FACTORS AFFECTING THE DISTRIBUTION OF THE INTERTIDAL ISOPODS *EURYDICE PULCHRA* LEACH AND *E. AFFINIS* HANSEN IN BRITAIN

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INTRODUCTION

Recent studies on the distribution of *Eurydice pulchra* Leach and *E. affinis* Hansen around the British coasts (Jones & Naylor 1967) have revealed that the latter species is restricted to the Bristol Channel area and, where these species occur together, they are seldom found in comparable densities. Salvat (1966, 1967) has shown some differences in the distribution of these species at Arcachon, south-west France, noting that *E. affinis* appeared to prefer semi-sheltered beaches, whilst *E. pulchra* occurred over a wide range of beaches, as is to some extent seen in Britain (Jones & Naylor 1967). Salvat also showed that the two species have different patterns of vertical zonation at Arcachon, but such differences have not been observed in British populations.

In view of the reported differences in the relative distribution of these species, both from beach to beach and on the same beach, detailed investigations have been carried out in Britain with a view to elucidating the factors controlling their distribution. Two beaches in South Wales, at Rotherslade and Oxwich near Swansea, were chosen for these studies, as preliminary sampling revealed wide and consistent differences in population densities of the two species on these beaches. The physical conditions of each beach have been measured, including factors such as sand grain size, salinity, oxygen content and exposure, and these have been related to the distribution and densities of the animals collected in quantitative samples over a period of 2 years. Experimental work on the behaviour of these isopods is also considered in conjunction with the physical factors listed above.

METHODS

Monthly quantitative samples of *Eurydice* were obtained from the sand, and at the water's edge above the sand, at six vertically equidistant stations situated between L.W.S. and H.W.S. on each beach over a period of 2 years. Sand samples were obtained by pressing a 25 × 25 × 15 cm deep square metal box frame into the sand at each station and sieving all the sand removed from the frame through 0·5 mm mesh netting, preserving all the animals retained. Plankton samples were taken over each station in approximately 0·5 m of water on both flood and ebb tides by towing a Colman & Segrove surf net for a standard 25 m distance across the beach. This apparatus was originally designed with two nets placed vertically one above the other sampling 2–8 and 8–16 in. above the sand (Colman & Segrove 1955), but was modified to hold a single net 12 in. high in the present investigations. Temperatures of the sand were taken at all stations sampled by inserting a thermometer to a depth of 5 cm. Salinities were measured using a salinometer and oxygen concentrations in the top 10 cm of sand using an E.I.L. dissolved oxygen meter. Sand

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samples were taken to the laboratory for particle size analysis, and the results of the analysis are expressed in the figures as cumulative percentage curves.

Laboratory experiments on the responses of the animals included substrate choice experiments, and responses to changes in hydrostatic pressure. Analyses of oxygen consumption were also carried out using a constant volume respirometer similar to that described by Davies (1966).

PHYSICAL FACTORS

(a) *Profiles and sand particle size*

Of the two beaches sampled (Fig. 1). Rotherslade faces south-west, and receives the full fetch of the Bristol Channel, but the sampling area at Oxwich faces south-east, thus receiving considerable shelter from Oxwich point. Beach profiles for each sampling area in May 1968 together with the median diameters of sand particles at each station are given in Fig. 2. From that figure it is clear that on the upper shore where *Eurydice* was most abundant, the sand was much coarser at Rotherslade (median diameter 375 μ) than at Oxwich (median diameter 250 μ). This difference, together with the steeper slope of the beach at Rotherslade confirms the greater exposure to wave action of that beach, since slope and particle size tend to increase in areas of greater wave action (Shepard 1950; Trask & Johnston 1955). Changes in profiles of these beaches were noted over the 2-year period of study and these appear to be typical of other sandy beaches (McIntyre & Eleftheriou 1968) in that deposition occurred on the upper part of the shore during calm weather, and storms resulted in destructive wave action which tended to flatten the profiles. On several occasions up to 30 cm depth of sand was removed from the H.W.N. region of Rotherslade by a single tide during autumn equinoctial gales.

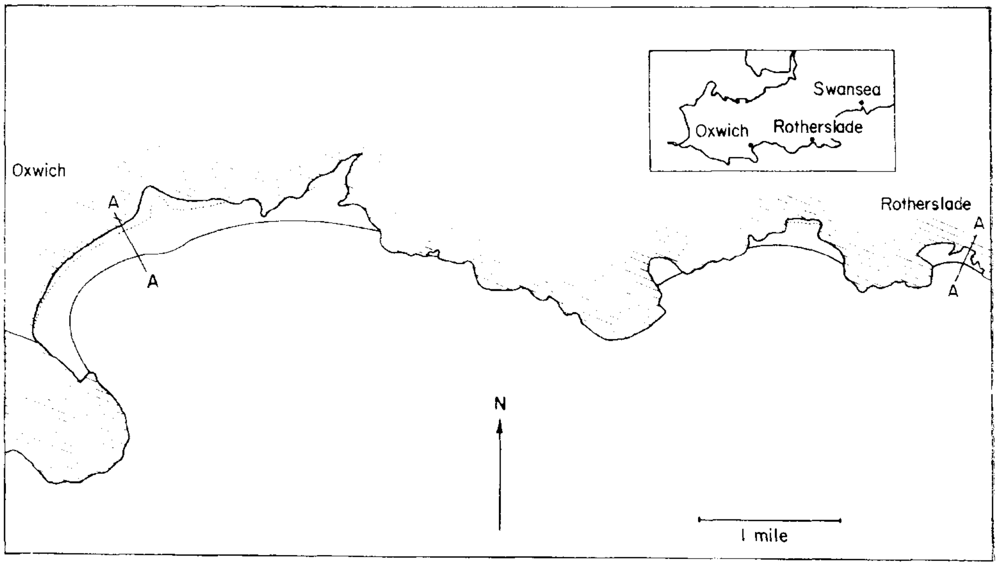

FIG. 1. Map showing position of Rotherslade and Oxwich (see insert) and sampling positions on these beaches (A–A).

(b) *Salinity*

The salinity of the intertidal sea water remained fairly uniform throughout the year, falling only slightly over the winter months (Fig. 3b). The range of sea water salinities was similar on the two beaches as were interstitial water salinities measured at each station on both beaches (Fig. 3c), which were chosen so as to avoid fresh water run-off.

(c) *Temperature*

Monthly sea and sand temperatures taken on the occasion of each sample are given for 1966 in Fig. 3(a). The sand temperatures were taken at 5 cm depth at the levels of H.W.N.T. and L.W.N.T., at the time of low tide. Sand temperatures were always taken on those low tides which occurred during the early afternoon, and are the average of 2-monthly readings taken on each beach. These monthly temperatures did not vary significantly from beach to beach over the period studied.

