 = 14 to 16 March 1977
12 = 4 to 7 Oct. 1976	24 = 28 March to 2 April 1977
	25 = 11 to 16 April 1977
	26 = 25 to 28 April 1977
	27 = 9 to 11 May 1977
	28 = 23 to 27 May 1977
	29 = 6 to 8 June 1977
	30 = 20 to 22 June 1977
	31 = 11 to 13 July 1977
	32 = 27 to 28 July 1977
	33 = 8 to 11 Aug. 1977

PERIOD Station	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
I	$^{-}$108	^{1}101	^{1}102	^{13}90	^{12}115	^{4}92	^{3}113	^{1}104	$^{-}$103	$^{-}$105	123	^{1}96	^{9}105	^{5}101										^{1}111	^{4}108	^{8}52	$^{-}$102	^{3}102	^{3}91	$^{-}$113	^{14}104	^{4}126	^{12}107
I S															^{20}84	$^{-}$-	^{4}90	$^{-}$-	$^{-}$-	$^{-}$-	^{1}111	$^{-}$109	^{6}94										
I L															^{81}25	^{38}96	^{49}63	^{19}94	^{20}73	^{37}54	^{1}97	^{10}27	^{7}24										
II	^{48}54	^{18}113	^{79}38	^{77}43	^{16}107	^{35}81	^{3}136	^{24}86	^{1}112	^{39}68	^{31}68	^{10}101	^{1}116	^{44}63	$^{-}$113	^{3}111	x	^{9}101	^{8}100	^{61}45	$^{-}$109	^{9}97	^{15}134	^{4}100	^{5}96	^{47}66	$^{-}$102	^{10}96	$^{-}$109	^{21}90	$^{-}$120	^{92}18	^{6}100
III	x	$^{-}$17	$^{-}$72	x	$^{-}$89	$^{-}$94	$^{-}$95	x	$^{-}$92	$^{-}$31	$^{-}$114	^{1}102	^{1}46	$^{-}$118	^{3}80	^{2}106	^{2}100	^{7}34	^{15}86	^{6}73	^{1}103	^{1}7	$^{-}$6	$^{-}$41	$^{-}$39	^{1}103	$^{-}$54	$^{-}$2	^{1}20	^{2}109	^{1}89	^{37}62	$^{-}$93
IV	^{4}86	$^{-}$107	^{1}96	^{94}20	^{4}86	^{6}103	$^{-}$101	^{15}116	^{8}96	$^{-}$107	^{1}118	$^{-}$107	^{3}123	$^{-}$104	$^{-}$101	$^{-}$117	$^{-}$104	$^{-}$101	$^{-}$103	$^{-}$98	$^{-}$95	^{1}105	^{8}93	$^{-}$105	$^{-}$108	^{1}111	^{4}98	^{5}91	^{3}91	$^{-}$113	^{12}106	^{2}140	^{6}114
V	$^{-}$x	x	$^{-}$41	x	$^{-}$27	$^{-}$30	$^{-}$6	x	$^{-}$1	$^{-}$4	$^{-}$2	$^{-}$-	$^{-}$7	$^{-}$10	$^{-}$11	$^{-}$6	$^{-}$6	$^{-}$--	$^{-}$105	$^{-}$9	$^{-}$-	$^{-}$5	$^{-}$23	$^{-}$38	$^{-}$5	$^{-}$9	$^{-}$21	$^{-}$5	$^{-}$4	$^{-}$5	$^{-}$1	$^{-}$-	$^{-}$2
VI	x	x	$^{-}$110	x	$^{-}$112	$^{-}$126	$^{-}$98	$^{-}$108	$^{-}$113	$^{-}$105	^{1}127	$^{-}$143	$^{-}$114	$^{-}$115	^{1}100	^{1}112	^{3}112	^{10}101	^{18}86	^{4}107	$^{-}$107	^{1}113	^{5}110	^{3}110	^{19}87	$^{-}$98	$^{-}$104	^{2}105	^{1}96	$^{-}$106	$^{-}$110	$^{-}$114	^{1}113
VII	x	x	$^{-}$27	x	$^{-}$19	$^{-}$5	$^{-}$11	x	$^{-}$13	$^{-}$50	$^{-}$45	$^{-}$21	$^{-}$19	$^{-}$-	$^{-}$97	$^{-}$116	$^{-}$26	$^{-}$91	$^{-}$40	$^{-}$48	$^{-}$17	$^{-}$78	$^{-}$17	$^{-}$20	$^{-}$32	$^{-}$79	$^{-}$15	$^{-}$7	$^{-}$7	$^{-}$4	$^{-}$16	$^{-}$34	$^{-}$24
