HABITAT SELECTION BY *Cheirimedon femoratus* (Pfeffer) AND *Tryphosella kergueleni* (Miers) (CRUSTACEA : AMPHIPODA)

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ABSTRACT. Field and laboratory investigations indicate that the size of particles composing the substrate, and also its compressibility, are important factors in determining the distribution of *Cheirimedon femoratus* and *Tryphosella kergueleni*. *C. femoratus* prefers finer softer sands, but *T. kergueleni* possesses a much wider tolerance of particle size and appears to select areas with firmer substrates in which to release its young.

ALTHOUGH the areas occupied by the sand-dwelling amphipods *Cheirimedon femoratus* (Pfeffer) and *Tryphosella kergueleni* (Miers) coincide for much of their life cycles, females of both species produce and maintain their broods in areas distinct from one another (Bregazzi, 1972). The result is the separation of their early juvenile stages, when food requirements are likely to be similar. This paper describes some field and laboratory studies designed to investigate habitat selection, and discusses possible factors which determine the local distribution of these species.

FIELD INVESTIGATIONS

Methods

In order to establish more accurately the differences in distribution of amphipods in the bottom sediments described previously, a transect line with seven stations marked at 30 m. intervals was laid along the bottom sand near the entrance to Factory Cove, Signy Island, South Orkney Islands (Fig. 1), which thereby included the areas where *C. femoratus* and *T. kergueleni* were known to release their broods, and also, the areas where late-stage ovigerous females of *T. kergueleni* were known to be present and absent (Bregazzi, 1972). The difference in depth between stations 1 and 7 was no more than 1–2 m. Samples of the amphipod fauna were taken with a hand dredge (Bregazzi, 1972) by divers at each station, between 21 and 29 January 1969. Amphipods were separated by sieving, and preserved in 5 per cent neutral formalin. Each sample was thoroughly mixed, and a 25 $cm.^3$ portion of animals, loosely shaken down in water, was removed for identification and counting.

During a dive at several points in the area around station 1 on 17 February 1969, it was apparent that the bottom sediment was unusually hard, so much so that it was found impossible to use the hand dredge in the accustomed manner. This was in contrast to the conditions that prevailed at station 7 where the bottom was, as usual, quite soft. These observations were made on the day following a north-easterly gale; there was a certain amount of surge around station 1 at the bottom and the bottom sediment was rippled.

The marked difference in bottom conditions between the ends of the transect raised the possibility that the hardness or compressibility of the substrate might be a factor in influencing the distribution of amphipods. Consequently, a device was constructed to provide a comparison in this respect at the different transect stations. It consisted of a cylindrical steel bar, 30 cm. by 4 cm. with a 70 cm. steel rod attached, supported in a Dexion frame (Fig. 2). The bar and rod together weighed 2·85 kg. in air. To operate, the steel bar was raised 30 cm. above the base of the frame, which stood on the sea bed, and released. The amount of penetration into the substrate was read from a scale, arbitrarily marked in centimetres, secured to the frame next to the tip of the rod. 20 such readings were made within a 5 m. radius of station 1 and also station 7 on 19 February 1969. At the same time, four 10 cm. diameter core samples were taken at each of these stations. The top 3 cm. of bottom sediments, containing the great majority of burrowing amphipods, was separated, and the proportions of particles of different diameters composing it were estimated by sieving in water through meshes of 500, 210 and 125 μm. The sediments were allowed to settle in measuring cylinders for 24 hr. and the volumes then recorded.

