THE BIOLOGY OF *CHAETOGAMMARUS MARINUS* (LEACH) AND *EULIMNOGAMMARUS OBTUSATUS* (DAHL)
with some notes on other intertidal gammarid species (Crustacea, Amphipoda)

by

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ABSTRACT

The reproductive cycles of *Chaetogammarus marinus* and *Eulimnogammarus obtusatus* in northern Brittany are compared, as well as the environmental conditions under which these gammarids live. Both species show reproductive activity throughout the year. The maximum rate of ovigerous ♀♀ was established for *E. obtusatus* in the months of February-March (the coldest period of the year), for *Ch. marinus* in December. The former species showed the lowest rate in August (the warmest month of the year) and the latter species in March.

Eulimnogammarus obtusatus lives in the lower half of more exposed beaches and was rarely found on a substrate containing mud, contrary to *Chaetogammarus marinus*. It was established that the southern distribution limit of *E. obtusatus* lies in Brittany.

Ecological data are given on a number of other gammarid species from the tidal zone of the Atlantic coast of France.

RÉSUMÉ

Les cycles de reproduction de *Chaetogammarus marinus* et *Eulimnogammarus obtusatus* provenant du N.-Finistère sont comparés, de même que les conditions du milieu dans lequel ces espèces furent trouvées. Les deux gammares se reproduisent pendant toute l'année. Le pourcentage maximum de ♀♀ ovigères fut établi pour *E. obtusatus* pendant les mois de février-mars (la période la plus froide de l'année), pour *Ch. marinus* au mois de décembre. Au mois d'août (le mois le plus chaud) la première espèce montre un pourcentage minimum de ♀♀ ovigères, tandis que ce minimum fut observé pour l'autre gammare au mois de mars.

Eulimnogammarus obtusatus fut rencontré dans les zones plus basses des plages plus exposées et ne fut que rarement trouvé sur un substrat de vase, au contraire de *Chaetogammarus marinus*. La limite de l'aire de répartition de *E. obtusatus* se trouve en Bretagne méridionale.

Quelques données écologiques sont mentionnées sur des autres Gammaridés de la zone de marées de la côte Atlantique française.

INTRODUCTION

According to Sexton & Spooner (1940) *Chaetogammarus marinus* (Leach, 1815) is associated with substrates varying from cobbles to soft mud, while *Eulimnogammarus obtusatus* (Dahl, 1938) occurs on less muddy and more stony grounds. Jones (1948) mentions similar data on these species. Moreover, he states that *Ch. marinus* can survive in entirely fresh streams for many hours.

Den Hartog (1964) has never found *Ch. marinus* on soft mud in the Deltaic region of the Netherlands. According to this author, the upper limit of this gammarid coincides more or less with mean H.W. mark, the lower limit lying always above the level of mean L.W. neap. In localities where *Ch. marinus* and *E. obtusatus* coexist, the former lives above mean sea level, the latter below this level. From the fact that on stations where *E. obtusatus* occurs alone, this species does not occur above mean sea level, Den Hartog concludes that, in places where both species occur together, the lower limit of *Ch. marinus* is determined by competition. He established no difference between the substrates on which *Ch. marinus* and *E. obtusatus* were found.

Vader (1965) questions the theory of Den Hartog (1964) about competition. This author found a clear difference in preference for a particular substrate for each of the above-mentioned species and suggests this to be a reason for their zonation: a combination of environmental factors which is favorable to *E. obtusatus* (being absent in places where this gammarid does not occur), could render the same biotope unfit for *Ch. marinus*. On very muddy substrates he found only the lat-

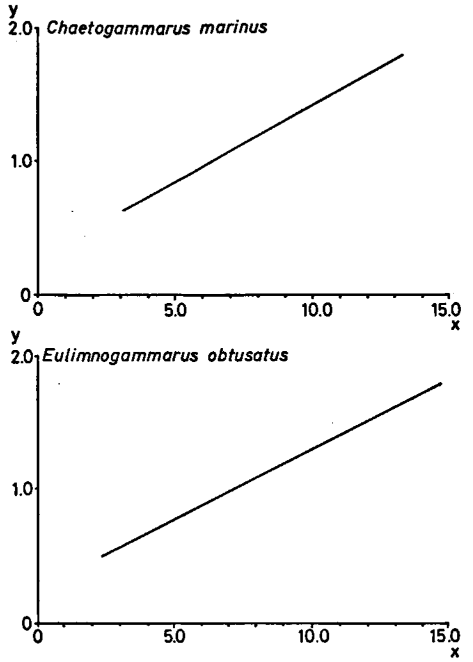

Fig. 1. The relation between body length (plotted on the X-axis) and cephalic length (Y-axis) in two species of gammarids. Top: *Chaetogammarus marinus* ($y = 0.119\ x + 0.241$; $N = 140$; correlation = 0.965; standard error $Y = 0.025$; standard error $X = 0.003$). Bottom: *Eulimnogammarus obtusatus* ($y = 0.105\ x + 0.256$; $N = 206$; correlation = 0.930; standard error $Y = 0.029$; standard error $X = 0.003$).

ter species and never *E. obtusatus*, whereas on grounds consisting of mere cobbles only this gammarid occurred.

The present investigations have been carried out to ascertain whether a difference in preference for a particular substrate does exist between the two species. Furthermore, monthly quantitative samples have been taken from populations of both gammarids to establish whether they reproduce during a different time of the year.

METHODS

As far as temperature readings have been made, a mercury thermometer was used (scale in 0.1°C). Salinities have been measured with the aid of a refractometer. Sampling of the animals was carried out by hand or with a dip net.

The monthly quantitative samples of *Chaetogammarus marinus* and *Eulimnogammarus obtusatus* have been obtained in the following way: in places, where these species sufficiently occurred, the animals were taken all at once (after removing the overlaying cobbles or algae), together with part of the underlaying substrate, and put into a bucket. Afterwards, in the laboratory, the gammarids were carefully separated from the substrate. These samples have been collected once a month, from December 1973 to December 1974, during a stay at the Biological Station of Roscoff (Brittany, France). *E. obtusatus* was sampled on the beach near Primel-Trégastel, N.E. of Morlaix, while *Ch. marinus* has been collected in the Aber de Roscoff in front of the Biological Station.

Since identification of the species in the field was impossible during the procedure mentioned above, a great number of specimens was collected to be sure of having a quantity of the present species that reflected the composition of the population at that time.

After establishing for both species a linear correlation between cephalic length and body length (fig. 1), the former has been used in determining the composition of the populations monthly. The measurements were made under a compound microscope with the aid of an eyepiece micrometer (for details on these measurements see Dennert et al., 1969).

In addition to the quantitative samples of the above-mentioned species, a number of qualitative samples of intertidal gammarids has been taken all along the Atlantic coast of France and northern Spain.

In August 1973 a simple experiment has been set up to observe differences in resistance to fresh water of some gammarid species from the tidal zone. A sample of about 350 specimens, consisting of *Gammarus finmarchicus*, *Gammarus locusta* and *Chaetogammarus marinus* was obtained from the Aber de Roscoff and divided equally over 12 basins. Each of these contained a liter of one of the following media (of each medium 4 basins):

seawater: 349 mg Ca/l, 19500 mg Cl/l;
brackish water: 244 mg Ca/l, 8900 mg Cl/l;
fresh water: 104 mg Ca/l, 223 mg Cl/l.

A few stones were placed as a substrate in the basins and the water was oxygenated. Every half hour the dead animals were removed and preserved in alcohol 70%. The experiment was started at 17.30 h. After 21.00 h the above-mentioned procedure was not repeated until 24.00 h and from then not till the next morning at 9.30 h. At this time the experiment has been brought to an end and the surviving animals were also preserved.