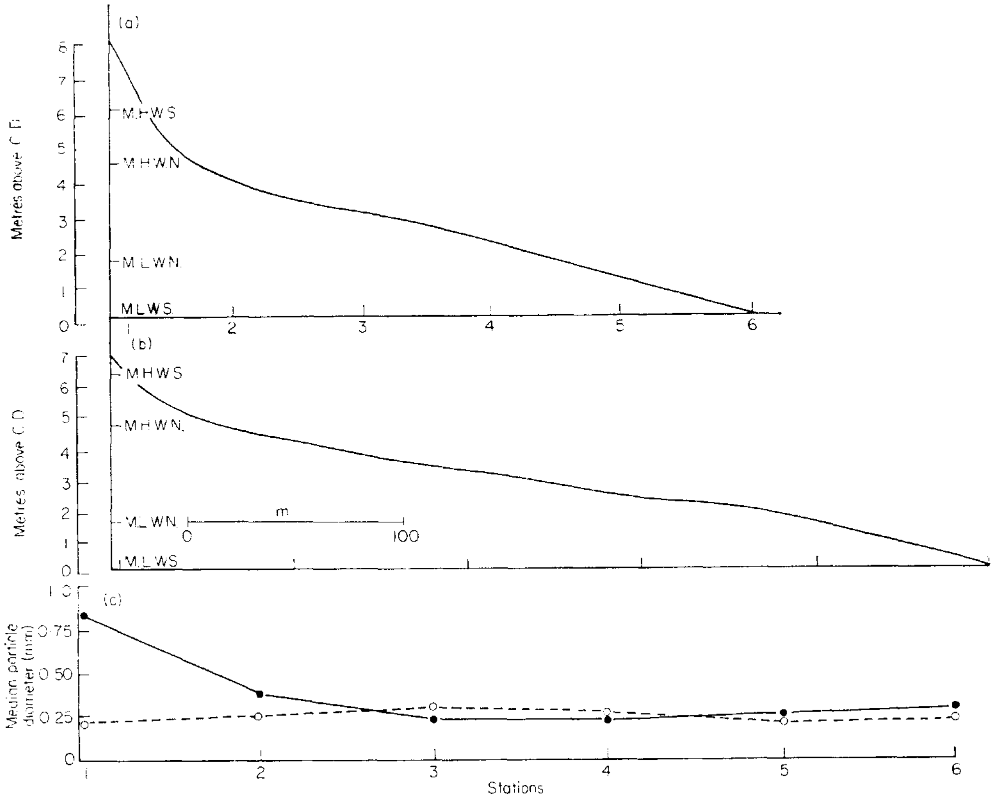

FIG. 2. Beach profiles of (a) Rotherslade, (b) Oxwich, showing sampling stations, and (c) median sand particle diameters at each station. ●, Rotherslade; ○, Oxwich.

(d) *Oxygen concentrations*

Fig. 3(c) gives values for the percentage saturation of oxygen at all stations on both beaches at a depth of 5 cm during May 1968 at the time of low tide. At Rotherslade the percentage oxygen saturation of the interstitial water at this depth fell significantly below 100% only at Station 6 whilst, at Oxwich, stations 4, 5 and 6 were all below 100%. These results are in agreement with Brafield (1965) and Jansson (1967a, 1968), who show that oxygen tensions are related to sand grain size and beach drainage, beaches containing a low percentage of 250–125 μ sized sand particles having a high oxygen content. Thus the region of Oxwich beach below M.T.L. which contained a high proportion of fine sand and which was poorly drained, contained less oxygen than the other regions of the beach. However, both beaches showed readings in excess of 100% oxygen saturation at station 2, the zone of maximum abundance of both species of *Eurydice*, where median particle diameters averaged 250–375 μ.

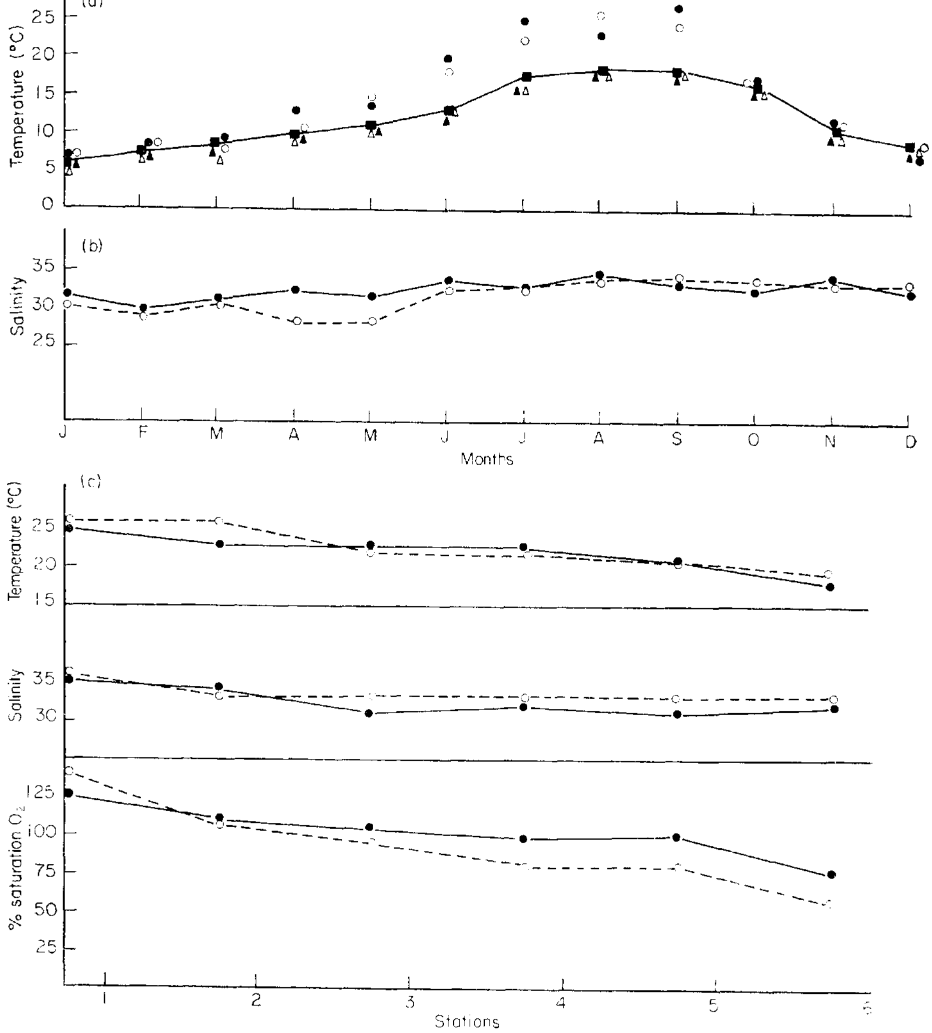

FIG. 3. (a) Monthly temperatures for 1966: ■, sea; ●, Rotherslade sand at H.T.; ▲, Rotherslade sand at L.T.; ○, Oxwich sand at H.T.; △, Oxwich sand at L.T. (b) Monthly salinities of sea water measured at H.T.: ●, Rotherslade; ○, Oxwich. (c) Sand temperatures, salinities and percentage saturation of oxygen of interstitial water at each station in June 1968: ●, Rotherslade; ○, Oxwich.