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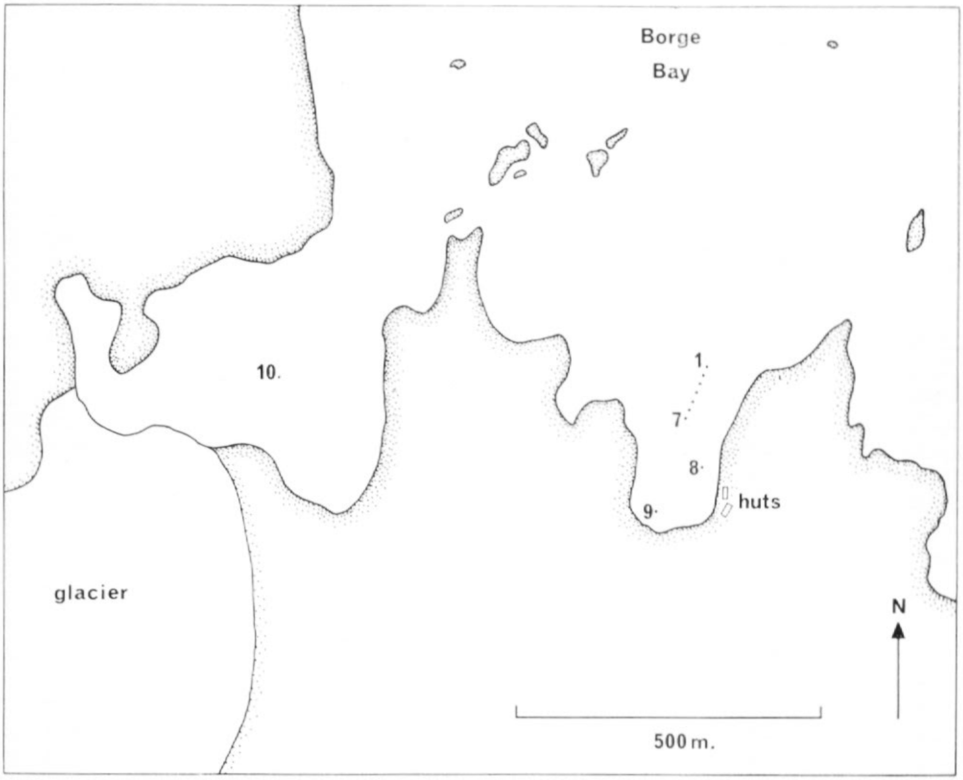

Fig. 1. Map of part of Borge Bay showing sampling stations 1–7, 8 and 9 (Factory Cove), and 10 (Elephant Flats).

Further readings with the hardness-testing device were made at transect stations 1, 4, 5, 6 and 7 on 27 and 29 March 1969 in the manner described above, and also, samples of the top 2–3 cm. of bottom sediment and the associated fauna were taken by means of a trowel and hand dredge at the same five stations. The sediment samples and amphipods were preserved in 5 per cent neutral formalin for analysis in the United Kingdom. Water temperatures were taken at the sea bed at the same time as each sample was collected.

Similar samples were taken and measurements made at three more stations. Two were in Factory Cove, station 8 at the eastern edge next to the boulder rim and station 9 at the head of Factory Cove. Station 10 was at Elephant Flats, a sheltered inlet 0·5 km. west of Factory Cove, into which Orwell Glacier flows (Fig. 1).

For sediment analysis, the samples were washed several times in tap water and left to settle for about 10 hr. between washings. After decanting most of the water, the samples were left to dry in open trays in a warm room for 1 week. Each dry sample was thoroughly mixed and about 100 g. of material was separated, weighed and placed in a nest of eight sieves, the mesh sizes of which ranged from 500 to 76 μm. After vibrating for 20 min. on a mechanical sieve shaker, the amount of sediment in each sieve was weighed to the nearest 0·01 g.

Results

The total number of all amphipods by species in the 25 cm.^{3} sample from each station is given in Table I, and the distribution of *C. femoratus* and *T. kergueleni* along the transect line, expressed as percentages of the total number of each category, is shown in Fig. 3. It can be seen that early stage ovigerous females and non-ovigerous *T. kergueleni* of more than 4 mm. are found at each station. The great majority of late-stage ovigerous females and juveniles of