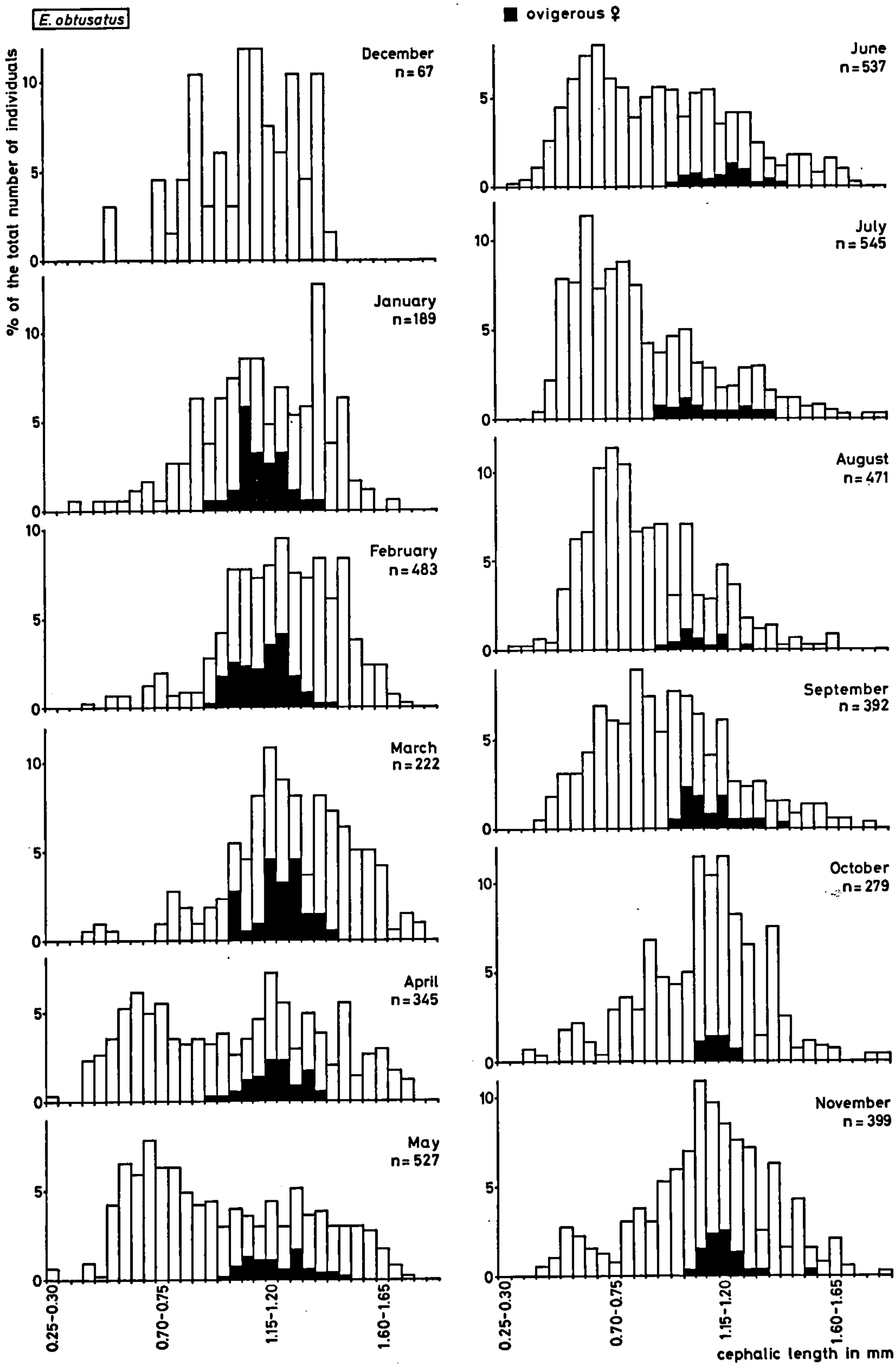

Fig. 2. Size composition, during a year, of a population of *Eulimnogammarus obtusatus*.

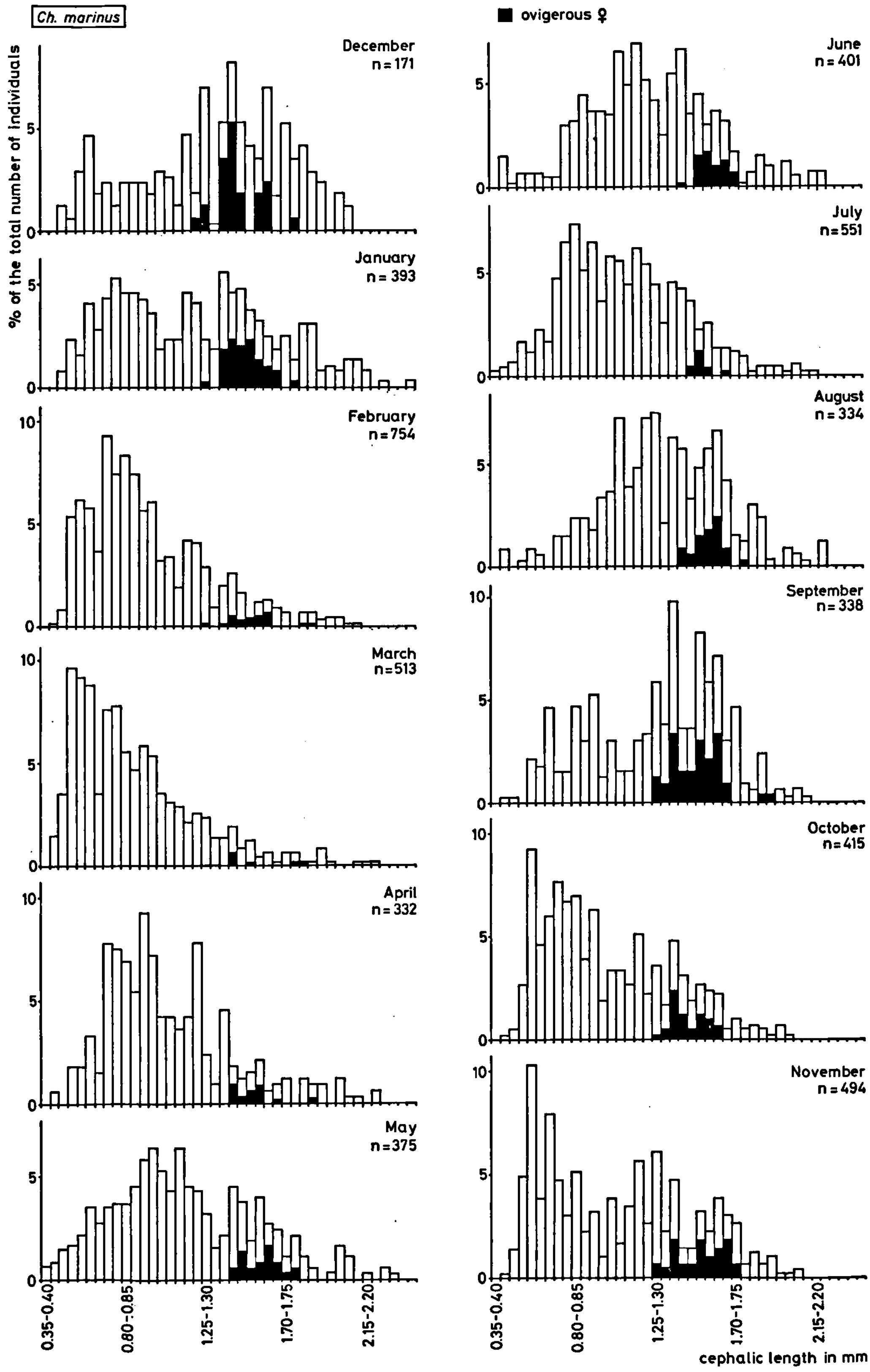

Fig. 3. Size composition, during a year, of a population of *Chaetogammarus marinus*.

Fig. 4. Rates of ovigerous ♀♀ in the monthly samples from a population of *Eulimnogammarus obtusatus* and of *Chaetogammarus marinus*.

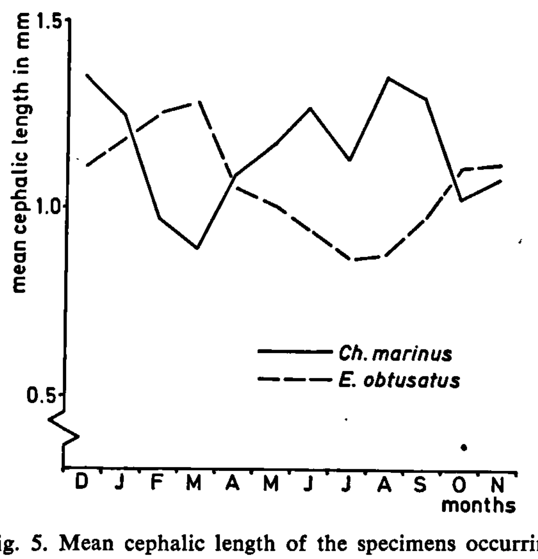

Fig. 5. Mean cephalic length of the specimens occurring in the monthly samples taken from a population of *Eulimnogammarus obtusatus* and of *Chaetogammarus marinus*.

RESULTS

I. Eulimnogammarus obtusatus & Chaetogammarus marinus

Reproductive cycles

Fig. 2 shows the composition of a population of *Eulimnogammarus obtusatus* at Primel-Trégastel during a year. Except in the month of December, all the monthly samples contained ovigerous ♀♀. Although the rate of ovigerous ♀♀ fluctuates throughout the year, it seems very likely that the absence of ovigerous ♀♀ in the sample of December is due to the relatively small number of specimens collected in this month. As shown in fig. 4, *E. obtusatus* has a maximum in reproductive activity during the months of February and March, and its lowest reproduction rate in August. These extremes coincide with the coldest and warmest period of the year, respectively.

Chaetogammarus marinus shows a maximum in reproductive activity earlier in wintertime, in the

Table I. Frequency of environmental factors and accompanying species (in %) at sampling stations where *Chaetogammarus marinus* and/or *Eulimnogammarus obtusatus* occurred.

	Ch. marinus	*E. obtusatus*
mud	43.4	2.4
sand	66.0	66.7
gravel	9.4	33.3
shingle	28.3	42.9
cobbles	77.4	83.3
rock	30.2	35.7
shells or shell grit	6.6	28.6
no vegetation	2.8	21.4
green algae	37.7	14.3
Pelvetia	3.8	0.0
Fucus ceranoides and/or *Fucus spiralis*	34.9	4.8
Fucus vesiculosus	65.1	66.7
Ascophyllum nodosum	37.7	26.2
Fucus serratus	12.3	19.1
detritus	4.7	16.7
Chaetogammarus marinus		40.5
Eulimnogammarus obtusatus	16.1	
Chaetogammarus pirloti	3.8	7.2
Chaetogammarus stoerensis	6.6	14.3
Gammarus finmarchicus	4.7	9.5
Gammarus locusta	16.1	21.4
Gammarus crinicornis	2.8	0.0
Melita palmata	28.4	45.2
Melita hergensis	0.0	7.1
other gammarid species	8.5	2.4
talitrid Amphipoda	32.1	21.4

month of December and has its lowest rate of ovigerous ♀♀ in March (fig. 4). For both species a secondary peak in reproductive activity has been established in early autumn. Like *E. obtusatus, Ch. marinus* shows reproductive activity throughout the year (fig. 3).