DISTRIBUTION OF *EURYDICE*

The relative abundances of both *E. pulchra* and *E. affinis* on beaches in the south and west of Britain (Jones & Naylor 1967) are given in Table 1. Sand samples were taken from the M.T. region on all these beaches and analysed for order of median particle size in the Table. On the two beaches sampled throughout the 2 years the percentage of *E. affinis* in the total *Eurydice* remained fairly constant, forming 60% at Oxwich with an average total density of *Eurydice* of 476/m^2 at the level of maximum abundance and 1·5% at Rotherslade where *E. pulchra* had an average density of 1862/m^2.

Table 1. *Results of sand analyses and quantitative samples of* Eurydice *from beaches in south and west Britain*

Beach	Median particle diameter (μ)	Nos. sieved from sand in approximately 15 min *E. pulchra*	*E. affinis*
Barry	160	3	0
Freshwater East (Pembroke)	165	5	0
Weston super Mare	177	24	0
Pendine	180	140	0
Looe	185	0	–
Margam	192	65	130
Borth	195	27	0
Burry Port	196	70	5
Oxwich (West)	200	45	5
Newgate	210	40	290
Minehead	220	35	21
Penzance	220	2	–
Fairlight cove	220	0	–
Newquay	225	40	45
Porthcawl	230	33	10
Rhossili	230	28	35
Bude	230	21	61
Ilfracombe	235	32	36
Oxwich (East)	250	125	240
Freshwater West (Pembroke)	255	650	1
Kennack sands	297	28	–
Treyarron Bay	300	45	10
Weymouth	320	1	–
St Ives	325	20	0
Bournemouth	325	35	–
Rotherslade	375	350	5
Par Sands	380	28	–
Perran Sands	380	285	0
Cuckhaven	565	17	–
Whitsand Bay (Plymouth)	670	225	–
Porthgain	1075	51	–

–, Outside geographical range; 0, absent.

Salvat (1966) working on French populations of *Eurydice* has shown that whilst *E. pulchra* and *E. affinis* may be found at any level of the beach, they form distinct zones of abundance. *E. pulchra* reaching a peak between M.T.L. and H.W.N. and *E. affinis* slightly higher with maximum densities at H.W.N. The quantitative sand samples taken at monthly intervals at Oxwich and Rotherslade (Fig. 4a and b) also indicate that *Eurydice* were most common on the upper part of the shore, but the zone of greatest abundance of *E. pulchra* coincided with that of *E. affinis*. The abundance of *Eurydice* at this level,

