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Environmental correlates with amphipod distribution in a Scottish sea loch

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Abstract : Over the period 1969 to 1980, 34 stations (both inter and subtidal) were visited in Loch Ewe, a fjordic sea loch on the west coast of Scotland. Amphipod densities were determined along with sediment particle size and levels of organic carbon and chlorophyll *a*. Multivariate analysis of these data indicates that depth and sediment organic carbon levels are the major determinants of amphipod assemblages in the loch, in contrast to previous studies which have variously implicated temperature, sediment granulometry and food availability.

Résumé: Au cours de la période 1969-1980, on a visité 34 stations (intertidales ou subtidales) dans le loch Ewe, bras de mer comparable aux fjords situés sur la côte occidentale de l'Écosse. Les densités d'amphipodes ont été déterminées, ainsi que, comme paramètres sédimentaires, la taille des particules et les teneurs en carbone organique et en chlorophylle *a*. Le traitement de ces données a l'aide de l'analyse factorielle multivariée indique que la profondeur et le contenu en carbonne organique des sédiments constituent les déterminants majeurs des assemblages d'Amphipodes se produisant dans le loch Ewe, ce qui est en désaccord avec les résultats d'études antérieures qui ont impliqué de diverses manières la température, la granulométrie sédimentaire et la disponibilité d'aliments.

INTRODUCTION

The factors which determine the distribution of amphipods, a dominant component of intertidal and shallow subtidal habitats, have been discussed by a number of authors. For example, Enequist (1949) considered that temperature range in a given habitat was important despite earlier indications that temperature *per se* had little effect on species distribution (Reid, 1941).

Later, Toulmond (1964) attempted to classify an intertidal habitat by relating the distribution of dominant species in respect to particle size. Several other studies have also implicated grain-size as an important determinant of amphipod distribution (Barnard, 1969; Fincham, 1969, 1973 ; Parker, 1984). The importance of food availability has been stressed by Buchanan (1963) and Parker (1984) and the role of pollutants in determining distribution has been considered by Bellan Santini (1980) and Anger (1975). To date, however, no clear consensus has been reached regarding the principal determinants of amphipod distribution, although, in general, particle size is most often cited.

In the present paper, amphipod distributions are defined for a sea loch on the west coast of Scotland, and species distributions are considered in relation to a number of environmental parameters.

MATERIALS AND METHODS

The study was conducted at Loch Ewe, Ross-shire, a sea loch situated on the fjordic coatline of the west of Scotland (Fig. 1 (inset)). The data presented here are from 34 intertidal and subtidal stations visited in summer or autumn between 1968 and 1980 (Fig. 1).

Five intertidal sand beaches (see Fig. 1) were sampled using 0.0625 m^2 metal quadrats driven into the substratum to a depth of 15 cm. Sampling sites were established at high, mid and low water with intermediate sites at 15 m intervals for beaches with extensive intertidal areas. In addition to the quadrat sample at each sampling site, two 2.2 cm internal diameter cores were taken for organic carbon and chlorophyll *a* determinations and a single 4.4 cm internal diameter core was taken for particle size analysis. For four of the beaches, data from each sampling site were combined to calculate mean abundance and environmental parameter values for the beach as a whole (stations 27, 28, 33 & 34). The fifth sandy beach was extensive, however, and sampling locations between high and low water were widely spaced ; each was, therefore, treated as a separate station (stations 29 to 32).

All subtidal stations were sampled with a 0.1 m^2 van Veen grab. A single haul was used to estimate amphipod abundance and cores for sediment, organic carbon and chlorophyll a determinations were subsampled from the same haul.

Chlorophyll *a* was analysed using a modification of the fluorimetric method outlined by Strickland and Parsons (1972). Instead of the filter paper used in water analysis, a 2 cm section of sediment was oven dried at 40°C, a subsample 0.1 to 1.0 g dry sediment was then ground in a mortar and the pigments extracted directly from the sediment with 90 % acetone. The fluorimetric assay for chlorophyll *a* was then conducted and results are expressed as µg chlorophyll *a* g^{-1} sediment.

The organic carbon content was determined using an adaptation of the wet oxidation technique described by Strickland and Parsons (1972), where 0.1 to 1.0 g of sediment was analysed instead of the filtrate used in water analysis. Estimation of the organic carbon level was performed by titration with ferrous ammonium sulphate (0.1 N) using dimethylferroin as the indicator. Results are expressed as µg C. g^{-1} sediment.