The decrease in mean cephalic length of *Ch. marinus* during the months of December to March, as can be seen in fig. 5, reflects the birth of many juveniles during this period. This also holds true for the decrease, although to a lesser degree, from August to October. *E. obtusatus* has its greatest mean cephalic length in March and from then on a decrease can be seen, reaching a minimum during July-August.

Ecology

In table I are figuring some ecological factors that are part of the littoral environment and some other gammarid species that occurred sometimes together with *Chaetogammarus marinus* or *Eulimnogammarus obtusatus*. For each component the percentage is given, in which it was present on the total number of samples, containing one or both of the above-mentioned species. From these data can be seen that mud is present in many places where *Ch. marinus* occurs, contrary to in those where *E. obtusatus* has been found. The biotope of the latter gammarid contains more often coarser substrates like gravel and shingle. Fig. 6 gives a survey of the rates of ecological factors of localities in which *Ch. marinus* or *E. obtusatus* was the only occurring gammarid species.

In table II the rates for ecological factors and

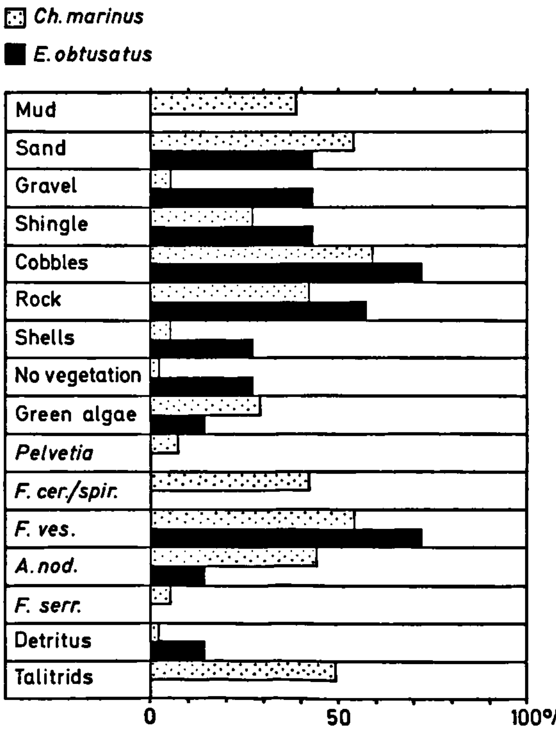

Fig. 6. The rates of occurrence of the ecological factors at localities where *Ch. marinus* or *E. obtusatus*, respectively, was the only gammarid species (*F. cer.* = *Fucus ceranoides*; *F. spir.* = *Fucus spiralis*; *F. ves.* = *Fucus vesiculosus*; *A. nod.* = *Ascophyllum nodosum*; *F. serr.* = *Fucus serratus*).

Table II. Frequency of environmental factors and accompanying species (in %) in those places where *Chaetogammarus marinus* and *Eulimnogammarus obtusatus* occurred in coexistence.

	Ch. marinus + *E. obtusatus*
mud	5.9
sand	64.7
gravel	23.5
shingle	41.2
cobbles	94.1
rock	23.5
shells or shell grit	17.7
no vegetation	11.8
green algae	17.7
Pelvetia	0.0
Fucus ceranoides and/or *Fucus spiralis*	5.9
Fucus vesiculosus	88.2
Ascophyllum nodosum	41.2
Fucus serratus	23.5
detritus	5.9
Chaetogammarus pirloti	5.9
Chaetogammarus stoerensis	17.7
Gammarus finmarchicus	0.0
Gammarus locusta	5.9
Gammarus crinicornis	0.0
Melita palmata	29.4
Melita hergensis	0.0
other gammarid species	0.0
talitrid Amphipoda	29.4

Table III. Rate of occurrence (in %) of factors indicative of a sheltered littoral biotope (A) and of freshwater influence (B) in places where *Chaetogammarus marinus* and/or *Eulimnogammarus obtusatus* have been found.

	Ch. marinus	*E. obtusatus*
A. mud + *Ascophyllum nodosum*	16.0	0.0
mud	43.4	2.4
Ascophyllum nodosum	37.7	26.2
B. *Fucus ceranoides* +/or *Fucus spiralis* + green algae	17.0	2.4
Fucus ceranoides +/or *Fucus spiralis*	34.0	4.8
green algae	37.7	14.3

accompanying gammarids are shown in those cases, where the above-mentioned species have been found in coexistence.

If one considers the presence of mud and algae like *Ascophyllum nodosum* characteristic of more sheltered beaches (or estuaries), *Ch. marinus* shows a clear preference for this kind of biotope, contrary to *E. obtusatus*, as can be concluded from the data in table III.

The presence in a biotope of green algae like *Ulva*, *Chaetomorpha* and *Enteromorpha*, is indicative for a certain degree of freshwater influence,

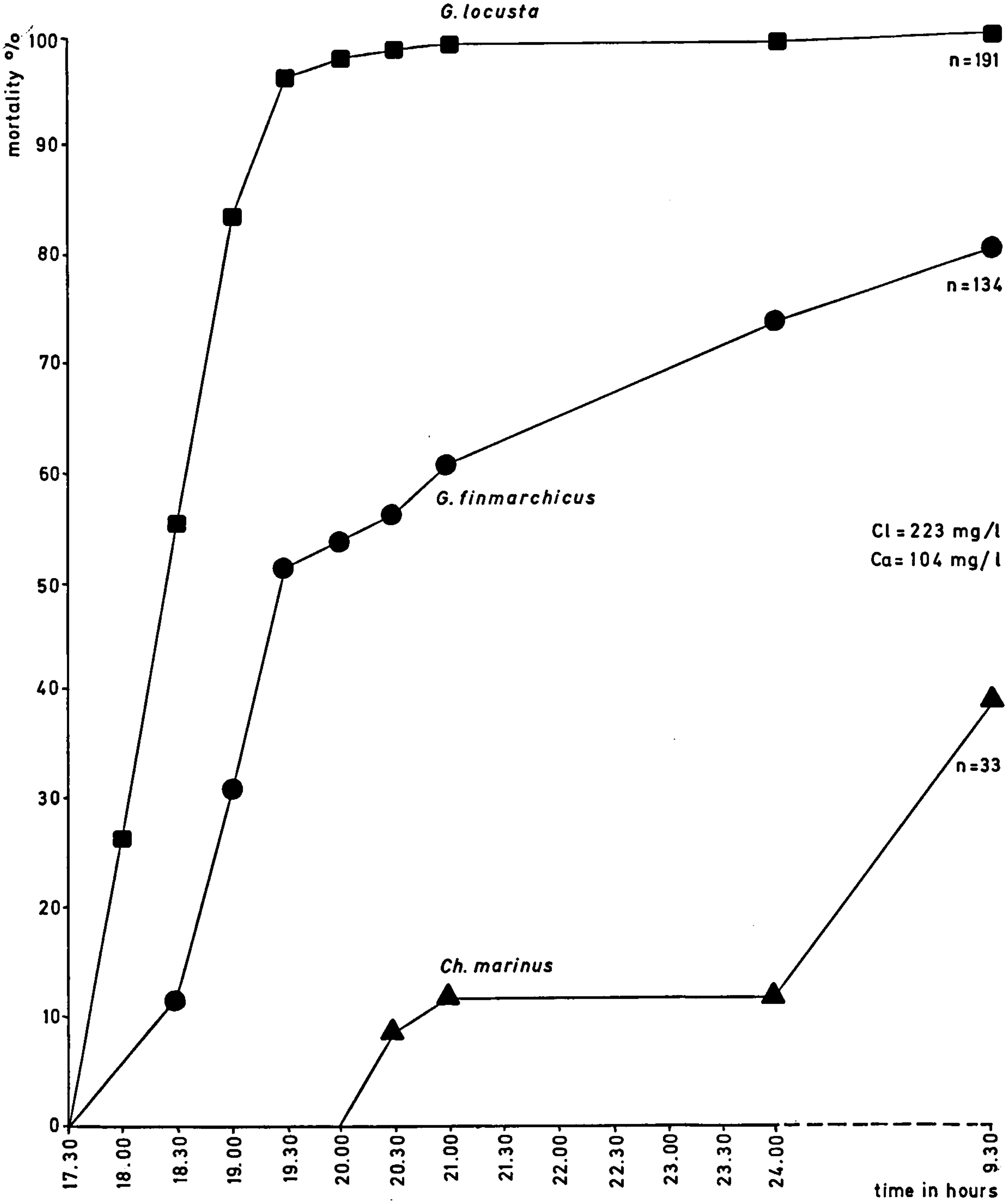

Fig. 7. Mortality rate of three intertidal species under freshwater conditions.

as is the occurrence of the *Fucus* species *ceranoides* and *spiralis*. Table III shows the difference in occurrence between the present gammarids among these kinds of algae.

The results from the experiment during which three littoral species have been submitted to different salinities for some hours, are given in fig. 7, so far as fresh water is concerned. In the basins containing seawater, only one dead specimen (*Gammarus finmarchicus*) was found alltogether. In the aquaria with brackish water only 3 out of 46 *Gammarus finmarchicus* and 10 out of 79 *Gammarus locusta* died.