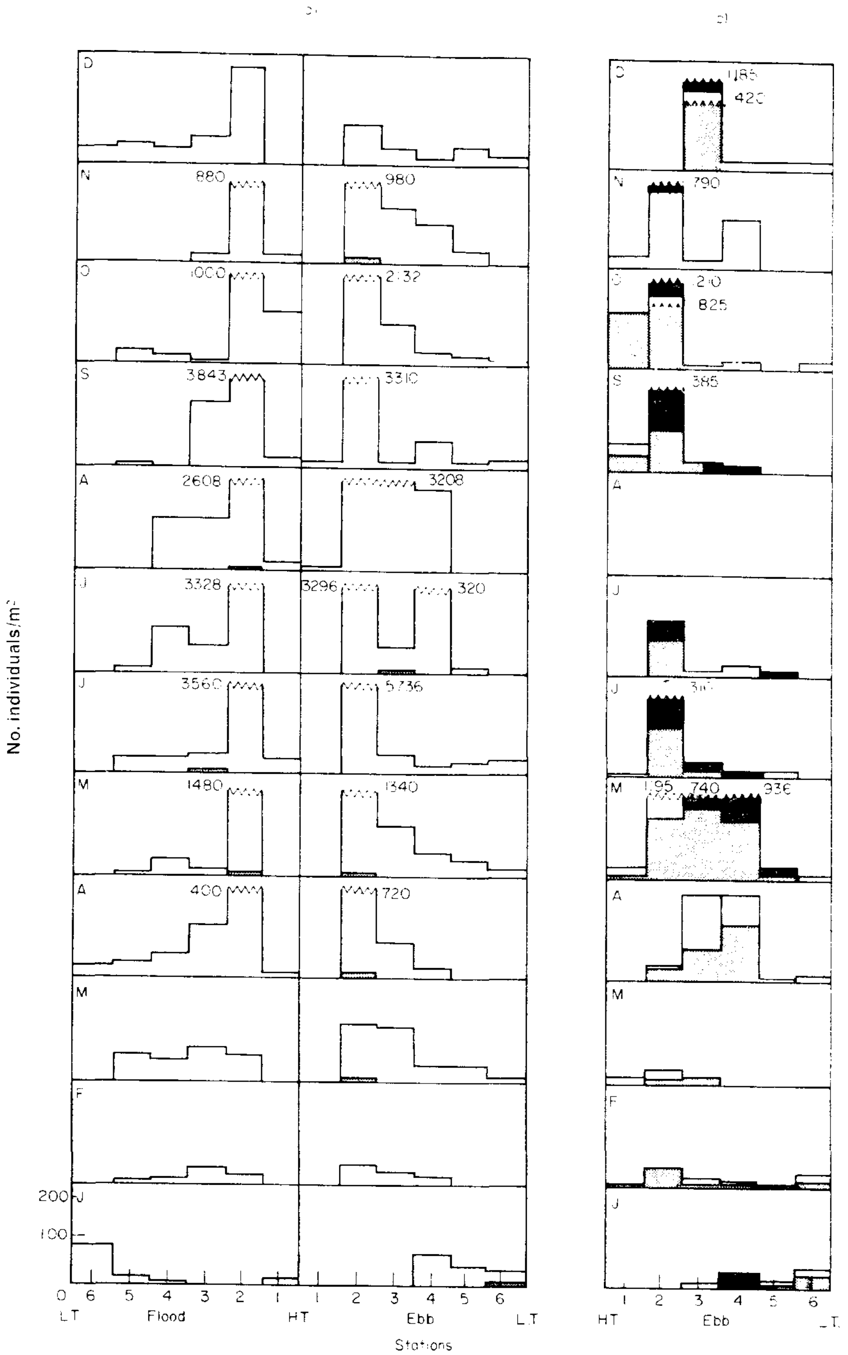

FIG. 4. Numbers of *Eurydice*/m² sieved from the sand at each station during 1966. (a) Rotherslade, samples taken on the flood and ebb tides in consecutive days. (b) Oxwich, samples taken on ebb tides. Open columns, *E. pulchra*; closed columns, *E. affinis*; stippled columns, both species.

apart from the winter months, has been reported by other authors (Brady 1943; Colman & Segrove 1955; Elmhirst 1932; Holme 1959; Lagardère 1966; Perkins 1956; Pirrie, Bruce & Moore 1932; Rees 1939; Scott 1960; Soika 1955; Watkin 1942). The only exceptions are Southward (1953) who reports maximum abundance of *E. pulchra* at M.L.W.N. at Derbyhaven, Isle of Man, stating however that this may be due to absence of silt at this level, and Crawford (1937) who found *Eurydice* in greater abundance below M.T.L. at Plymouth. Present investigations showed peak abundances of both species on the lower shore during January and February, in agreement with Elmhirst (1932) who reported a downshore migration during the winter for *E. pulchra*.

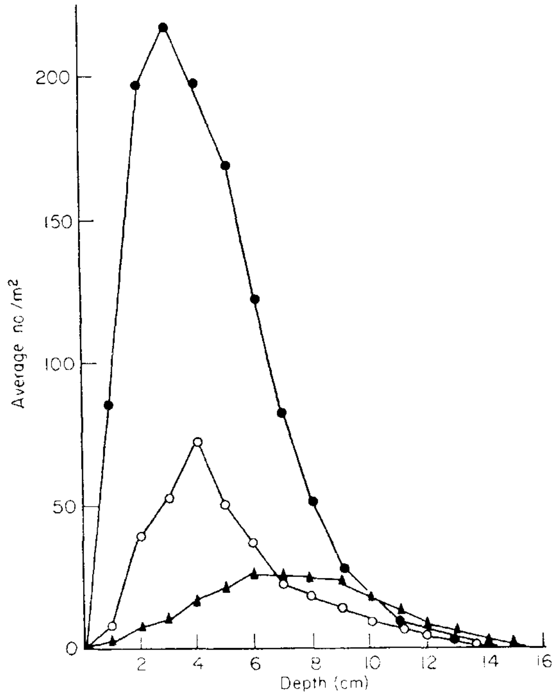

FIG. 5. Depth distribution of *Eurydice* in the sand; samples taken at station 2 at time of L.T. ●, *E. pulchra*; ▲, *E. pulchra* ovigerous females; ○, *E. affinis*.

The restriction of *Eurydice* to the top 20 cm of sand during their inactive phase has been observed by Watkin (1942) and Salvat (1966). Present studies using many samples from various depths indicate that the optimum depth for non-breeding populations of both species lies between 2 and 8 cm (Fig. 5), whilst *E. pulchra* ovigerous females burrowed to an optimum of 6–10 cm.

EXPERIMENTAL WORK

From the field work described above it appears that *Eurydice* populations show characteristic patterns of distribution both from beach to beach and on the same beach, and further that both species show a depth zonation during their inactive phase. In an attempt to explain these distributional patterns a series of experimental studies were conducted with both species in the laboratory.

(a) *Substrate choice*

In view of the differences in median particle size between the two beaches at the zones of maximal abundance of the two species (Station 2), it was decided to investigate whether the species were selective of particle size. For these experiments both graded glass beads and sand were used, the grades falling within the natural range of beach sands. All substrates were dried in an oven at 60° C for 12 h before use to eliminate any naturally occurring organisms which may have been adhering to the sand grains, and then re-wetted and placed in crystallizing dishes. In multichoice experiments these dishes were placed at equal intervals inside the perimeter of a large circular tank in a dark room. Small and large grade sizes were placed in alternate dishes and the tank was filled with sea water. In some experiments two dishes containing the differing grades of sand were placed at each end of a rectangular tank, and in all experiments a dim red light illuminated the tanks from above. Animals collected from Oxwich were introduced into the vessels which were then left undisturbed for a period of 6 h, after which time the dishes were removed and the substrates sieved to remove any buried animals. Preliminary experiments showed that for any one species, animals of different sizes showed no significant preference for different particle sizes, but nevertheless animals of similar size were used in each experiment. Neither species exhibited any preference between washed beads and sand where these were used together.

Table 2. *Multichoice experiment in which eighty-three specimens of both species were given five choices of bead size* (χ^2 *test to compare each of these distributions with random occurrence gives* $P<0{\cdot}2$ *for* Eurydice affinis *and* $P<0{\cdot}01$ *for* E. pulchra)

Grade size (beads) (μ)	*E. pulchra*	*E. affinis*
31	0	9
79	9	11
157	21	20
315	15	12
444	25	14

Table 3. *Multichoice experiment in which eighty-two specimens of both species were given three choices of bead size* (χ^2 *test to compare each of these distributions with random gives* $P<0{\cdot}01$ *for* Eurydice affinis *and* $P<0{\cdot}001$ *for* E. pulchra)

Grades (μ)	Average	*E. pulchra*	*E. affinis*
10–210	(157)	12	28
295–590	(444)	20	11
500–1000	(750)	40	14

The results of a multichoice experiment in which eighty-three specimens of each species were given five choices of bead size are presented in Table 2. Both species appear to show some choice, tending to avoid very fine grades and *E. pulchra*, in particular seeming to prefer coarse particle size. In a second series of multichoice experiments with an extended range of grades (Table 3) *E. affinis* showed a significant tendency to occupy finer grades than *E. pulchra* which again preferred coarse grades.

Two-choice experiments. In these experiments animals were offered a choice between five pairs of grades within the size range found on the beach (Table 4). In four out of the five tests with *E. pulchra* greater numbers burrowed into one grade than the other and in all four the coarser grade was preferred. In two out of these four tests the differences were highly significant at the 0·1% level. With *E. affinis*, in only two out of the five experiments were there much larger numbers in one of the pairs of grades offered, and in neither of these were the differences in numbers significantly different at the 5% level. However, where differences occurred, *E. affinis* burrowed most abundantly in the finer of the pairs of grades offered.