Particle size analysis was conducted using a combination of dry sieving the sand fraction and pipette analysis of the silt-clay fraction (<63 µm) as described by Holme and McIntyre (1971).The results are presented as sediment median diameters in microns.

In the case of carbon and chlorophyll, only data from the top 2 cm of each core are presented here ; particle size data are presented for the top 4 cm.

Multivariate Analysis

Large data sets, as presented here (Table I), are best analysed by multivariate techniques such as ordination that reveal any underlying trends in the species abundance patterns. The ordination techniques used in the present study are based on correspondence analysis (Hill, 1973, 1974), detrended to remove the arch effect that confounds the interpretation of many

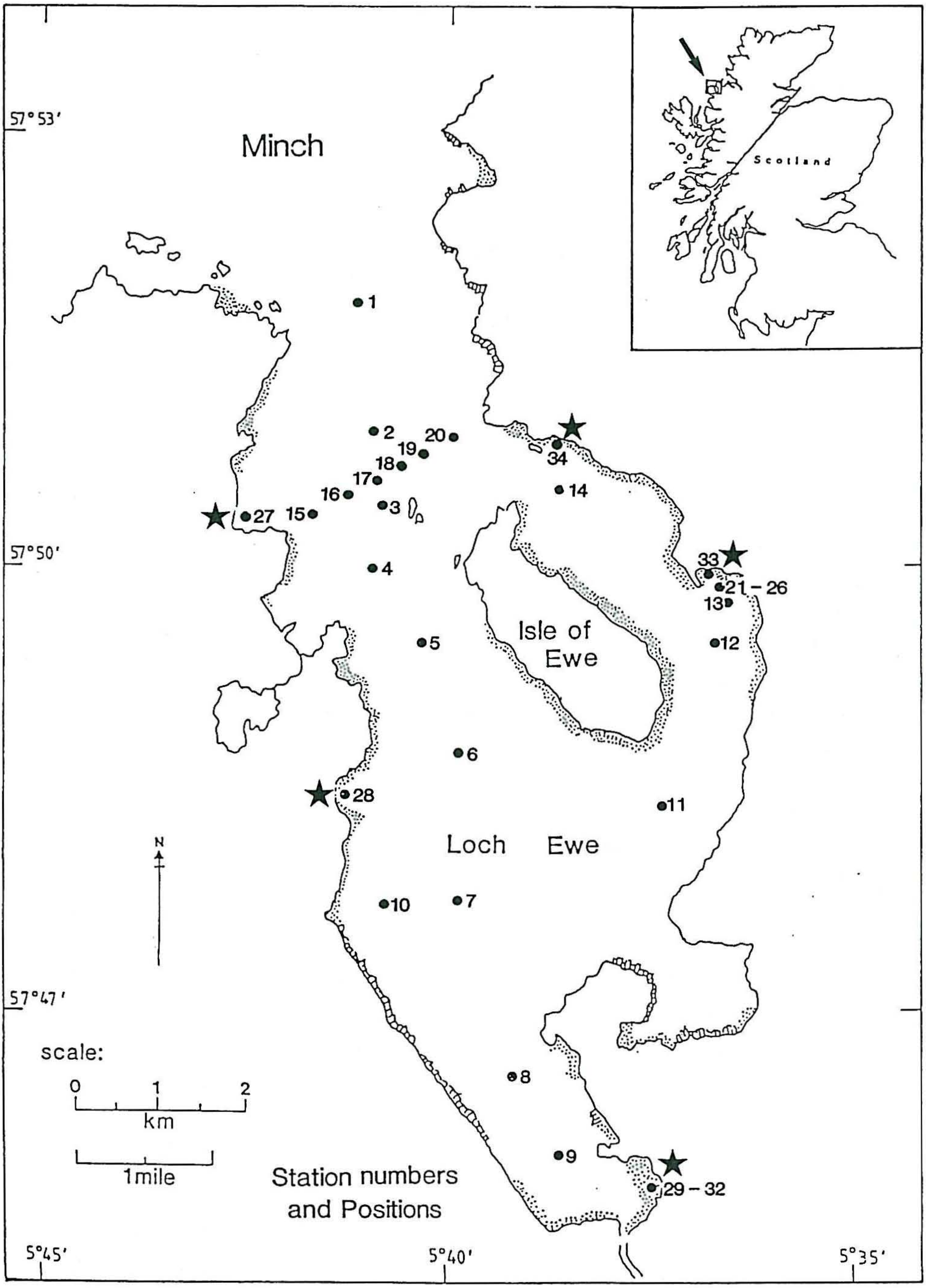

Fig. 1 : Sampling stations within Loch Ewe, Ross-shire, Scotland (★ denotes intertidal sand beach stations). Inset figures : arrow shows geographical location.