Geographic distribution

The map in fig. 8 shows that *Eulimnogammarus obtusatus* was not found south of Brittany (southernmost locality: le Passage, S.E. of Vannes, Golfe du Morbihan). *Chaetogammarus marinus* reaches its southern distribution limit not until N. Portugal (Viano do Castelo), as was established earlier (Van Maren, 1975).

II. Some other gammarid species from the tidal zone

Besides the above-mentioned gammarids, the following species occurred in the samples collected during the present investigations:

Chaetogammarus stoerensis (Reid, 1938)
Chaetogammarus pirloti (Sexton & Spooner, 1940)
Gammarus finmarchicus Dahl, 1938
Gammarus locusta (Linnaeus, 1758)
Gammarus crinicornis Stock, 1966
Gammarus salinus Spooner, 1947
Gammarus zaddachi Sexton, 1912
Gammarus chevreuxi Sexton, 1913
Pectenogammarus planicrurus (Reid, 1939)
Melita palmata (Montagu, 1804)
Melita hergensis Reid, 1939
Pherusa fucicola Leach, 1814

With the exception of *M. palmata* and *G. locusta* which occurred in a considerable number of sampling stations and *P. planicrurus* which was found only in one locality, ecological data on stations where one or more of the above-mentioned species have been collected, are given in table IV.

Chaetogammarus stoerensis was never found on a substrate consisting of mud, but often on grounds containing coarser elements like gravel. The present gammarid lives in the *Fucus spiralis* and *Fucus vesiculosus* zones of the beach, often among the particles of the substrate, where vegetation is lacking. Ovigerous ♀♀ were present in samples collected in January and February.

In most places where *Chaetogammarus pirloti* occurred, gravel, shell grit or shingle was part of the substrate. This gammarid lives in the higher and middle zones of the beach. Although often found at reduced salinities (in pools, near fresh streams and upwelling groundwater), the present species seems to resist to almost marine conditions as well, at least temporarily. In samples from September, October and February ovigerous ♀♀ were observed.

From the ecological data on *Gammarus finmarchicus* can be seen, that this gammarid lives mainly in the *Fucus vesiculosus* zone. It seems to prefer less muddy substrates. The salinities measured indicate marine conditions. Ovigerous ♀♀ occurred in the samples from December, but not in those from August, September and November. During the present investigations *Gammarus finmarchicus* has not been found South of Brittany (southernmost locality: Lanvoy, W. of le Faou, S.-Finistère).

According to the data in table IV, *Gammarus crinicornis* shows a preference for living in pools with a vegetation of green algae like *Ulva* and *Chaetomorpha*. The salinities measured for this gammarid vary from entirely marine to slightly reduced.

Gammarus salinus was found in places with chlorinities varying from 500 to 21100 mg/l. In most cases, mud formed part of the substrate. In samples from December and February ovigerous ♀♀ have been observed.

The samples containing *Gammarus zaddachi* originate from estuaries or small streams in the tidal zone. At station EX 16, however, this gammarid lived in a green zone on the beach consisting of a great amount of *Ulva* overlaying sand, in water with a depth of some centimeters.

Gammarus chevreuxi has been found under environmental conditions resembling those of *G. zaddachi*.

Pectenogammarus planicrurus has been sampled only in one locality: Plovan-sur-Mer near Audierne (Brittany, S.-Finistère). It occurred on a subtrate of sand, shingle, cobbles and rock, devoid of vegetation (temperature 20°C).

Melita hergensis (table IV) seems to be a much rarer species than *Melita palmata* along the Atlantic coast of the European continent (fig. 9). During the present study it has never been found

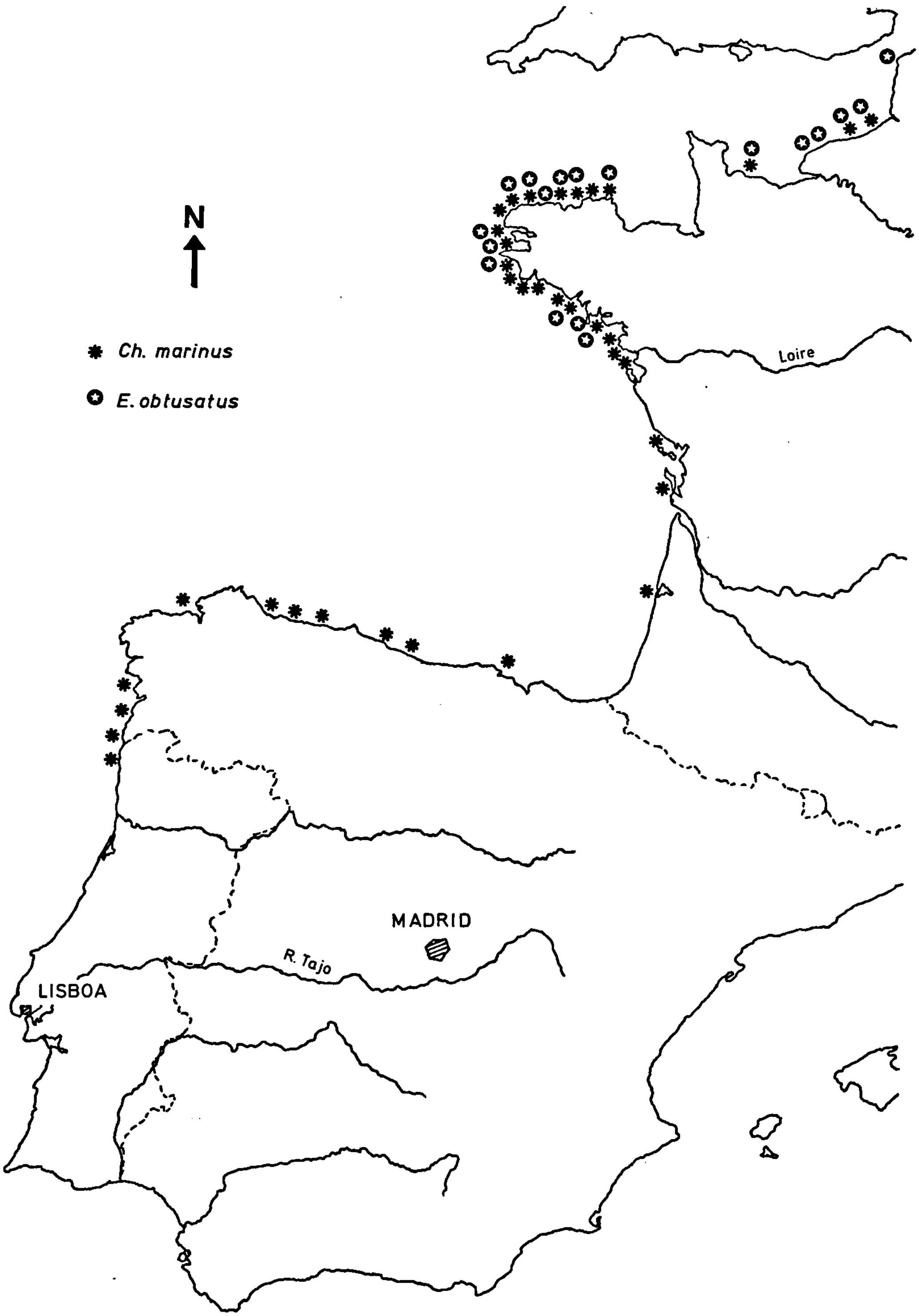

Fig. 8. Geographic distribution of *Eulimnogammarus obtusatus* and *Chaetogammarus marinus* along the Atlantic coast of France and of the Iberian peninsula (Iberian localities mainly after Van Maren, 1975).

Table IV. The occurrence on a number of sampling stations*) of the following species: *Chaetogammarus stoerensis* (1), *Chaetogammarus pirloti* (2), *Gammarus finmarchicus* (3), *Gammarus crinicornis* (4), *Gammarus salinus* (5), *Gammarus zaddachi* (6), *Gammarus chevreuxi* (7), *Melita hergensis* (8), *Pherusa fucicola* (9).