Table 4. *Two choice experiment in which equal numbers of both species were offered a choice between two grades of bead size (significantly different from random at the* 0·1% *level)*

Grades (μ)	Average	*E. pulchra*	*E. affinis*	Totals used	Significance level *E. pulchra*	 *E. affinis*
10–53	(31)	10	14	60	$P<0{\cdot}001$	$0{\cdot}2>P>0{\cdot}1$
149–250	(200)	34	6			
149–250	(200)	17	22	60	$0{\cdot}2>P>0{\cdot}1$	$P<0{\cdot}97$
297–590	(444)	27	23			
297–590	(444)	13	19	65	$P<0{\cdot}001$	$P<0{\cdot}99$
500–710	(665)	43	18			
500–710	(665)	26	20	54	$P<0{\cdot}99$	$0{\cdot}05>P>0{\cdot}02$
710–1000	(855)	25	11			
710–1000	(855)	12	14	60	$0{\cdot}2>P>0{\cdot}1$	$P<0{\cdot}99$
1000–4000	(2000)	21	12			

Table 5. *Results of experiment in which* 200 *specimens of both species were offered a choice between sand taken from a similar level (Station* 2) *on both Oxwich and Rotherslade beaches*

Species	Oxwich sand (235 μ)	Rotherslade sand (380 μ)	Significance
Eurydice affinis	119	50	$P<0{\cdot}001$
E. pulchra	69	103	$P<0{\cdot}01$

Table 6. *Results of an experiment designed to test the effect of different grade sizes upon the speed of burrowing and depth reached by* Eurydice pulchra

Grades (μ)	Depth attained (cm) and time taken 15 min	 30 min	 75 min	 3 h	 16 h
530	2·5	4·0	6·0	9·0	11·0
330	2·0	3·5	5·0	8·0	8·5
237	3·5	3·5	4·25	4·5	6·0
157	1·5	2·5	2·5	2·75	3·0
79	0·15	0·5	0·5	1·0	1·0
31	0	0	0	0	0

In other two-choice experiments samples of sand were taken from Station 2 at Rotherslade and Oxwich, oven-dried for particle size analysis (380 μ and 235 μ) before rewetting, and then offered as a choice to 200 specimens of each species (Table 5). Here a highly significant choice was evident in *E. affinis* for Oxwich sand and in *E. pulchra* for Rotherslade sand.

Finally the effect of different size grades of sand on burrowing was tested (Table 6), when it was found that the depth burrowed by *E. pulchra* was related to the particle size of the substrate, with the animals burrowing deepest in coarse grades.

These experiments clearly show the ability of both species to select between the sand samples taken from Oxwich and Rotherslade. Taken in conjunction with the results of the choice experiments, there is some indication that they have preferences, *E. affinis* for fine grades and *E. pulchra* for coarse grades, which may be an important factor in determining their zonation and relative geographical distributions. Further confirmatory evidence is presented on Table 1, where *E. affinis* is shown to be restricted to beaches of median particle size ranging from 192 to 375 μ and occurred abundantly within the range

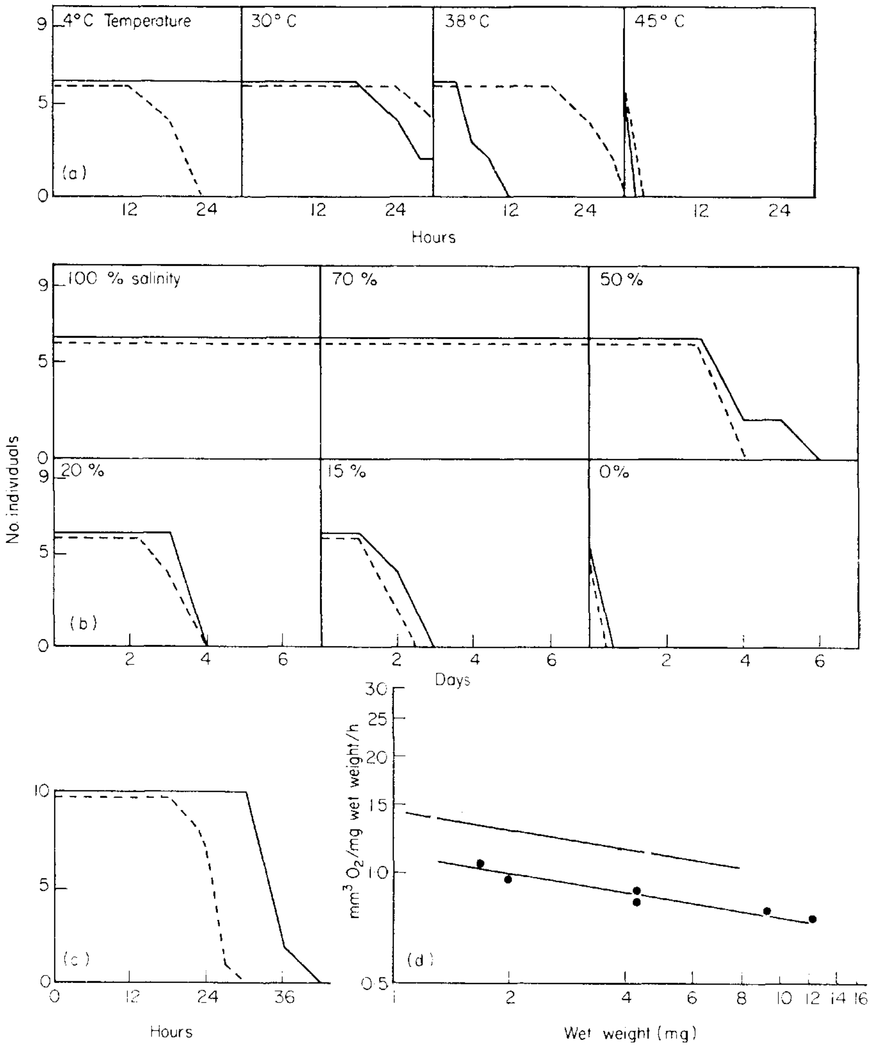

FIG. 6. (a) Survival rates at various temperatures of *Eurydice pulchra* (——) and *E. affinis* (----). (b) Survival rates at various salinities of *E. pulchra* and *E. affinis*. (c) Survival rates in sealed tubes of *E. pulchra* and *E. affinis*. (d) Oxygen consumption rates of *Eurydice* at various sizes with fitted regression lines. ●, *E. pulchra*; ○, *E. affinis*.

of 200–250 μ. *E. pulchra* was found on beaches sampled over a range of 160–1075 μ, occurring abundantly over a range of 250–670 μ.