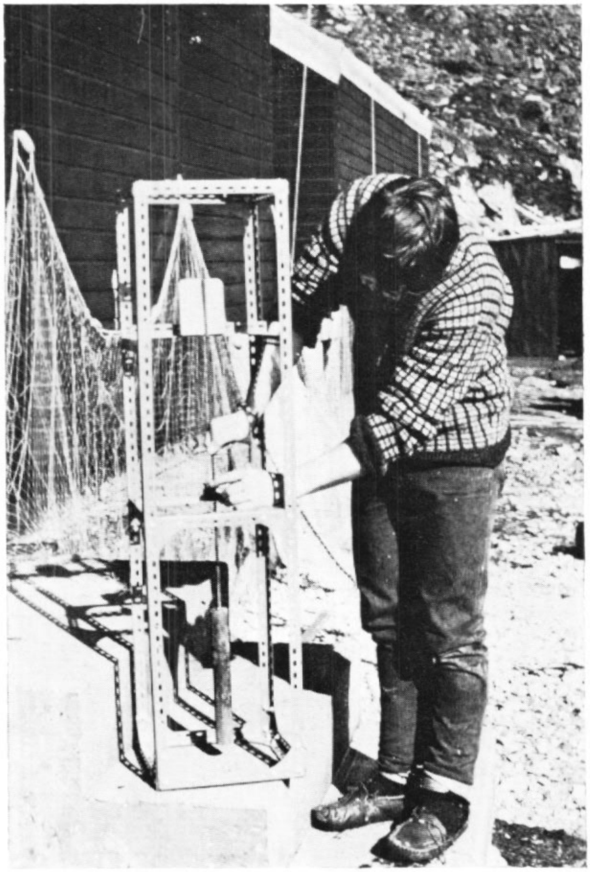

Fig. 2. Device for testing hardness of marine bottom substrates.

less than 4 mm., however, are found at stations 1–4. All categories of *C. femoratus* are virtually restricted to stations 6 and 7. Station 5 may represent a region of slight overlap between those categories of both species which are for the most part separated. The small numbers of these species taken at station 5 may be due to the large numbers of *Pontogeneiella brevicornis* (Chevreux) greater than 6 mm. taken at this station. The distribution of *C. femoratus* and *T. kergueleni* along the transect line is in agreement with that reported in Bregazzi (1972) for site A and site B.

The mean volumes of sand particles of different sizes in the four cores taken at stations 1 and 7 on 19 February 1969, expressed as a percentage of the total volume for each core, are given in Fig. 4. It is seen that the highest proportions of finer particles occur at station 7.

The results of the more detailed analysis of particle size of the top 2–3 cm. of sediment from stations 1 and 4–7, taken on 27 and 29 March 1969, are shown in Table II. In order to compare with earlier measurements and also the laboratory substrate selection experiments described later, the weights are shown as percentages of total sediment at each station for the same three categories of particle size used previously. The values for stations 1 and 7 agree with those made at the earlier date in the field in that a higher proportion of sediment of the finest category was found at station 7.

The comparative measurements for hardness of substrate at stations 1 and 4–7 are also given in Table II. The two values taken 1 month previously (i.e. 2 days after the unusual hardness conditions at station 1 were first noted) are shown in brackets. The values obtained at each of

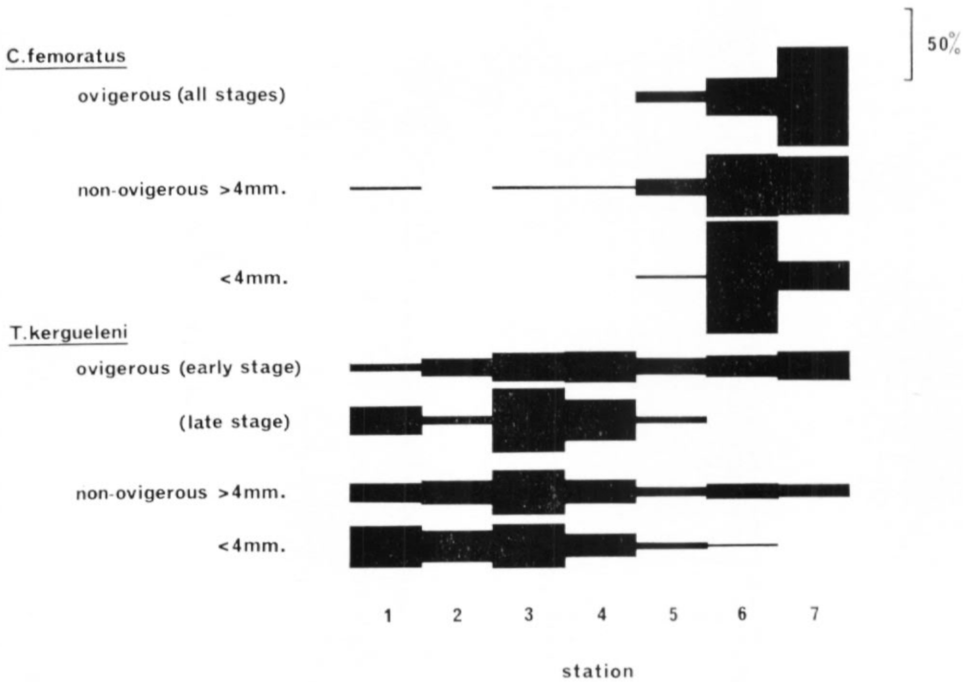

Fig. 3. Percentage distribution of each class of *C. femoratus* and *T. kergueleni* at stations 1–7.