STATION	SUBSTRATE	VEGETATION	FURTHER PARTICULARS	1	2	3	4	5	6	7	8	9
EX 4	m+s+c	*Chaet.*+*F. ves.*	under cobbles			×						
EX 7	m+s	*F. spir.*+green algae	20.0°C; 209 mg Ca/l; 2100 mg Cl/l					×				
EX 8	m+s	*Ent.*	149 mg Ca/l; 1400 mg Cl/l					×				
EX 9	s+c	*F. spir.*+*F. ves.*	on wet sand, under algae; many specimens			×						
EX 10	s+c	*F. ves.*+*F. serr.*	on wet sand; under algae			×						
EX 11	s+c	*Ent.*+*Ulva*+*F. ves.*	in tide creek; 25.0°C; 285 mg Ca/l; 18200 mg Cl/l			×						
EX 16	s	*Ulva*	24.0°C						×			
EX 17	m+s+sh	*Ulva*+*Chaet.*	19.5°C; 30 mg Ca/l; 114 mg Cl/l						×			
EX 18	s+sh+c	*Ent.*	17.0°C; 30 mg Ca/l; 64 mg Cl/l						×			
EX 22	m+s	*Ulva*	in pools; 22.0°C; 407 mg Ca/l; 18600 mg Cl/l				×					
EX 24	s+d	*Ulva*	in pool; 23.0°C; 384 mg Ca/l; 16100 mg Cl/l				×					
EX 29	s	*F. serr.*	on boulder				×					
A 2	s+sh+c	—	13.5°C; 375 mg Ca/l; 21100 mg Cl/l; 1 specimen					×				
NF 2	s+r+shl	—	10.5°C; 354 mg Ca/l; 19200 mg Cl/l; among *Mytilus*, on limestone rock			×						
NF 5	s+sh+c+r	*F. ves.*	11.5°C; 373 mg Ca/l; 18100 mg Cl/l; 1 specimen					×				
NF 9	s+sh+c+d	—	in pools; 12.0°C; 346 mg Ca/l; 16700 mg Cl/l				×					
NF 10	s+sh+c	green algae	in small pools; 11.3°C; 318 mg Ca/l; 17000 mg Cl/l				×					
NF 11	s+sh+c+r	*F. ves.*+*F. spir.*	1 specimen	×								
NF 12	s+c	*F. spir.*+ green algae	90 mg Ca/l; 800 mg Cl/l	×								
NF 14	s+c	*F. spir.*	113 mg Ca/l; 221 mg Cl/l; „résurgence"	×								
NF 15	s+c+d	—	in small pools; 370 mg Ca/l; 17800 mg Cl/l				×					
NF 17	s+c+d	—	under cobbles; many specimens		×							
NF 18	s+sh+r	*F. spir.*+*Pelv.* + green algae	in pools; 10.8°C; 364 mg Ca/l; 19100 mg Cl/l		×		×					
NF 19	s+sh+c+r	—	in pools; 390 mg Ca/l; 17900 mg Cl/l		×		×					
NF 20	s+c	*F. spir.*+*F. ves.*+*A. nod.*	under cobbles		×							
NF 21	s+c	*F. serr.*+*A. nod.*	in pool; 348 mg Ca/l; 18900 mg Cl/l				×					
AA 3	c	*F. spir.*	on boulder, among algae				×					
BR 1	s+sh+c	*Chaet.*	9.5°C; 104 mg Cl/l						×	×		
BR 2	m+s	—	500 mg Cl/l					×		×		
BR 3	m+s+c	*F. ves.*					×	×				
BR 6	m+s+c	*Chaet.*							×	×		
BR 7	m+c	*F. spir.*	88 mg Cl/l						×	×		
BR 15	s+sh	*F. serr.*									×	
BR 20	s+c	*Chaet.*+*Ulva* +red algae									×	×
BR 21	s+c	—					×					
BR 22	s+sh+c	—	below the *Fucus* zone				×					

Table IV (continued)

STATION	SUBSTRATE	VEGETATION	FURTHER PARTICULARS	1	2	3	4	5	6	7	8	9
BR 27	s+sh+c	*F. spir.*+ green algae	next to stream							×		
BR 34	s+c	*F. ves.*+*F. serr.*	18300 mg Cl/l				×					
BR 36	gr+c	*F. ves.*+*A. nod.*	under cobbles	×		×						
BR 39	gr+c+r	*F. ves.*		×	×	×						
BR 40	gr+c+r	*F. spir.*		×		×						
BR 43	m+s+c	*F. ves.*+*F. serr.*	seawater				×					
BR 49	s+sh+c	*F. ves.*+*A. nod.*	under cobbles			×						
BR 51	m+sh+r	*A. nod.*				×						
BR 52	s+c+r	*F. serr.*									×	
BR 53	s+c	*F. ves.*									×	
BR 54	s+sh+c+r+ shl	—									×	
BR 56	m+sh	*F. spir.*+ *F. ves.*	10.1°C						×	×		
BR 68	m+s+c+d	*F. serr.*	under cobbles		×		×					×
BR 71	gr+sh+c+d	*F. serr.*	under cobbles	×			×					×
BR 78	s+c	*A. nod.*+*F. ves.*	under cobbles, on wet sand		×							
BR 79	s+sh+c+d	green algae			×							
BR 82	gr+c	*A. nod.*+*F. ves.*										×
BR 83	s+c+r	*F. spir.*+*Pelv.* +green algae	in rock pools	×								
BR 89	s+sh+c	*F. cer.*+ green algae					×					
BR 93	m+s+sh+c	*A. nod.*+*F. ves.* + green algae			×							
BR 94	gr+c+r	*F. ves.* + *A. nod.*	temp. seawater 9.8°C	×								
BR 103	m+s+c	—	11.0°C; in a lagoon					×				
BR 104	gr+c+d	—	8.8°C; under cobbles, in small stream		×							
BR 105	m+s+gr+c	*F. spir.*+*F. ves.* + *Chaet.*		×								
BR 106	gr+c+d	—				×						
BR 112	s+c	*F. cer.*+*F. spir.* + *Ent.*	11.7°C; in small stream							×		
BR 115	gr+c+r	*F. ves.*	rather exposed beach	×								
BR 117	m+s+gr+c	*F. spir.*+*Ent.*	temp. seawater 18.5°C		×							
BR 120	s+r	*F. ves.*+*Ent.*	in pools; exposed beach		×							
BR 123	s+sh+c	—	in rock pools								×	
NS 5	sh+c+d	—	16.5°C; 38‰ S								×	×
NS 8	m+s+sh+c	—	15.2°C; fresh water							×		
NS 10	s+c	*F. cer.*	15.0°C; fresh water							×		
NS 11	gr+c+d	*Zostera* sp.	38‰ S									×
NS 18	s+sh+c+r	*F. ves.*+*Ulva* +*Chaet.*	in small pools; 41‰ S								×	
NS 19	s+c	*Chaet.*	in pools; 16.8°C				×					

c = cobbles
d = detritus
gr = gravel
m = mud
r = rock
S = salinity
s = sand
sh = shingle
shl = shells or shell grit

A. nod. = *Ascophyllum nodosum*
Chaet. = *Chaetomorpha*
Ent. = *Enteromorpha*
F. cer. = *Fucus ceranoides*
F. serr. = *Fucus serratus*
F. spir. = *Fucus spiralis*
F. ves. = *Fucus vesiculosus*
Pelv. = *Pelvetia*

*) For the position of the sampling stations mentioned in this table, see the appendix.

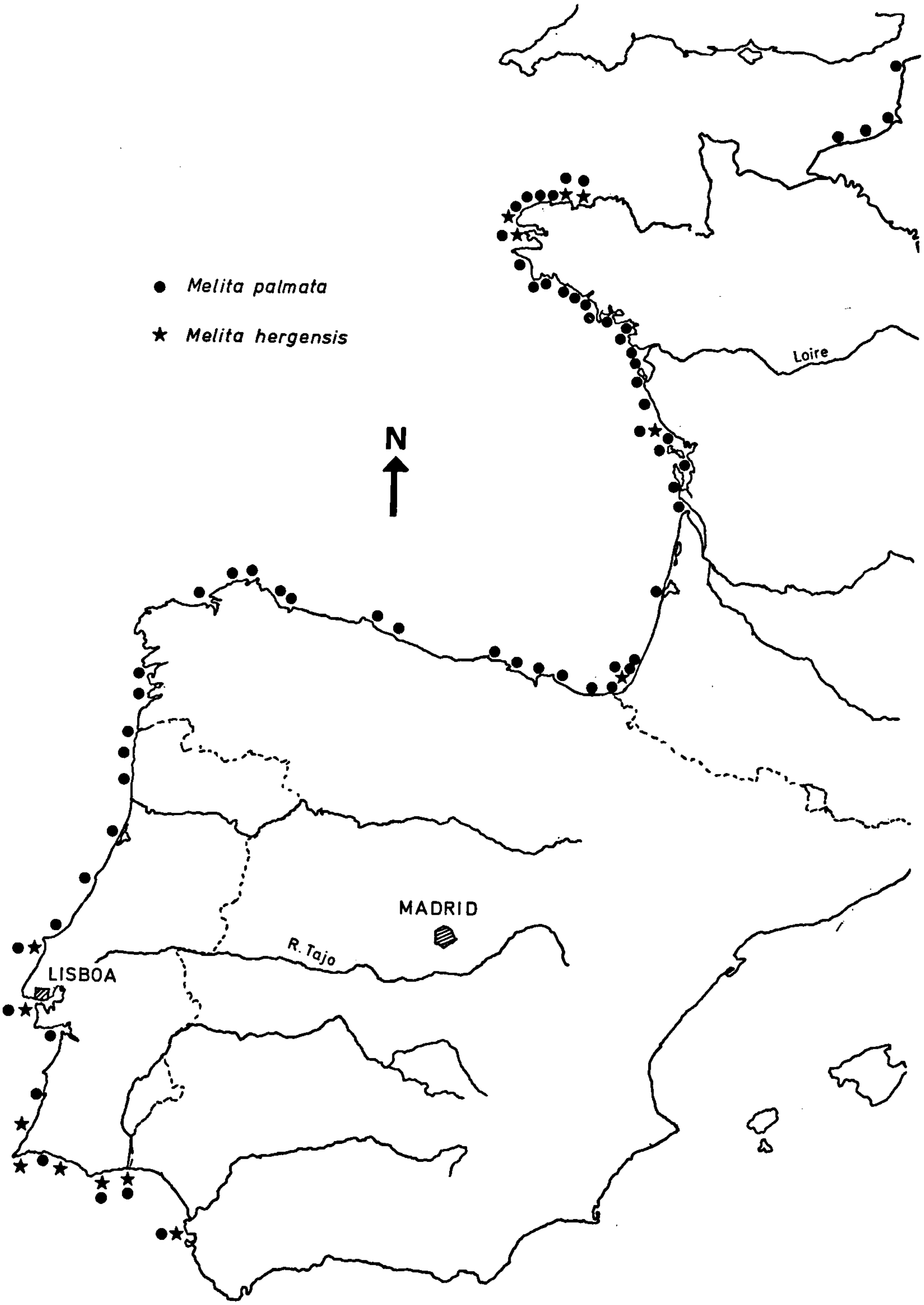

Fig. 9. Geographic distribution of *Melita palmata* and *Melita hergensis* along the Atlantic coast of France and of the Iberian peninsula (Iberian localities mainly after Van Maren, 1975).

on mud, but always on more stony and exposed beaches. This gammarid was not observed in estuaries and only once in the direct neighbourhood of a river mouth (Morlaix River). Ovigerous ♀♀ were present in a sample collected in October.