(b) *Temperature, salinity and oxygen requirements*

Fig. 6(a) shows the survival times of the two species in sea water over a range of temperatures. The animals employed in this experiment included males, females and juveniles of each species, and the sea water was aerated at all times. Particularly striking is the poorer survival of *E. affinis*, compared to *E. pulchra* at 4° C and the better survival of *E. affinis* at 38° C. These results are of interest in view of the fact that *E. affinis* has a more southerly range than *E. pulchra* and reaches the northern limit of its range in south-west Britain.

From salinity tolerance experiments conducted with males of both species (Fig. 6b) it appears that both are to some extent euryhaline, each tolerating up to 50‰ S.W. for up to 5 days. No differences in survival rates were observed when using small specimens and ovigerous females.

The relative oxygen requirements of *E. pulchra* and *E. affinis* were investigated in two ways. Initially specimens of a similar size of both species were placed in sealed tubes and survival rates were noted (Fig. 6c). Secondly (Fig. 6d) oxygen consumption rates of both species were measured when buried in glass beads in a respirometer. Oxygen consumption rates were measured in animals of different sizes and are expressed as double logarithmic plots on the graph (Fig. 6d), each point representing the average hourly rate measured over 18 h for each animal. Oxygen consumption is related here to weight rather than length^2 (see Bertalanffy & Krywienczyk 1951), as the former could be determined far more accurately for small individuals. The results (Fig. 6c and d) indicate that *E. affinis* possesses a higher respiratory rate per gram weight than *E. pulchra* under similar conditions and that in both species oxygen uptake per unit time is proportional to between 0·6 and 0·8 of the weight as is seen in other crustacea (Wolvekamp & Waterman 1960).

(c) *Wave action*

Whilst wave action operates indirectly upon these isopods during their inactive phase through its control of particle size and beach oxygenation, it will also have a direct effect upon them during their active phase. This active feeding phase is initiated as the rising tide reaches the sand in which the isopods are buried (Elmhirst 1932; Watkin 1942; Salvat 1966), and is maintained during high tide by an endogenous activity rhythm, the animals reburrowing into the sand on the ebb (Jones & Naylor 1970). When *Eurydice* are brought into the laboratory and placed in aquaria with sand and sea water, they remain in the sand and have only rarely been observed to re-emerge. Experiments involving the addition of sea water at outside temperatures have failed to evoke the swimming response from animals. The only method achieving any success was mechanical stirring of the sand, when both species swam free and began their activity cycles. In the laboratory it was observed that both species, when placed on damp sand, are positively geotropic and negatively phototactic burrowing rapidly downwards. Neither species was observed to burrow upward out of the sand in the laboratory, and it appears that in the field these isopods rely upon wave action to wash them out of the sand on each tide.

In an attempt to confirm that wave action controls the emergence of these isopods, a series of quantitative hauls with a Colman & Segrove net were made on Rotherslade beach as the flood tide covered Station 2. The height of waves, taken from the beach to the crest just before they broke, was measured and the numbers of isopods caught in each haul plotted against average wave height (Fig. 7). This graph shows a direct relationship between the numbers of animals swimming and the height of the waves on any day. The depth of disturbance of sand by a wave is in direct proportion to its height, providing that the slope of the beach and the median particle size of the sand remain constant (King 1959), and the numbers of *Eurydice* washed out varied accordingly.

King (1959) has calculated that for a beach with a Md of 0·25 mm there is an approximate increase of 1 cm depth of disturbance for every 1 ft wave height, and that for a beach with 0·4 mm Md sand the increase is approximately 3 cm depth of disturbance for every 1 ft wave height. The depth of penetration also increases as the beach slope becomes steeper, for the zone in which the wave energy is dissipated becomes relatively narrower. If the depth of wave penetration between the tidemarks is plotted for Rotherslade (Fig. 8), it shows a sharp increase towards high tide mark where the gradient is steepest and particle size largest.

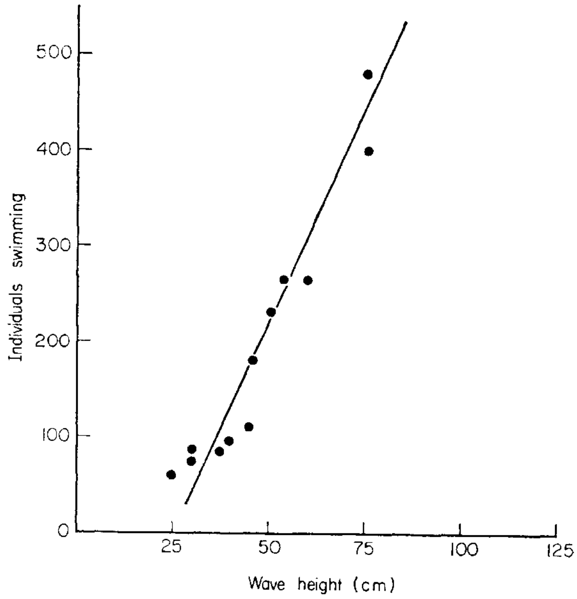

FIG. 7. The relationship between the height of waves and the numbers of *Eurydice* swimming in the surf.

Since it has been shown that *Eurydice* swim free from the sand in response to increased wave action, one would clearly expect that in the sand they would concentrate within the range of depth penetration by wave action. Reference to Fig. 5 shows that this is in fact so, for the depth distribution shown by both juvenile and adult *Eurydice* places them within the depth penetration range of average wave action (Fig. 8).

(d) *Depth of burrowing*

The factor or mechanism controlling the depth of burrowing in these isopods is of considerable interest as the mechanisms which initiate burrowing, negative phototropism and positive geotropism, do not in themselves constitute any depth regulatory mechanism. The influence of physical factors which might be considered to exert some control over depth regulation were examined both on the beach and in the laboratory.

During the summer months a clear gradient in temperature is present in the top 20 cm of the beach during daytime when the tide is out (Salvat 1966). However, samples taken during June and July showed the same population depth distribution as those taken in September and October when this temperature gradient was virtually absent. Also laboratory experiments involving heating the sand surface with a lamp failed to induce any change in depth distribution of animals when compared to unheated controls.