VIII	^{23}83	x	^{6}60	x	^{18}62	^{10}2	^{7}99	^{3}90	^{1}98	^{7}26	$^{-}$41	$^{-}$5	$^{-}$10	^{4}18	^{4}40	$^{-}$117	^{6}18	^{5}39	^{26}78	^{6}33	^{1}21	$^{-}$-	^{7}11	^{5}8	^{12}8	^{11}6	$^{-}$5	^{25}77	^{71}30	^{25}71	^{97}7	^{77}30	^{107}-
IX	x	x	^{70}2	x	^{78}-	^{43}31	^{68}22	^{98}13	$^{-}$22	$^{-}$-	^{37}-	^{24}-	^{4}1	^{3}-	^{1}9	$^{-}$1	$^{-}$-	^{48}2	^{17}2	^{92}1	^{97}1	^{110}-	^{109}-	^{114}-	^{105}-	^{110}-	^{97}-	^{98}-	^{83}-	^{115}-	^{137}-	^{104}-	^{105}-
X	^{1}62	^{9}114	^{9}86	$^{-}$140	$^{-}$9	$^{-}$111	$^{-}$126	$^{-}$102	$^{-}$104	$^{-}$105	$^{-}$107	$^{-}$105	$^{-}$110	^{2}105	^{1}111	$^{-}$110	$^{-}$104	^{19}98	^{7}100	$^{-}$118	^{37}71	$^{-}$99	^{11}119	^{1}95	$^{-}$119	$^{-}$140	$^{-}$105	^{7}99	^{6}97	$^{-}$124	^{16}100	^{33}62	^{56}67
XI	$^{-}$7	x	$^{-}$8	x	$^{-}$94	$^{-}$1	$^{-}$10	x	$^{-}$1	$^{-}$-	$^{-}$2	^{3}-	$^{-}$14	$^{-}$-	$^{-}$-	^{3}7	$^{-}$14	$^{-}$-	$^{-}$5	$^{-}$26	$^{-}$28	$^{-}$24	$^{-}$6	$^{-}$20	$^{-}$9	$^{-}$2	$^{-}$6	$^{-}$2	$^{-}$5	$^{-}$23	^{2}17	^{2}35	$^{-}$9
XII	$^{-}$144	$^{-}$137	$^{-}$99	$^{-}$127	$^{-}$108	$^{-}$141	$^{-}$123	$^{-}$94	^{1}102	^{1}109	$^{-}$97	$^{-}$124	$^{-}$113	$^{-}$119	$^{-}$98	^{1}93	$^{-}$100	^{2}98	^{4}99	$^{-}$103	$^{-}$104	$^{-}$111	^{1}107	^{5}100	^{76}31	^{15}93	^{28}80	^{63}41	^{39}51	^{56}43	^{121}-	^{88}-	^{107}-
XIII	^{26}25	^{67}57	^{38}92	^{35}81	^{63}101	^{104}-	^{93}19	^{115}1	^{108}26	^{15}104	^{78}21	^{11}110	^{37}74	^{101}14	^{27}84	^{86}16	^{8}97	^{74}32	^{63}38	^{7}98	^{5}104	^{27}84	^{52}43	^{46}68	^{119}-	^{103}-	^{95}3	^{98}6	^{95}3	^{109}5	^{124}2	^{104}-	^{37}-
XIV	^{28}92	x	^{94}9	x	^{8}131	$^{-}$134	$^{-}$141	$^{-}$107	$^{-}$119	$^{-}$116	$^{-}$98	$^{-}$103	$^{-}$101	$^{-}$93	$^{-}$104	^{4}100	^{18}81	^{33}77	^{70}22	^{14}98	^{31}81	^{25}86	^{19}84	^{13}89	^{5}106	^{1}107	$^{-}$96	^{1}127	$^{-}$96	$^{-}$128	$^{-}$168	$^{-}$129	^{3}118
XV	^{2}99	x	$^{-}$4	x	$^{-}$2	$^{-}$80	x	x	$^{-}$98	$^{-}$117	$^{-}$122	$^{-}$120	$^{-}$127	$^{-}$109	$^{-}$113	$^{-}$124	$^{-}$105	^{2}107	^{1}107	$^{-}$18	$^{-}$111	$^{-}$109	$^{-}$110	$^{-}$97	$^{-}$63	$^{-}$108	$^{-}$47	^{1}103	$^{-}$62	$^{-}$113	^{3}103	^{6}89	^{18}89
XVI	^{6}-	x	^{75}19	x	^{28}49	^{32}89	^{1}139	$^{-}$126	$^{-}$109	$^{-}$112	^{1}138	$^{-}$113	$^{-}$109	$^{-}$135	$^{-}$141	^{2}118	$^{-}$103	$^{-}$109	^{68}34	$^{-}$93	^{63}65	^{63}48	^{82}48	$^{-}$109	$^{-}$110	$^{-}$113	$^{-}$96	$^{-}$100	^{1}107	$^{-}$131	^{1}144	$^{-}$132	^{3}158