In four of the five stations where *Pherusa fucicola* was collected, the substrate consisted of gravel and/or shingle. In all cases it coexisted with *Gammarus locusta*, in three cases with *Melita hergensis*.

Melita palmata occurs all along the Atlantic coast of France and the Iberian peninsula as is shown in fig. 9. The salinities measured for this species, during the present investigations, vary from 4‰ (in an estuary) to 44‰ (in pools). From table V it appears that in most of the stations with *M. palmata* cobbles and sand form part of the substrate, though it occurs on muddy grounds and other substrates as well. The present species shows a preference for the *Fucus vesiculosus* zone, occurring to a lesser degree among *Ascophyllum nodosum* or *Fucus serratus*. In the lower zones of its vertical distribution on the beach, it was often accompanied by *Gammarus locusta*. Ovigerous ♀♀ were present in the samples from September and October.

Gammarus locusta lives mainly in the middle and lower parts of the tidal zone, among *Fucus vesiculosus* and *Fucus serratus* (table V). It was found rarely among *Fucus spiralis*, but green algae show a rather great frequency in places with *G. locusta*. The lowest chlorinity measured for the present species was 3900 mg/l. Ovigerous ♀♀ were observed in samples collected during the period of August-October and of December-February. *Gammarus locusta* occurs all along the Atlantic coast of France and the Iberian peninsula, as was established previously (Van Maren, 1975) (fig. 10).

Table V. Frequency of environmental factors and accompanying gammarid species (in %) at sampling stations where *Melita palmata* occurred (total number of samples containing *M. palmata* = 68) and at sampling stations with *Gammarus locusta* (total number of samples containing *G. locusta* = 64).

	M. palmata	*G. locusta*
mud	25	39
sand	78	75
gravel	25	19
shingle	25	36
cobbles	91	78
rock	28	22
shells or shell grit	22	9
no vegetation	16.2	12.5
green algae	41.1	36.0
Pelvetia	0.0	0.0
Fucus ceranoides and/or *Fucus spiralis*	8.8	4.7
Fucus vesiculosus	54.5	50.0
Ascophyllum nodosum	23.6	21.9
Fucus serratus	29.4	39.0
detritus	20.6	28.2
Chaetogammarus marinus	25.0	26.6
Eulimnogammarus obtusatus	22.0	15.6
Chaetogammarus pirloti	5.9	7.8
Chaetogammarus stoerensis	2.9	6.3
Gammarus finmarchicus	4.4	6.3
Gammarus locusta	30.9	
Gammarus locusta (occurring alone)		20.4
Gammarus crinicornis	4.4	14.1
Melita palmata		39.0
Melita palmata (occurring alone)	30.9	
Melita hergensis	5.9	6.3
other gammarid species	5.9	12.5

DISCUSSION

According to Sheader & Chia (1970), who studied an *Eulimnogammarus obtusatus* population in England, this gammarid does not show a distinct reproduction period, although an increase in the rate of ovigerous ♀♀ was established from December to March. The data on *E. obtusatus* obtained during the present study are in agreement with theirs.

Steele & Steele (1970), investigating a population of *E. obtusatus* living close to its northern distribution limit in the northwestern Atlantic, did not find hatched juveniles before May or June and mention a decrease in the size composition of the population in early summer. The present population from Brittany shows a minimum in mean cephalic length in August, a maximum in February-March, coinciding with the lowest and the highest rate of ovigerous ♀♀, respectively (figs. 3 and 4). This means that the young are released from April to August.

The annual seawater temperatures never drop below 5°C in Brittany (see also Faure, 1959). The temperatures mentioned by Steele & Steele (1970) for their study area (Conception Bay, Newfoundland) did not rise above 0°C until April. The duration of the development of the eggs of *E. obtusatus* at a mean temperature of 0°C is 117 days, at a mean temperature of 10°C it is 26 days and at a mean temperature of 13°C it is 22 days (Steele & Steele, 1973). This may explain the fact that hatching of the young takes place earlier in spring in the Brittany area than in Newfoundland.

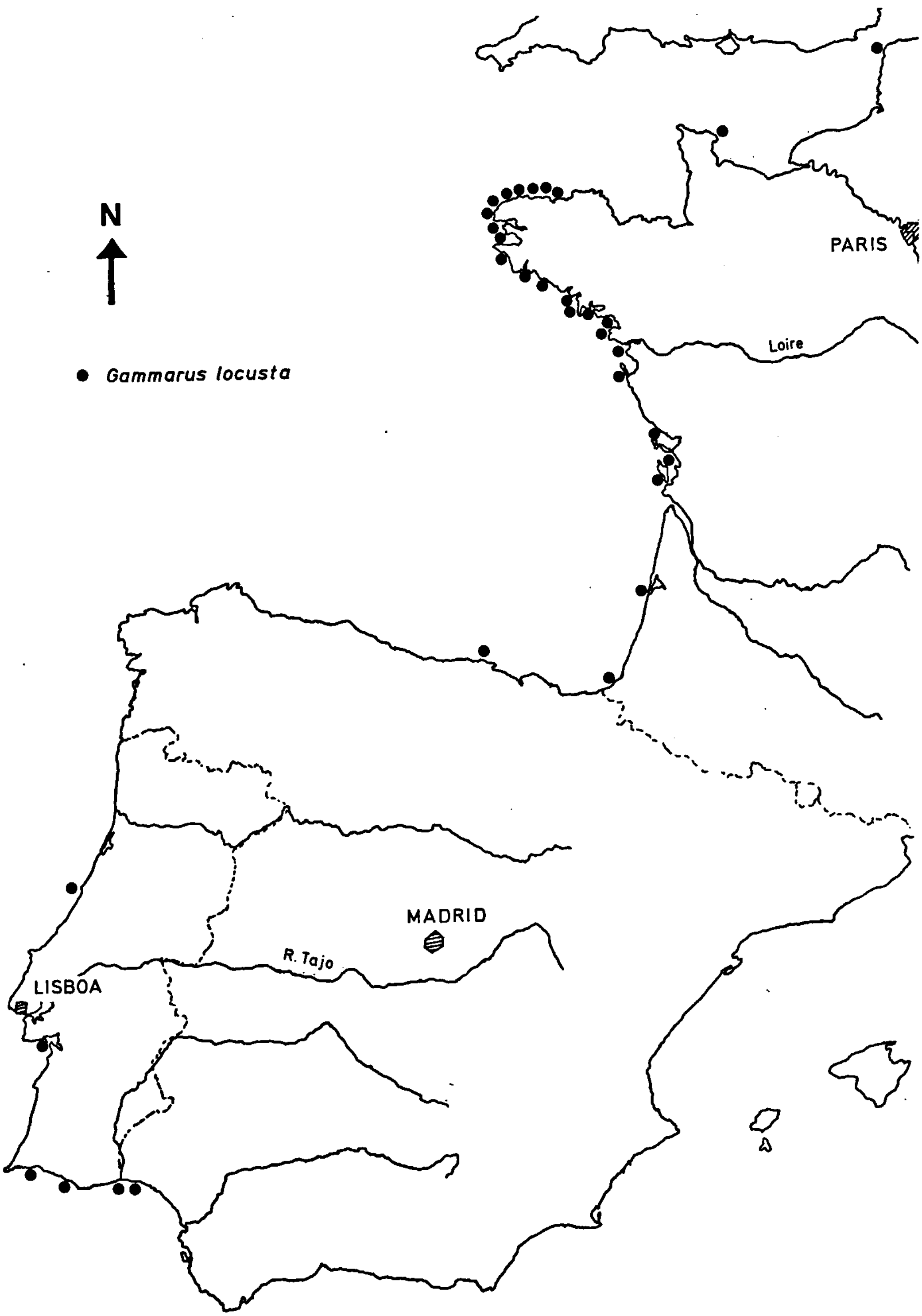

Fig. 10. Geographic distribution of *Gammarus locusta* along the Atlantic coast of France and of the Iberian peninsula (Iberian localities mainly after Van Maren, 1975).

The major and minor peak in the rate of ovigerous ♀♀ of *E. obtusatus* coincide with the greatest increase and decrease, respectively, in the seawater temperature during the year (fig. 3). Amanieu (1971) states that the beginning of many reproduction cycles is correlated with critical climate periods, the moments that temperature inversion takes place being also the times during which temperature differences are largest.

Vlasblom (1969) established that the *Chaetogammarus marinus* population occurring in the Oosterschelde (the Netherlands) does not show a distinct season during which only resting females are present. The annual temperature fluctuations affect the rate of ovigerous ♀♀, but lie between such limits that reproduction is possible the whole year round (temperatures varying from about 2° to 20°C). He observed a maximum in the number of ovigerous ♀♀ during the month of May and a second but lower peak in September. The lowest rate of ovigerous ♀♀ occurred in January and another minimum was found in June. The present *Ch. marinus* population from Brittany shows a maximum in the rate of ovigerous ♀♀ in September and a second peak in December. Furthermore, a slight increase during the months of May and June can be seen (fig. 3). In March the lowest percentage of ovigerous ♀♀ occurred.