TABLE I

Loch Ewe amphipods (nos m^{-2})

		Station number																																	
Species name and authority	Family	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Acidostoma obesum (Bate and Westwood)	Lysianassidae									3										5															
Hippomedon denticulatus (Bate)		3																																	
Lysianassa plumosa Boeck								8																		46	8								
Tryphosella horingi (Boeck)																									3	3									
T. sarsi Bonnier									63																										
Ampelisca brevicornis (Costa)	Ampeliscidae			5	8		3			3	13		3	3	10						10	3	5	6					4					2	
A. diadema (Costa)						13			28											5	5						33								
A. tenuicornis Liljeborg																10	5	30	20	20	25														
A. typica (Bate)			3	5		3			15	10																									
Iphimedia minuta (Sars)	Acanthonotozomatidae																						3				3								
Gitana sarsi Boeck	Amphilochidae			3					20	5																									
Leucothoe lilljeborgi Boeck	Leucothoidae							5				5	3		3		5																		
Stenothoe marina (Bate)	Stenothoidae		3	3			5									1	5																		
Hyale nilssoni (Rathke)	Hyalidae									3																									
H. pontica Rathke																														16					
Gammarus locusta (Linnaeus)	Gammaridae																								3										
Cheirocratus intermedius Sars	Melitidae																								6										
C. sundevallii (Rathke)				3		8			13					3				15						3			3								
Maera othonis (Milne-Edwards)									3								5									8									
Bathyporeia elegans Watkin	Pontoporeiidae	5			23																35	18						30	268						3
B. guilliamsoniana (Bate)																					118		321	20	8						32	48		160	
B. pelagica (Bate)																					8							48	108						7
B. pilosa Lindstrom																					8								92					2	170
Urothoe elegans (Bate)	Urothoidae				5																														
Argissa hamatipes (Norman)	Argissidae				5	5										5																			
Monoculodes carinatus (Bate)	Oedicerotidae								10	3																									
Perioculodes longimanus (Bate and Westwood)					8					3												55	23	58	3				132						
Pontocrates altamarinus (Bate and Westwood)																												7							
Synchelidium haplocheles (Grube)		3	3	3	3	5	3									5			5						16	10	5								
Westwoodilla caecula (Bate)							3																												

		Station number																																	
Species name and authority	Family	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Harpinia antennaria Meinert	Phoxocephalidae			23		5	5							3		5	30			15					3		83								
H. crenulata (Boeck)																										20									
Metaphoxus fultoni (Scott)									43	8													3	3	3	373	11								
Paraphoxus oculatus Sars																									3										
Megaluropus agilis Hoeck	Melphidippidae																				10														
Apherusa bispinosa (Bate)	Calliopiidae			3		5		5	3																	5									
A. jurinei (Milne-Edwards)																								3											
Calliopius laeviusculus (Kroyer)					5																								4						
Atylus falcatus Metzger	Atylidae																																2		2
A. swammerdami (Milne-Edwards)																																	32		2
A. vedlomensis (Bate and Westwood)									10																										
Dexamine spinosa (Montagu)	Dexaminidae																								3										
D. thea Boeck									20	8																8									
Guernea coalita (Norman)		3	5						33																	8									
Sunamphitoe pelagica (Milne-Edwards)	Amphithoidae																								3										
Aora gracilis Kroyer	Aoridae		5							50															48										
Lembos longipes (Liljeborg)		18																																	
Leptocheirus pectinatus (Norman)																										283	18								
Microprotopus maculatus Norman	Isaeidae																					6													
Corophium crassicorne Bruzelius	Corophiidae				3																	182	91	3	51						32	48	112		
Siphonoecetes kroyeranus Bate		3																		30															
Phtisica marina Slabber	Caprellidae						8		20	3															8	6									
Podalirius typicus Kroyer			3						28	3																									

other ordination methods (Hill & Gauch, 1980 ; Greig-Smith, 1983 ; Gauch, 1982). Two complementary analyses were carried out : detrended correspondence analysis and two-way indicator species analysis, using the programmes DECORANA and TWINSPAN (Hill, 1979 a, b).