XVII	x	x	^{110}3	x	^{70}48	^{101}20	^{4}145	^{7}91	$^{-}$111	$^{-}$128	^{79}58													^{36}56	^{19}91	^{70}39	^{53}64	^{1}112	^{18}83	$^{-}$14	^{78}24	$^{-}$126	$^{-}$129
XVII S												^{11}105	^{3}115	^{1}132	$^{-}$104	^{33}113	$^{-}$-	$^{-}$-	$^{-}$-	$^{-}$-	$^{-}$-	$^{-}$-	$^{-}$-										
XVII L												^{6}-	^{95}10	^{91}15	^{98}12	^{1}99	^{98}22	^{13}114	^{2}113	^{5}97	^{7}107	^{7}107	^{30}87										
XVIII	x	x	^{44}40	x	^{2}143	^{12}106	$^{-}$104	$^{-}$105	$^{-}$115	$^{-}$104	$^{-}$118	^{6}103	$^{-}$112	$^{-}$-	^{7}5	^{40}60	^{6}109	^{73}24	^{47}52	^{3}104	^{85}19	^{19}85	^{69}53	^{58}44	^{23}92	^{15}108	^{30}71	^{8}121	^{2}113	$^{-}$140	^{4}240	^{30}107	^{14}99
XIX	^{92}32	^{7}103	^{32}59	^{10}118	^{8}92	^{83}23	^{7}100	^{82}38	$^{-}$117	$^{-}$113	$^{-}$112													^{45}61	^{84}36	^{85}21	^{21}78	^{16}109	^{26}67	^{11}95	^{11}101	^{46}70	^{105}37
XIX S												^{3}136	^{2}100	^{2}109	$^{-}$113	^{3}108	$^{-}$113	$^{-}$-	$^{-}$-	$^{-}$-	$^{-}$-	$^{-}$-	$^{-}$-										
XIX L												^{98}27	^{88}34	^{57}30	^{76}23	^{84}21	^{33}55	^{88}12	^{39}59	^{21}80	^{59}40	^{88}18	^{54}43										
XX	x	x	^{101}1	^{138}-	^{65}62	^{27}86	^{16}99	^{31}71	^{14}89	$^{-}$113	^{7}91													^{6}99	^{48}63	^{117}-	^{20}87	$^{-}$-	^{4}-	$^{-}$-	^{6}1	^{95}-	^{98}-
XX S												^{8}96	^{3}103	^{7}96	^{22}75	$^{-}$-	$^{-}$-	^{1}107	$^{-}$-	$^{-}$-	$^{-}$-	$^{-}$-	$^{-}$-										
XX L												^{99}21	^{114}10	^{55}28	^{76}28	^{79}30	^{33}46	^{27}77	^{94}6	^{15}81	^{1}106	^{14}105	^{14}81										
XXI	x	x	$^{-}$110	x	$^{-}$64	$^{-}$107	x	x	$^{-}$125	$^{-}$105	$^{-}$106	$^{-}$109	$^{-}$120	$^{-}$129	$^{-}$116	$^{-}$108	^{2}96	$^{-}$108	$^{-}$104	$^{-}$108	$^{-}$117	$^{-}$112	$^{-}$109	$^{-}$100	$^{-}$99	$^{-}$111	$^{-}$98	$^{-}$28	$^{-}$14	$^{-}$121	^{1}40	^{43}59	^{81}19
XXII	x	x	^{1}86	x	^{1}98	^{23}10	x	x	$^{-}$114	^{10}11	^{12}66	^{4}22	^{7}44	^{6}7	^{7}3	^{22}10	^{98}10	^{103}12	^{97}9	^{97}5	^{98}15	^{110}3	^{81}21	^{73}25	^{33}71	^{42}68	^{25}78	^{64}38	^{84}12	^{86}27	^{94}3	^{110}-	^{108}-
XXIII	^{100}11	^{90}17	^{136}3	^{120}19	^{91}11	^{116}-	^{8}103	^{107}60	^{9}108	$^{-}$85	^{68}47																	^{88}5	^{73}56	^{66}38	^{74}-	^{5}118	^{116}3
XXIII S												^{15}112	^{10}109	^{43}57	^{16}99	^{12}88	$^{-}$96	^{2}96	$^{-}$-	$^{-}$-	$^{-}$-	$^{-}$-	$^{-}$-	$^{-}$111	$^{-}$-	^{95}16	$^{-}$-						
XXIII L												^{107}25	^{108}8	^{110}1	^{76}26	^{70}30	^{92}20	^{73}34	^{93}9	^{106}-	^{108}5	^{112}2	^{50}53	^{91}7	^{50}59	^{32}65	^{35}66						