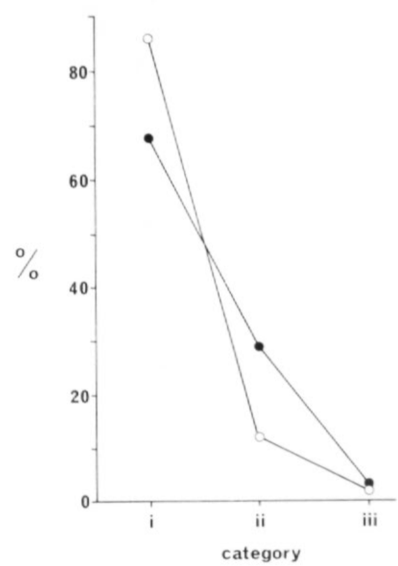

Fig. 4. Mean percentage of different categories of sand particle size from stations 1 (solid circles) and 7 (open circles).
i. Up to 125 μm. diameter; ii. 125–210 μm. diameter; iii. 210–500 μm. diameter.

Table I. Numbers of different species of amphipod in 25 cm^3 portions of samples from different stations

	21/29 January 1969							1 April 1969		20 March 1969
Station:	1	2	3	4	5	6	7	8	9	10
Cheirimedon femoratus										
Ovigerous	—	—	—	—	4	16	42	37	8	1
More than 4 mm.	4	—	2	3	39	158	147	156	105	49
Less than 4 mm.	—	—	—	—	1	105	26	62	10	8
Tryphosella kergueleni										
Ovigerous (early)	12	29	48	54	26	36	48	—	1	—
Ovigerous (late)	7	2	16	10	1	—	—	—	—	—
More than 4 mm.	166	195	376	194	59	116	108	5	34	—
Less than 4 mm.	183	141	198	99	17	5	2	—	—	—
Pontogeneiella brevicornis										
More than 6 mm.	18	25	18	50	116	26	23	67	191	18
Less than 6 mm.	—	—	—	3	62	135	41	—	2	—
Parharpinia rotundifrons										
More than 2 mm.	150	72	54	26	17	11	42	25	91	1
2 mm.	Many	Many	31	15	3	21	15	—	38	—
Lepidepecreum cingulatum	1	—	—	—	10	8	20	5	13	4
Monoculodes scabriculosus	1	1	—	6	—	7	—	—	1	—
Pontongeneia antarctica	—	—	—	—	—	—	—	—	2	1
Paramoera walkeri	—	—	—	—	—	—	—	—	—	29

TABLE II. PERCENTAGE BY WEIGHT OF DIFFERENT DIAMETERS OF PARTICLE SIZE FROM EIGHT SAMPLING STATIONS, WITH CONCURRENT COMPRESSIBILITY MEASUREMENTS

	27/29 March 1969					1 April 1969		20 March 1969
Station:	1	4	5	6	7	8	9	10
More than 500 μm.	0·01	0·03	0·03	0·01	0·01	7·20	4·86	0·08
210–500 μm.	1·77	0·95	0·28	0·35	1·94	5·25	5·73	0·28
125–210 μm.	36·42	29·51	12·33	10·98	30·37	29·39	65·92	2·24
Less than 125 μm.	61·80	69·53	87·36	88·66	67·68	58·16	23·49	97·40
Mean compressibility (arbitrary units)	1·37 (1·08)	2·02	2·72	3·26	2·72 (3·83)	3·90	2·45	12·30
Standard deviation (±)	0·36 (0·38)	0·57	0·94	0·56	1·04 (0·75)	2·20	0·58	2·00

Brackets: readings taken 1 month earlier at stations 1 and 7.

stations 1 and 7 at 1 month's interval differ from each other as if the bottom at station 7 had hardened, and the bottom at station 1 had softened somewhat over the course of the month. The softest bottom conditions appear at station 6 and so does the greatest proportion of smallest particle sizes. Further measurements of the hardness of the bottom sediment were made from July to December 1969 at station 1. The results are given in Table III and show some variation in hardness over this period of time within the range 0·62–1·70.