The possibility that changes in salinity might regulate burrowing was discarded as there are only minor differences in the salinities in the top 20 cm of sand on the beach (Pirrie *et al.* 1932). A further factor, the degree of saturation of the sand by sea water, varies considerably with the state of the tide. The sand is fully saturated at the time of burrowing but later the water table drops at least 20 cm below the surface at Station 2 on both beaches. This, however, is well below the depth of greatest abundance of *Eurydice* and can also be discounted as a depth regulatory factor. Salvat (1966) also showed that the depth distribution of both species of *Eurydice* was not correlated with the movement of the water table. Finally it is unlikely that interstitial oxygen conditions would affect the depth distribution, for Jansson (1966) has shown that in beaches similar to those considered in the present work there is usually an excess of oxygen available on the top 20 cm of sand, and also that oxygen content does not necessarily follow a gradient from the sand surface downwards.

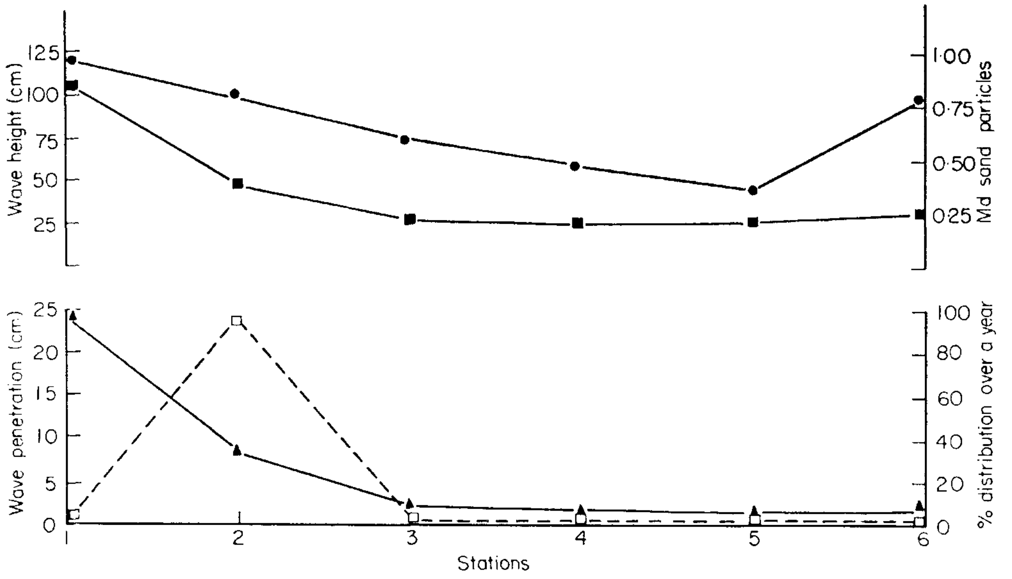

Fig. 8. The relationship between wave height (●), median particle diameter (■) and wave penetration (▲) at Rotherslade. □, Percentage distribution of *Eurydice*.

The effect of different size grades of sand upon burrowing has already been examined (Table 6), when it was found that the depth burrowed by *E. pulchra* was related to the particle size of the substrate, so that animals buried deepest in coarse grades. This could be related to the avoidance of very fine sand by both species, but other factors may also

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be involved. It is possible, for instance, that the animals burrow for a relatively constant length of time on entering sand, thus tending to burrow further into coarser, less densely packed sand.

The former suggestion is certainly supported in experiments when the 31 μ grade sand was offered, since experimental animals made no attempt to burrow in that deposit. The second suggestion seems less likely from evidence in field samples and laboratory experiments. Table 7 shows that different sized *Eurydice* burrow at different rates yet the peak depth reached in the sand contains animals of varying sizes (see Fig. 5). Thus some animals must burrow for longer periods than others, and time cannot be the overriding factor controlling depth distribution.

Table 7. *Results of an experiment devised to examine burrowing speeds and depth distribution of* Eurydice pulchra *of different sizes*

Eurydice pulchra Size (mm) and sex	Depth burrowed (cm) together with time taken			
	10 min	30 min	90 min	120 min
6·0♀	5·0	7·0	10·0	15
6·0♀	4·5	6·0	9·0	14·5
4·5♂	3·0	4·0	6·0	15
4·25♀	3·25	4·5	7·0	15
3·0	2·0	3·0	5·0	14·8

Table 8. *Results of an experiment in which burrowing* Eurydice pulchra *were subjected to different hydrostatic pressures*

Sand depth (cm)	Water height above sand (cm)			
	0	5	10	20
1	7	35	35	68
2	27	49	80	43
3	31	41	11	14
4	16	4	3	7
5	8	10	14	6
6	8	5	0	2
7	6	1	0	2
8	6	1	6	5
9	3	3	0	1
10	0	5	0	1
11	6	5	0	0
12	0	0	0	0
13	1	0	0	0
14	2	0	0	0
15	1	0	0	0
16	0	0	0	0
17	0	0	0	0
18	0	0	0	0
19	0	0	0	0
20	0	0	0	0
Totals	149	149	149	149

Contingency table test shows that the difference between 5, 10 and 20 cm columns is on $P < 0{\cdot}01$ level.

Another factor which may influence the depth of burrowing is that of rising pressure with increased depth. Table 8 shows the results of an experiment in which animals were subjected to pressure differences by being allowed to burrow in sand under water columns of various heights. The results obtained in the Table were tested for significance using a contingency table method assuming a null hypothesis that there was no association between depth burrowed and water height. There was a significant difference at the 1% level between the control column and 5, 10 and 20 cm columns of water, and also between the 5 and 10 cm columns, thus a marked correlation exists between depth burrowed and height of water above the sand.

DISCUSSION

Consideration of the effects of the physical environmental factors prevailing at Rotherslade and Oxwich have shown that most appear to have little influence on the distribution of *Eurydice pulchra* and *E. affinis*, both from beach to beach and on the same beach. Sea water salinities did not vary significantly on either beach and both species were shown experimentally to have similar tolerances to salinity fluctuations. Salvat (1966) further demonstrated that both species fell in numbers at the same rate where a fresh water stream crossed the beach.

Whilst there does appear to be some differential in survival rates to extreme temperatures (Fig. 6a), this would have little effect on the local distribution of these species in Britain. Both species undergo migrations into the sublittoral during winter escaping extreme temperatures, a factor perhaps responsible for their high survival rate after the severe winter of 1962–63 (Crisp *et al.* 1964). At Arcachon the sand temperatures reach 40° C in the summer months (Salvat 1966) and it is suggested by this author that temperature is the main factor responsible for the separate zonation of *E. affinis* and *E. pulchra* in these latitudes. Present temperature tolerance experiments (Fig. 6a) would appear to confirm this view since *E. pulchra*, the species occupying the lower shore in France, was unable to survive temperatures of 40° C for more than a few hours.