XXIV	x	x	$^{-}$97	x	$^{-}$138	$^{-}$142	x	x	$^{-}$116	$^{-}$112	$^{-}$109	$^{-}$115	$^{-}$89	$^{-}$41	$^{-}$105	$^{-}$101	$^{-}$111	$^{-}$112	$^{-}$103	$^{-}$104	$^{-}$112	$^{-}$110	$^{-}$115	$^{-}$93	$^{-}$18	$^{-}$40	$^{-}$18	^{8}24	^{1}8	$^{-}$10	^{4}101	$^{-}$125	^{46}66
XXV	x	x	^{19}39	x	^{1}87	^{2}115	x	x	^{2}123	$^{-}$116	$^{-}$115	$^{-}$122	$^{-}$116	$^{-}$13	x	$^{-}$129	$^{-}$-	$^{-}$104	$^{-}$105	^{6}86	^{1}113	^{19}97	^{3}117	^{9}102	^{2}17	^{2}30	$^{-}$53	^{71}24	^{37}57	^{15}58	^{15}74	^{66}45	^{104}8
XXVI	^{97}1	^{123}3	^{121}2	^{88}9	^{34}117	^{21}122	^{8}130	^{11}109	$^{-}$110	^{6}103	^{104}3													^{108}9	^{90}14	^{102}-	^{25}82	^{85}7	^{96}20	^{49}60	^{1}115	$^{-}$120	^{18}183
XXVI S												^{6}106	$^{-}$-	$^{-}$-	$^{-}$-	^{8}89	$^{-}$-	$^{-}$-	$^{-}$-	$^{-}$-	$^{-}$-	$^{-}$-	$^{-}$-										
XXVI L												^{97}2	^{67}27	$^{-}$-	^{61}25	^{27}62	^{86}9	^{77}35	^{93}6	^{99}4	^{105}9	^{109}2	^{102}5										
XXVII	x	x	^{108}-	x	^{91}3	^{144}9	x	x	^{65}50	^{33}55	^{13}98	^{6}79	^{27}11	^{9}13	^{80}9	^{17}101	^{76}20	^{107}2	^{107}-	^{97}10	^{116}3	^{105}3	^{111}3	^{37}77	^{94}22	^{109}-	^{94}1	^{84}24	^{101}-	^{97}12	^{92}23	^{77}27	^{110}-
XXVIII	x	x	^{1}104	x	^{3}41	^{2}99	x	x	$^{-}$113	$^{-}$107	$^{-}$119	$^{-}$122	$^{-}$108	$^{-}$127	^{3}98	$^{-}$127	^{1}91	^{2}123	^{111}3	^{16}77	$^{-}$106	^{11}102	^{12}36	^{3}77	^{7}112	^{9}124	^{2}53	^{12}46	^{3}68	^{8}117	^{20}86	^{57}41	^{57}65
XXIX	^{98}12	^{135}4	^{57}7	^{84}10	^{102}13	^{110}7	^{127}-	^{102}6	^{116}-	^{89}8	^{89}23	^{98}5	^{99}15	^{100}6	^{95}10	^{94}7	^{90}4	^{108}2	$^{-}$115	^{98}9	$^{-}$136	^{104}1	^{122}12	^{107}2	^{118}1	^{97}4	^{92}-	^{103}-	^{102}-	^{105}-	^{105}-	^{108}-	^{103}-
XXX	x	x	^{1}78	x	^{1}100	$^{-}$110	x	x	$^{-}$100	$^{-}$66	$^{-}$38	$^{-}$105	$^{-}$90	^{1}51	^{1}113	$^{-}$107	^{4}108	$^{-}$122	^{1}100	^{2}121	^{116}-	^{3}125	^{3}153	^{1}121	$^{-}$125	$^{-}$125	$^{-}$151	^{1}110	$^{-}$139	^{2}108	$^{-}$110	$^{-}$100	$^{-}$119
XXXI	^{84}-	^{118}3	^{93}1	^{119}-	^{121}18	^{60}58	^{128}59	^{103}43	^{103}5		^{107}10													^{120}3	^{114}13	^{81}36	^{105}7	^{36}58	^{85}15	^{19}88	^{29}76	^{11}89	^{68}41
XXXI S										^{11}94		^{90}17	$^{-}$-	^{5}101	^{8}98	^{8}49	$^{-}$-	^{12}110	$^{-}$-	$^{-}$-	$^{-}$-	$^{-}$-	$^{-}$-										
XXXI L										^{95}10		^{124}2	^{134}-	^{94}27	^{100}24	^{55}71	^{96}-	^{108}7	^{106}-	^{107}-	^{99}5	^{120}3	^{74}31										