The amphipod content of stations 1 and 4–7 made during the collection of the sediment samples and compressibility measurements agree closely with those made 2 months previously (Table I).

Data for the non-transect stations (8, 9 and 10) are given also in Tables I and II.

At the time of sample collection along the transect line, the temperature difference between stations 1 and 7 did not exceed 0·05° C.

TABLE III. VARIATION IN COMPRESSIBILITY IN ARBITRARY UNITS OF THE BOTTOM SEDIMENT AT STATION 1

	Mean	*Standard deviation (±)*	*Number of readings*
1969			
19 February	1·08	0·38	20
27 March	1·37	0·36	20
12 July	0·62	0·23	12
7 August	0·73	0·31	19
3 September	1·32	0·29	20
6 October	0·82	0·29	20
3 November	0·92	0·18	20
3 December	1·57	0·35	20
13 December	1·70	0·30	20

LABORATORY INVESTIGATIONS

The laboratory investigations examined the extent to which different stages of both species are able to distinguish between substrates composed of sand particles of different sizes.

Methods

Samples of washed bottom sand were separated into different fractions by sieving in sea-water. The following five categories of particle diameter were used: up to 125, 125–210, 210–500 and 500–1,000 μm., and pebbles of about 5 mm. diameter.

For each experiment, the five fractions were placed in five or ten 5 cm. diameter crystallizing dishes to a depth of 1 cm., and these were introduced into an aquarium tank with water at 0–3° C. The tank was shielded from directional light but otherwise was in natural light conditions. Animals were introduced into the tank and left overnight, after which the dishes were removed and contents counted. For successive experiments, substrate dishes were always placed in different relative positions. Most experiments were carried out using all non-juvenile categories of one species at the same time, but juveniles were treated separately. The number of experiments carried out, and the mean number of animals used in each experiment are given in Table IV. All animals were taken, by hand dredge or trap, at or near station 7, Factory Cove (Fig. 1).

TABLE IV. NUMBER OF SUBSTRATE SELECTION EXPERIMENTS CARRIED OUT

	Number of experiments	*Mean number of animals per experiment*
C. femoratus		
Ovigerous	3	16
Non-ovigerous	7	69
Juveniles (less than 4 mm.)	3	298
T. kergueleni		
Ovigercus (early stage)	7	33
Non-ovigerous females	6	12
Males	7	25
Juveniles (less than 4 mm.)	2	73

Two additional experiments were conducted using ovigerous females of *T. kergueleni*, some with early-stage and some with late-stage broods, taken by divers at station 1 (Fig. 1).

Results

The results, expressed as mean percentage of each category of animal in the different substrates, are given in Fig. 5. A clear preference for the sand composed of particle diameters of less than 125 μm. is shown by *C. femoratus*. *T. kergueleni*, however, appears to possess a wider range of tolerance, with most being found in the sand with particle diameter of 125–210 μm.

The results of the additional experiments with early and late-stage ovigerous *T. kergueleni* are given in Fig. 6. There is no obvious difference between the two stages in respect of their preferences for substrates of different particle size.

DISCUSSION

Several amphipod species are thought to discriminate between substrates on the basis of particle size. Jones (1950) drew attention to the importance of this in determining the distribution of many bottom-dwelling gammaridean amphipods. Toulmond (1964) has classified intertidal sand on the basis of particle size and the dominant species of amphipod therein, and Fincham (1969) regarded the nature of the bottom sediment as probably being the most important environmental factor which determines the distribution of amphipods in the sand communities of the northern Irish Sea. Fincham (1971) reported the importance of particle size for sand-dwelling amphipods of the intertidal and shallow sub-littoral regions. Wieser (1959) considered that the distribution of at least some intertidal organisms is determined by the grades of substrate rather than tidal levels. *Corophium volutator* Pallas prefers a fine grade of sand but *C. arenarium* Crawford has a much wider range of tolerance (Meadows, 1964*a*). Where salinity is greater than 5‰, the nature of the substrate is more important than salinity in determining the distribution of *C. volutator* (McClusky, 1968). *Pectenogammarus planicrurus* Reid inhabits shingle beaches and maximum densities occur where the median