In Britain sand temperatures rarely exceed 25° C (Fig. 3a) and both species occupy the same zone. The overall geographical range of *E. affinis* is however undoubtedly affected by temperature (Jones & Naylor 1967), the northward spread of this species probably being limited by the restrictive effect of the low average summer temperatures upon the breeding period.

Respiration rates are high in comparison with some other isopods (Wieser 1962), although values may not be excessive when the small size and high activity rate are taken into consideration. It is clear that the respiration rate of *E. affinis* is generally higher than that of *E. pulchra*, but since both beaches studied were well oxygenated except at L.W., oxygenation probably has little influence on the distribution of these species. When considering distribution over a wide range of beaches (Table 1) the absence of *E. affinis* from beaches of fine sand (160–185 μ), where *E. pulchra* was present despite its preference for coarser grades may be related to oxygenation.

Thus sand particle size remains as the major factor determining the relative distribution of these isopods both between Oxwich and Rotherslade and on the same beach where these species occur together, *E. affinis* exhibiting some preference for fine grades and *E. pulchra* a marked preference for coarse grades. Particle size is in turn related to overall exposure and wave action experienced on the shore (King 1959). Thus though both species may occur on a wide range of shores *E. pulchra* is characteristic of exposed shores and *E. affinis* of semi-exposed beaches, particularly in geographical areas where they occur together. Recent work in the Aegean (Jones 1969) has shown that the distribution of other intertidal members of the genus may also be correlated with beach exposure in a similar manner.

It has already been shown that factors such as salinity and oxygen levels do not vary sufficiently to account for the marked zonation seen in both species between the tide marks. Nor does there appear to be a critical immersion or emersion time, for both have survived continuous immersion in the laboratory for over 2 years. On both beaches studied in present work, maximum abundance of both species was centred around M.T.L.–H.W.N., part of the zone of intense wave action which extends up to H.W.S. (Fig. 8). Burrowing is however usually impractical above H.W.N. for these species as the beach is often pebbly and the length of exposure between spring tides provides a physical barrier (Salvat 1966). Thus the area from M.T.L. to H.W.N., which offers few other advantages to these isopods during their inactive buried phase, provides the coarsest particle sizes on the beach available to these animals into which they burrow deepest. Moreover it is subject to intense wave action during flood tides, releasing maximum numbers of animals from the sand into the tidal waters which will contain an abundant food supply in the form of flotsam and jetsam at H.T. It is suggested that it is for this main reason that *Eurydice* reaches its highest densities at this level of the beach, forming such distinct zonation patterns.

Table 9. *Total numbers of tidal plankton organisms in comparable* 25 *m hauls with a* 1 *mm mesh net in June–August at Oxwich and Rotherslade*

	Rotherslade	Oxwich
Chaetognatha	5	–
Ctenophora	63	–
Amphipoda	250 (eight species)	398 (ten species)
Isopoda (excluding *Eurydice*)	47 (three species)	44 (four species)
Decapoda (Brachyura)	11 adult (two species)	16 adult 297 (megalopa) (two species)
Caridea	151 young 2 adult (two species)	470 young 28 adult (two species)
Mysidacea	326 (four species)	1903 (six species)
Cumacea	–	14 (two species)
Young fish larvae	142 (one species)	88 (five species)
Medusae	4 (one species)	169 (two species)

E. pulchra has been shown to be pressure sensitive, responding to pressures equivalent to 50 cm of water by upward swimming (Knight-Jones & Morgan 1966; Knight-Jones & Qasim 1967; Singarajah 1966), and it appears from Table 8 that pressure may also be concerned in the depth distribution of this species in sand. Whilst the pressures experienced at the optimal depth distributional zone in the sand are equivalent to 18–27 cm of water, somewhat lower than previous minimal pressures eliciting a swimming response, it does not seem unreasonable to suggest that depth zonation in sand may be controlled by a similar pressure mechanism to that controlling upward swimming in water. This mechanism would thus control the depth of burrowing by the animals enabling them to remain within the depth of penetration by waves.

Actual population densities are discussed in relation to reproductive capacities of both species elsewhere (Jones, unpublished) where it was concluded that factors such as relative egg production and length of breeding period, did not fully explain the observed densities of these isopods in the sand at Oxwich and Rotherslade. At Oxwich during

June–August 1966–67 the average densities of total *Eurydice* populations were $510/m^2$, whilst at Rotherslade a density of $4000/m^2$ was recorded for the same period. Thus markedly fewer *Eurydice* occurred at Oxwich despite the fact that tidal plankton, an important part of the food supply (Jones 1968), was more abundant at Oxwich at this time (Table 9).

It is suggested therefore that the larger population densities of *Eurydice* observed at Rotherslade may be related to the greater amount of wave action received by this beach. Perhaps it ensures that the isopods are released from the sand more often, enabling them to spend a proportionately greater time feeding on surf plankton. This is emphasized by reference to Fig. 8, which shows that waves of 50 cm height release twice the number of animals compared with waves of half this height.

The importance of exposure and wave action in regulating both distribution and population densities of *Eurydice* is borne out by a comparison of the abundance of these animals sampled on a series of beaches of ranging exposure and median particle size (Table 1). Beaches such as Freshwater West and Whitsand Bay, Plymouth, like Rotherslade, also receive heavy wave action and support large populations of *Eurydice*. Slightly reduced wave action resulting in shortened available feeding times, perhaps explains why *E. affinis* is able to compete so successfully with *E. pulchra* on semi-exposed beaches in Britain (Table 1), the former species perhaps being able to satisfy its feeding requirements more quickly due to its smaller size (Jones & Naylor 1967).

SUMMARY

Habitat preference studies on *Eurydice pulchra* and *E. affinis* in south Wales suggest that sand particle size is of primary importance in determining their relative geographical distribution in areas where these species occur together, *E. pulchra* favouring coarse sand, *E. affinis* fine sand. Both species occur predominately between M.T.L. and H.W.N. on the shore. This zone receives intense wave action and experiments show that the animals rely upon this factor to wash them out of the sand for the commencement of their active feeding phase. They burrow to an optimal depth of about 4 cm in the sand, which is within the depth of disturbance by waves at that level. The depth of burrowing varies experimentally according to the depth of water above them and may be controlled by a pressure response. High densities of *E. pulchra* found on very exposed beaches are not entirely explained by reproductive potentials and may relate to the more frequent feeding times available to them on such wave beaten shores.

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