In detrended correspondence analysis (DECORANA), as in other ordination models, the order of the stations on the ordination axes can be compared with the environmental characteristics of those stations and this may allow identification of the environmental gradients underlying the distribution and abundance of the fauna. Here the associations between axes scores and sediment median diameter, organic carbon and chlorophyll *a* were assessed by Spearman's rank correlations.

Two-way indicator species analysis (TWINSPAN) is also an ordination based method which divides the stations into groups occupying separate parts of the main ordination axis (i.e environmental gradient). It then identifies any species which are good indicators of these groups and hence characteristic of different parts of the gradient. The axis division process is progressively dichotomous and generates a branching tree, superficially similar to that derived by a cluster analysis. However, it must be stressed that two-way indicator species analysis is an ordination method and not a cluster analysis technique.

A full account of the use of these methods for community analysis is given in Greig-Smith (1983) and Gauch (1982).

Basford *et al.* (1989a), Basford *et al.* (1989b) and Eleftheriou & Basford (1989) provide examples of the use of the techniques for marine benthic assemblages.

RESULTS

Environmental Characteristics

Data for environmental parameters in the loch are presented in figures 2a to d. Depth data (Fig. 2a) were obtained from both Admiralty charts and from direct echosounder measurements. Data for the construction of figures 2b to d were obtained from the sampling stations described above and from additional stations visited during the period of study for which environmental, but not faunal data, were available.

Figure 2b shows that the largest part of the floor of the loch consists of fine sand while the finer sediments accumulate in the deeper parts of the loch to the west and to the east of the Isle of Ewe. The coarser sediments occur at the mouth of the loch and in small patches to the west of the main island.

This sediment distribution is consistent with the circulation and exposure pattern of the loch whereby fine sediments are transported from the high energy shallower environments in the periphery of the loch and deposited in the deeper lower energy areas to the south and east of the Isle of Ewe.

In general, organic carbon levels (Fig. 2c) mirror sediment distribution ; the highest levels are recorded in association with fine sediments in the deeper parts of the loch while the lowest levels are generally found in association with coarse sediments at the mouth and along the western shore.