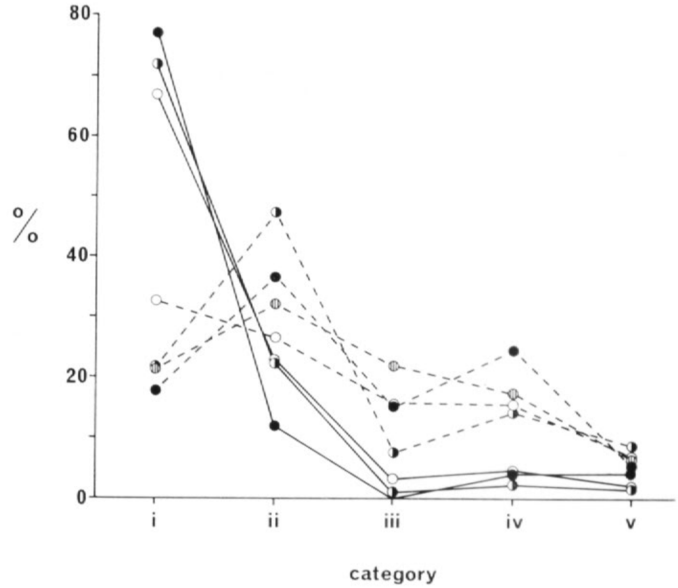

Fig. 5. Mean percentage of each class of *C. femoratus* and *T. kergueleni* in different categories of sand particle size.
Continuous line: *C. femoratus*; broken line: *T. kergueleni*.
● Ovigerous female. ◍ Male.
◑ Non-ovigerous. ○ Juvenile.
i. Up to 125 μm. diameter; ii. 125–210 μm. diameter; iii. 210–500 μm. diameter; iv. 500–1,000 μm. diameter; v. About 5 mm. diameter.

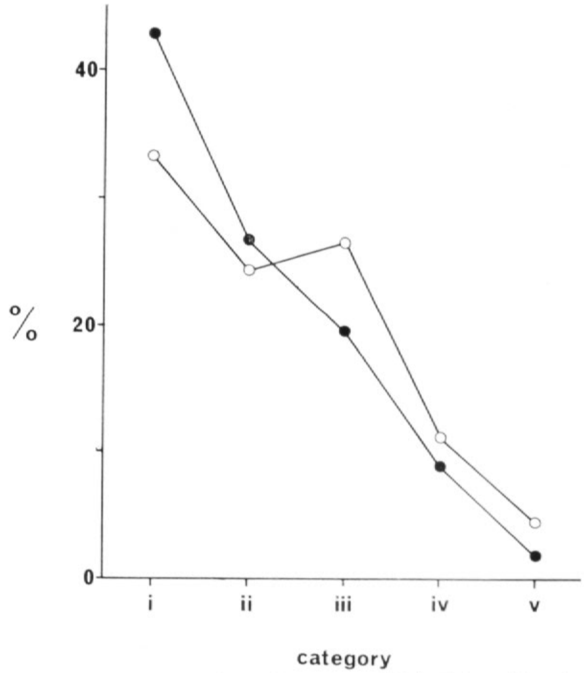

Fig. 6. Mean percentage of ovigerous *T. kergueleni* with early (solid circles) and late (open circles) stage broods, in different categories of particle size. Particle-size categories as in Fig. 5.

particle diameter is 4·0 mm. and where there is good sorting (Morgan, 1970). The semi-terrestrial amphipods *Talitrus saltator* (Montagu) and *Talorchestia deshayesi* (Audouin) show different particle-size preferences from each other, with *T. deshayesi* replacing *T. saltator* in the finest sand (Dahl, 1946).

The laboratory studies in the present investigation show that particle size has some significance for *C. femoratus* and *T. kergueleni*, and this is likely to account, at least in part, for their occurrence in the field. The wider tolerance of *T. kergueleni* is reflected in the wider distribution of this species in the field investigations. *C. femoratus*, apparently preferring sands of finer particle size, was more restricted in distribution along the transect line (Fig. 3).

However, it is clear from the data in Tables I and II that particle size is not the only factor governing the distribution of these species in the field. The percentages of different particle sizes at station 7 is closely similar to that of station 4 and not very different from station 1 (Table II), and yet station 7 has a very different amphipod content. Station 9 has a lower proportion of the finest sediment than any transect station and yet it contains many *C. femoratus*, including ovigerous stages. It appears to be well established that ovigerous *T. kergueleni* move to areas distinct from those occupied by *C. femoratus* in order to produce and release their broods (Bregazzi, 1972), but the results of the substrate-selection experiments with late- and early stage ovigerous *T. kergueleni* would suggest that the distinction between different habitats is made, in this case, on some basis other than particle size alone. Differences between the data for ovigerous females of *T. kergueleni* in Figs. 3 and 6 underline the probability that particle size is not the only factor involved.