From experiments by Vlasblom (1969) a rapid increase in the rate of development from egg to hatching stage in *Ch. marinus* appears at temperatures from 5° to 10°C, almost reaching an optimum at 20°C. The greatest yield of juveniles, however, was reached at about 15°C. In Brittany the annual seawater temperatures never drop below 5°C and reach a maximum in August (about 18°C in 1974). The drop in temperature to about 15°C during the month of September might be responsable for the peak in the number of ovigerous ♀♀ in that month. The other peak, although lower, occurring in May coincides with a temperature of about 15°C as well. The temperatures of the seawater in Brittany, not falling below 10°C before the month of January, make possible that a third maximum in the rate of ovigerous ♀♀ can be reached in December. However, in the northern *Ch. marinus* population, as studied by Vlasblom, the low temperatures during wintertime depress the number of ovigerous ♀♀ and retard the embryonic development. Water and air temperatures may remain for a considerable period below 5°C.

Comparing the mean cephalic length of the *E. obtusatus* population and the *Ch. marinus* population, it can be seen that at the time that the former species shows a maximum in mean cephalic length, a minimum is established for the latter, and vice versa. The highest rate of juveniles of *Ch. marinus* occurs in early spring, while this can be observed for *E. obtusatus* during summer.

E. obtusatus, reaching in Brittany the southern limit of its distribution area, shows only one distinct peak in reproductive activity, while in the *Ch. marinus* population, living in Brittany in its mean distribution area, an obvious maximum in reproduction is attained twice a year. Steele & Steele (1970) state that *E. obtusatus* has a low biotic potential due to the production of a small quantity of relatively large eggs in addition to a small number of broods produced during a year. Also Cheng (1942) established a low fecundity for this species compared to *Ch. marinus*.

As to the southern limit of *E. obtusatus* in the northwestern Atlantic, Steele & Steele (1970) mention that annual temperatures are always above 0°C and rise to a maximum of 18°C in August. This is in agreement with the data obtained in Brittany, the southern distribution limit of the present species in the northeastern Atlantic.

From table III and fig. 6 it can be seen that, contrary to *E. obtusatus*, *Ch. marinus* prefers muddy substrates and more sheltered biotopes. The experiment executed to obtain data on the freshwater tolerance of some intertidal gammarid species, has demonstrated that *Ch. marinus* can survive for several hours in entirely fresh water (fig. 7). This explains its ability to penetrate in estuaries over a considerable distance (Spooner, 1947; Salmon, 1962; Van Maren, 1974) and its occurrence in the higher parts of the littoral. The data mentioned above are in agreement with those of Jones (1948).

Although *E. obtusatus* often occurred among *Fucus vesiculosus*, it seems to be less associated with the presence of vegetation than *Ch. marinus*. Vegetation was lacking in more than 20% of the cases in which *E. obtusatus* was found against in only 3% of the places with *Ch. marinus*. Algal remains (especially from the large brown algae and the red algae of the infralittoral zone) were found to a higher degree in stations with *E. obtusatus* than in those with *Ch. marinus*.

Mud formed never part of the substrate in places where *E. obtusatus* was the only occùrring gammarid species (fig. 6). This gammarid shows a clear preference for coarser substrates such as gravel and shells or shell grit. Its occurrence on this kind of substrates was already mentioned in literature (e.g. Vader, 1965).

In places where both species lived in coexistence, *Fucus vesiculosus* shows the highest rate of occurrence (table II), the substrate mostly consisting of sand and cobbles in these cases.

In disagreement with the statements of Den Hartog (1964), it can be concluded from the present data that a difference in preference for a particular substrate does exist between the two gammarid species. This confirms the hypothesis assumed by Vader (1965), explaining the difference in vertical distribution between *E. obtusatus* and *Ch. marinus* from a difference in substrate preference.

The euryhalinity of *Ch. marinus* (Jones, 1948; Den Hartog, 1964; Van Maren, 1975) and the stenohalinity of *E. obtusatus* (Goodhart, 1941; Tzvetkova, 1968) can form a further explanation for their occurrence in different parts of the tidal zone.

The fact that both species lived in coexistence in part of the stations visited, does not necessarily mean they are competing each other, as Den Hartog (1964) supposed, since they show a distinct difference in reproduction season (figs. 4 and 5).

According to Den Hartog (1964) *Ch. marinus* shows a more extended vertical distribution in places where *E. obtusatus* is absent. During the present investigations no such different vertical zonation has been established, nor has *Ch. marinus* been found in lower parts of the tidal zone south of the distribution limit of the other gammarid.

— The occurrence of *Chaetogammarus stoerensis* on substrates like gravel and shell grit at reduced salinities is in accordance with the data mentioned in literature on this gammarid (e.g. Vader, 1964; Van Maren, 1975). This species has often been found living among the particles of a substrate devoid of vegetation. Its vertical distribution extends over the *Fucus spiralis* and *Fucus vesiculosus* zones. *Ch. stoerensis* occurred mostly near small streams or upwelling groundwater on the beach. This confirms the observation by Vader (1964). He states that freshwater influence is of little importance to this species (under experimental conditions it survived for several months in seawater), but of primary interest is the fact that the substrate remains humid during low tide.

The presence of ovigerous ♀♀ of *Ch. stoerensis* in the samples from January and February is not in contradiction with the data in literature (e.g. Brattegard, 1966; Vader, 1964).

— *Gammarus finmarchicus* was mainly found living lower in the littoral than *Ch. marinus* and higher than *G. locusta*. This is in agreement with the difference between these three gammarids in resistance to freshwater conditions, as resulted from the experiment described earlier. Its low resistance to reduced salinities is also mentioned by Werntz (1963) and Tzvetkova (1968). Jones (1948) supposed that *G. finmarchicus* shows a tendency to live in places that do not dry up completely during low tide. Tzvetkova (1968) stated this gammarid to be less resistant to higher temperatures than, for example, *E. obtusatus*. In places where at low tide some water remains, temperature fluctuations will be less extreme.

G. finmarchicus shows a geographic distribution comparable to the other amphi-atlantic species, *E. obtusatus*, as was established by Steele & Steele (1974). During the present study neither of the two gammarids has been found south of Brittany along the Atlantic coast.

In samples from December ovigerous ♀♀ of *G. finmarchicus* were observed, and not in the samples from August, September and November. Up to now, no data were available in literature on the reproduction activity of this species.

— *Chaetogammarus pirloti* was found in the higher and middle parts of the tidal zone, often at reduced salinities (in pools, near streams and upwelling groundwater), mostly on coarser substrates. These observations confirm the data in literature (Sexton & Spooner, 1940; Jones, 1948; Duhig & Humphries, 1955; Martin, 1966).

During the present investigations, in some of the sampling stations *Ch. pirloti* was observed living at rather high salinities, which is in agreement with the statement of Jones (1948), who found it also in seawater flowing down the beach. Furthermore, Tulkki (1963) established its occurrence near L.W. mark.

Ch. pirloti has hitherto been recorded from Great Britain (Sexton & Spooner, 1940), from the western coast of Norway (Tulkki, 1963), and from Brittany (Dennert, 1975: fig. 4). During the present study it has not been found south of the Pointe du Percho, Presqu'île de Quiberon, in southern Brittany.

From the data obtained on *Ch. pirloti* it appears that this gammarid can reproduce at almost marine salinities. The observations of ovigerous ♀♀ in the samples from September, October and February are the first data on the reproduction activity of this gammarid.

— The Grève de Quillec in northern Brittany is a good example of a typical *Gammarus crinicornis* biotope: this species occurred here in large numbers in small pools filled with *Ulva lactuca*, at some distance from the riverbed. Stock et al. (1966) found *G. crinicornis* in a similar biotope. During the present investigations it occurred mainly in samples from sandy substrates and has been found only a few times in more sheltered places. This confirms the data on this gammarid mentioned by Stock (1967). The salinities measured for *G. crinicornis* indicate marine or almost marine conditions.

— *Gammarus locusta* has been found mainly in the lower parts of the littoral (*Fucus vesiculosus* and *Fucus serratus* zones). Not seldom mud and/or detritus were part of the substrate. This is in agreement with the data of Truchot (1963), who also did not find *G. locusta* in more exposed places, entirely devoid of detritus.

The rather high salinities measured under natural conditions for the present species are in accordance with the data resulting from the experiment on its resistance to reduced salinities and confirm the statements in literature on *G. locusta* (Bassindale, 1942; Den Hartog, 1964; Jażdżewski, 1973; Van Maren, 1975).

According to Den Hartog (1964) *G. locusta* occurs mainly in the sublittoral. In the lower part of the eulittoral he has found only small numbers of this species. During the present study not seldom green algae like *Ulva, Chaetomorpha*, and *Enteromorpha* were present at sampling stations with *G. locusta*. This confirms the earlier observations about the biotope of this gammarid on the Atlantic coast of the Iberian peninsula (Van Maren, 1975).

The frequent occurrence of *G. locusta* in places where some water remains during low tide, such as pools, tide creeks and for example the *Zostera* meadow in the Aber de Roscoff, might indicate a preference for biotopes that do not emerge completely at L.W., rather independent of their position on the shore and on condition that salinity reductions are limited.

The presence of ovigerous ♀♀ in samples from September and October is not in contradiction with the data provided by Den Hartog (1964).