The small scale of differences in temperature and depth between the two ends of the transect line suggest that it is most unlikely that these influence the local distribution of amphipods in the area under consideration.

The comparative data for the hardness of bottom sediments (Table II), although limited, indicates another possible factor concerned with the distribution of the sand-dwelling amphipods in this investigation. It can be seen that all categories of *C. femoratus* are virtually restricted to sediments, the compressibility of which, in the arbitrary units employed here, is within the range 2·72–12·30. Likewise, late-stage ovigerous *T. kergueleni* and very small juveniles of the same species are restricted to sediments with a compressibility which is within the range 1·08–2·02. The hardness of the substrate at station 1 between February and December 1969 (Table III) shows some variation with time, but this is over a narrow range and does not approach those values for the stations where *C. femoratus* was found.

The hardness of a bottom sediment is governed by several factors, of which proportions of different particle sizes, shape of the particles, the extent and type of water movement and the length of time a sediment has been in position are the most important (Richards, 1967). Visual observations have suggested that surging of the water layer next to the sandy bottom occurs quite often in the area of stations 1–3. It is possible that this type of water movement serves not only to remove some of the finest sand particles and deposit them elsewhere, but also causes the sediment to settle and become more compact and harder.

In situ measurements of the compressibility of submarine sediments has only been undertaken within the past 10 years or so, and these have been made in geological and marine engineering studies. It seems that there is no information of this factor with specific regard to infaunal content, although some workers have investigated the hardness of undisturbed intertidal sand. Perkins (1958) demonstrated a tidal, and also probably a seasonal, cycle of hardness in intertidal sand. He used a penetrometer, described by Chapman (1949), which measured in g./cm.^{2} the weight necessary to cause a 3 cm. penetration of a disc of known cross-sectional area into the substrate. Chapman and Newell (1947) also showed that the thixotropic properties of sand, which depend upon water content, are important for the burrowing polychaete *Arenicola marina* L. Wieser (1959) remarked that sands with different grain-size and shape are of different hardness, which will affect the number and distribution of organisms.

Enequist (1949), in his study of the soft-bottom amphipods of the Skagerak, pointed out the probable ecological importance of firmness of bottom sediments and he cited Ekman (1947) as attempting measurements of this. The technique adopted by Ekman, however, involved the disturbance of the bottom material before measurements were made, and they are therefore of limited value.

It is suggested that *in situ* compressibility measurements, over such a period of time as would give adequate knowledge of the degree of change of bottom conditions in different areas, are necessary in order to help establish clearly the substrate preferences of burrowing crustaceans and other organisms in the field. The present paper should be considered a pilot study in this respect, and future work might benefit from using a method similar to that which has been described. The hardness-testing device is quite convenient to use underwater and it avoids the need for the operator to force the rod into the bottom sediment, a characteristic of such a penetrometer as described by Carruthers (1954) which makes its handling by divers difficult, particularly when water movements are present.

Some information on the substrate preferences of other amphipod species can be gained from the data in Table I. *Paramoera walkeri* (Stebbing) was found only at station 10, in the softest and finest sediment, where 85 per cent by weight of the particles were smaller than 76 μm. *T. kergueleni* was not taken at this station. *Pontogeneiella brevicornis* was found at every station but most individuals and virtually all the smallest juveniles occurred in the finest sands. *Parharpinia rotundifrons* Barnard, also taken at all stations, appears to prefer the coarser and firmer sediments.

The content of organic material in bottom sediments may influence the distribution of burrowing organisms, particularly those which are detrital feeders, and such content could vary appreciably even over such small distances as considered here. There was a high level of phytoplankton in the water during most of the investigations. In view of this and also the method of collecting and separating the sediment samples from the associated amphipods, which could have resulted in the loss of some fine organic material, there is probably little value in analysing the present samples in this respect.

Finally, it may be noted that *Corophium volutator* is influenced in choice of substrate by the presence of a primary film of bacteria on the constituent particles (Meadows, 1964*b*), and Marzolf (1965) has shown that the distribution of *Pontoporeia affinis* Lindström is related to the count of bacteria in the sand, and not depth, particle size or organic matter estimates.

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