— The salinities established for *Melita palmata* are in agreement with the data on its euryhalinity known from literature (Den Hartog, 1964; Van Maren, 1972, 1974, 1975). Den Hartog (1964) mentions *M. palmata* to be most abundant near L.W. mark, but it may be very numerous also in the upper fringe of the sublittoral of the Dutch Deltaic region, where *M. hergensis*, which in other areas replaces *M. palmata*, does not occur. The present observations are in agreement with this statement.

At a considerable number of sampling stations with *M. palmata*, the substrate contained mud. This also agrees with the data of Den Hartog, who stated that it lives by preference in places where silt is deposited, avoiding exposed beaches.

A sample collected in northern Brittany during the month of September and a sample collected near Bordeaux in October contained ovigerous ♀♀ of *M. palmata*. According to Den Hartog (1964) reproduction of this species in the Dutch Deltaic region takes place in summer.

— Contrary to *M. palmata*, *Melita hergensis* was never found on muddy grounds. This is in agreement with the observations in its biotopes along the Atlantic coast of the Iberian peninsula (Van Maren, 1975). The present gammarid lives in the lower part of the tidal zone among *Fucus serratus* and *Fucus vesiculosus*. When occurring in the latter (higher) *Fucus* zone, it was often found together with species like *Eulimnogammarus obtusatus* and *Melita palmata*. In the lower range of its vertical distribution the accompanying gammarids were *Pherusa fucicola* and *Gammarus locusta* (among *Fucus serratus* and red algae). The coexistence with *G. locusta* at L.W. mark was already mentioned by Jones (1948). *M. hergensis* was found living in tide pools among a vegetation of *Chaetomorpha* and/or *Ulva* as well.

M. hergensis occurred at marine or almost marine salinities. In agreement with the observations of Truchot (1963), this species was never found in estuaries.

Although *M. hergensis* is much rarer along the Atlantic coast than *M. palmata* (fig. 9), it seems to have a wide geographic distribution. Reid (1939) mentioned the present gammarid from the British Isles and Naples. Myers (1969) has found *M. hergensis* in the Aegean Sea (Island of Khios), though he states that his material does not meet exactly the original description by Reid (1939).

During the present investigations, a sample from October contained ovigerous ♀♀ of *M. hergensis*. Previously, ovigerous ♀♀ were found to occur also in April (Van Maren, 1975).

— *Pherusa fucicola* lives down on the beach near L.W. mark. It seems to prefer marine or almost marine conditions. Except from the tidal zone, this species is known from other biotopes where slight salinity reductions may take place, such as the "foces" (mouths) of the brackish lagoons near Naples (Van Maren, 1973).

— The occurrence of *Pectenogammarus planicrurus* on a substrate of sand and gravel, devoid of vegetation, is in agreement with the data mentioned on this gammarid in literature (Morgan, 1970; Kant et al., 1968; Van Maren, 1975).

— In a small stream on "la Grande Grève" near Carantec (Brittany), where *Gammarus salinus* was found together with *G. chevreuxi*, the chlorinity was 500 mg/l. This is the lowest Cl value measured for *G. salinus* during the present study. At another sampling station, where a chlorinity of 21100 mg/l was established, only one specimen of this gammarid was found together with many *G. locusta*. In agreement with this are the data of Den Hartog (1964) from the Dutch Waddenzee (at marine or almost marine conditions), who found only a few *G. salinus* together with enormous numbers of *G. locusta*. Like Den Hartog, who collected *G. salinus* also in larger inland pools in the Dutch Deltaic region, we sampled it during the present study in a lagoon near Guisseny in northern Brittany.

Den Hartog (1964) observed ovigerous ♀♀ of *G. salinus* during the months of March to November. The occurrence of ovigerous ♀♀ of this species in samples from December and February taken in Brittany, may be explained by the relatively high winter temperatures in this region.

— *Gammarus zaddachi* was always found living under estuarine conditions, in streams running over the beach or in the riverbed of estuaries. This confirms the data in literature on this gammarid (e.g. Stock et al., 1966; Dennert et al., 1969). In Brittany it often occurs together with *G. chevreuxi*, penetrating somewhat more seaward than the latter gammarid (Van Maren, 1974).

In August, specimens in precopulation of *G. zaddachi* have been found on a sandy substrate among *Ulva lactuca* (temp. 24°C), where a small streams discharges on the beach of St. Michel-en-Grève (Brittany).

— Like *G. zaddachi*, *Gammarus chevreuxi* was found in small streams in the tidal zone and in estuaries, under freshwater conditions or at slightly raised salinities. According to Girisch et al. (1974) this gammarid does not reproduce in entirely fresh areas.

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APPENDIX

Position of the sampling stations as mentioned in table IV

STATION	DATE	POSITION	DEPARTMENT
EX 4-EX 11	9/10-VIII-'73	Roscoff, l'Aber	N.-Finistère
EX 16-EX 18	12-VIII-'73	St. Michel-en-Grève, beach	N.-Finistère
EX 22-EX 29	13-VIII-'73	Sibiril, Grève de Quillec	N.-Finistère
A 2	11-IX-'73	Audresselles, beach near Hotel de la Plage	Pas-de-Calais
NF 2	13-XI-'73	Le Tréport, S. of the harbour, limestone rock	Seine-Maritime
NF 5	14-XI-'73	Les Grandes Dalles, cliff coast and beach of boulders	Seine-Maritime
NF 9	15-XI-'73	Courseulles-sur-Mer, near wooden jetty, on the right bank of the river Seulles	Calvados
NF 10	16-XI-'73	Vierville-sur-Mer, Omaha Beach	Calvados
NF 11-NF 14	16-XI-'73	Vierville-sur-Mer, Pointe et Raz de la Percée	Calvados
NF 15	16-XI-'73	Grandchamp-les-Bains, next to the pier	Calvados
NF 17-NF 21	16-XI-'73	Montfarville, bay near Pointe du Moulard	Manche
AA 3	26-X-'73	Cap Griz Nez, beach	Pas-de-Calais
BR 1-BR 3	3-XII-'73	Carantec, la Grande Grève	N.-Finistère
BR 6	3-XII-'73	Estuary of Le Penzé, small affluent, downstream of the Pont de la Corde	N.-Finistère
BR 7	4-XII-'73	Le Dourduff, tributary of the Morlaix River, downstream of the water mill	N.-Finistère

STATION	DATE	POSITION	DEPARTMENT
BR 15	5-XII-'73	Roscoff, l'Aber	N.-Finistère
BR 20-BR 21	11-XII-'73	Le Conquet, beach near Pointe des Renares	N.-Finistère
BR 22	11-XII-'73	Grève d'Illien, N. of le Conquet	N.-Finistère
BR 27	11-XII-'73	Porspol, S. of the Aber-Ildut, beach	N.-Finistère
BR 34	14-XII-'73	Grèves de Lilia, N.W. of Plouguerneau	N.-Finistère
BR 36	14-XII-'73	Grève de Zorn, N.E. of Plouguerneau	N.-Finistère
BR 39-BR 40	14-XII-'73	Plage de Pors Guen, W. of Plouescat	N.-Finistère
BR 43	18-XII-'73	Roscoff, l'Aber, near Centre Hélio-Marin	N.-Finistère
BR 49	21-XII-'73	Gouermel-Plage, N.W. of Tréguier	Côtes-du-Nord
BR 51	8-I-'74	Lanvoy, W. of le Faou, beach	S.-Finistère
BR 52-BR 54	8-I-'74	Larmor, S.W. of Plougastel-Daoulas, beach	N.-Finistère
BR 56	10-I-'74	Le Dourduff, tributary of the Morlaix River, in small affluents of the estuary	N.-Finistère
BR 68	14-I-'74	Presqu'île de Quiberon, Pointe du Percho	Morbihan
BR 71	14-I-'74	Port-Louis, beach	Morbihan
BR 78	28-I-'74	Audierne, left bank of the river Goyen, near Poulgoazec	S.-Finistère
BR 79	28-I-'74	Audierne, right bank of the river Goyen, near Lervily	S.-Finistère
BR 82-BR 83	13-II-'74	Carnac-La Trinité, Baie de Quiberon, beach	Morbihan
BR 89	14-II-'74	Penerf, S.E. of Vannes, left bank of the river Penerf	Morbihan
BR 93-BR 94	12-II-'74	Port-Louis, beach near the fortifications	Morbihan
BR 103	14-II-'74	Guissény, lagoon W. of the village	N.-Finistère
BR 104-BR 106	14-II-'74	Plage de Pors Guen, W. of Plouescat	N.-Finistère
BR 112	9-V-'74	Dellec, W. of Brest, Goulet de Brest	N.-Finistère
BR 115	9-V-'74	Trégana, beach W. of Brest, E. of Pointe St. Mathieu	N.-Finistère
BR 117	14-VI-'74	Lesconil, S. of Pont l'Abbé, right bank of the estuary, E. of the harbour	S.-Finistère
BR 120	14-VI-'74	Poulhan, beach, S.E. of Audierne, Baie d'Audierne	S.-Finistère
BR 123	18-VIII-'74	Morgat, caves	S.-Finistère
NS 5	4-X-'74	Biarritz, beach	Pyrénées-Atlantiques
NS 8	4-X-'74	Capbreton, N. of Bayonne, estuary	Landes
NS 10	4-X-'74	Vieux-Boucau, mouth of the lagoon	Landes
NS 11	5-X-'74	Arcachon, Bassin d'Arcachon, next to the jetty of the "petit port de plaisance"	Gironde
NS 18	7-X-'74	Les Sables d'Olonne, beach "la Rudelière"	Vendée
NS 19	7-X-'74	Croix-de-Vie, N.W. of Les Sables d'Olonne, mouth of the river Vie	Vendée

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