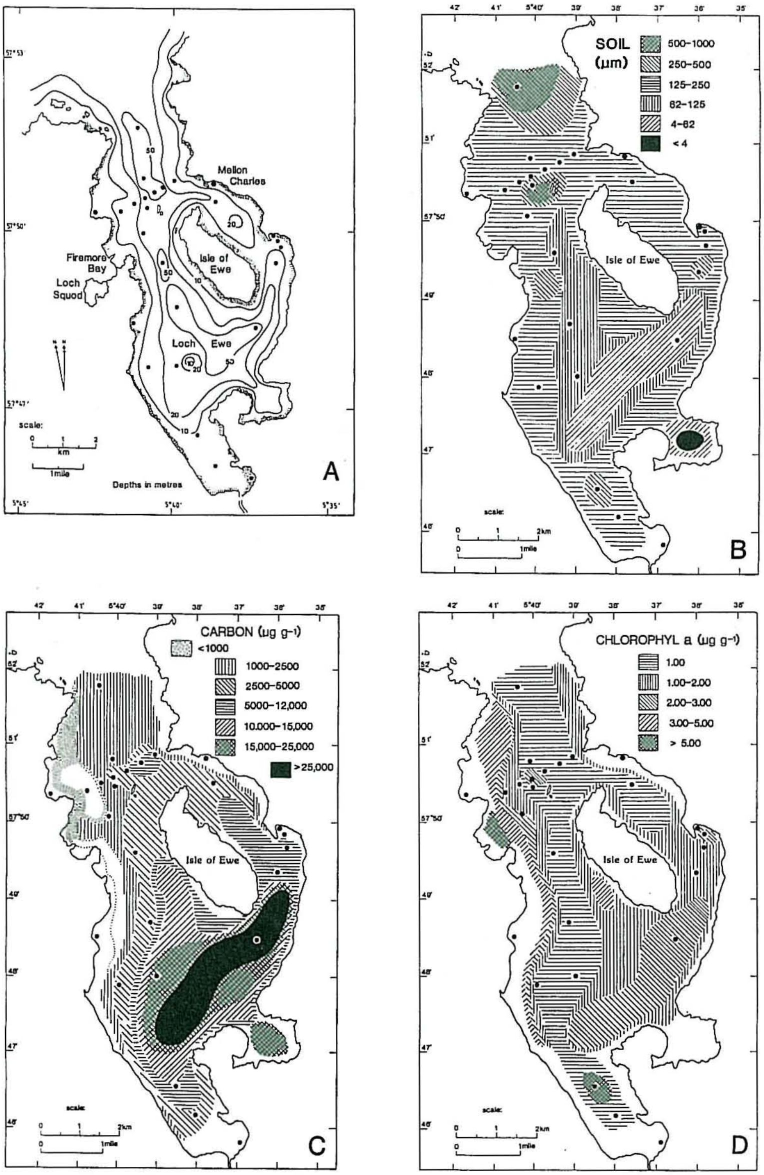

Fig. 2 : A) BATHYMETRY (m)
B) SEDIMENT median diameter (µm)
C) ORGANIC CARBON (µg g^{-1}) content of sediment
D) CHLOROPHYLL *a* (µg g^{-1}) content of sediment

Chlorophyll *a* levels (Fig. 2d) appear to be inversely related to water depth ; the highest levels are found in shallow water especially along the western shore and in other shallow subtidal sand regions. The lowest chlorophyll *a* levels were recorded in the outer part of the loch, and in the main north to south axis in the deep channel to the west of the Isle of Ewe.

The Amphipod Community

A total of 53 amphipod species representing two suborders and 23 families was collected from the Loch Ewe area during this survey (Table I). The Gammaridean suborder was by far the most dominant, represented by 22 families to which Lysianassids, Oedicerotids, Ampeliscids, Pontoporeids and Phoxocephalids contributed most species.

During the present survey, specimens were collected from different sedimentary environments ranging from medium sandy intertidal deposits to fine or very fine sands and silts at depths in excess of 50 metres.

If those strictly intertidal species such as *Bathyporeia pilosa* are excluded, then the faunal asemblages of the sandy areas could be loosely ascribed to the boreal shallow sand/boreal offshore sand association of Jones (1950) where Pontoporeids such as *Bathyporeia pelagica*, *B. elegans* and *B. guilliamsoniana*, Corophiids such as *Corophium crassicorne* and some Oedicerotids such as *Perioculodes longimanus* are the dominant species.

The deeper areas, consisting of a wide range of sediments containing an appreciable amount of silt, had a fauna dominated by the Oedicerotidae (*Synchelidium haplocheles*), Phoxocephalidae (*Harpina antennaria*), Ampeliscidae (*Ampelisca tenuicornis, A. brevicornis*), Melitidae (*Cheirocratus sundevallii*) and Leucothoidae (*Leucothoe lilljeborgi*) which could be ascribed to the boreal offshore muddy sand association as described by Jones (1950).

Frequency of Occurrence

The number of species per station ranged between 1 and 15. However, only 12 % of the stations had more than 10 species while the majority (47 %) had between 4 and 10 species. The species distribution, as indicated by the frequency of occurrence (Table II), showed that *Ampelisca brevicornis* and *Synchelidium haplocheles* were the most widely distributed species, found in 14 (41 %) and11 (32 %) of the sampled stations respectively.

Other amphipods which were found in more than 20 % of the stations were *Harpinia antennaria, Corophium crassicorne, Cheirocratus sundevallii, Bathyporeia elegans, B. guilliamsoniana, Perioculodes longimanus* and *Metaphoxus fultoni,* while 44 others showed a very limited distribution, appearing in less than 6 out of the total of 34 stations.

Dominance

The survey produced a total of 4435 specimens of amphipods. The ranking of the most abundant species was calculated as the abundance of each species expressed as a percentage of the total number of the amphipods collected.

TABLE II

Frequency of occurrence (ƒ 5 stations)

	N° of stations	% of stations
Ampelisca brevicornis	14	41.18
Synchelidium haplocheles	11	32.35
Harpinia antennaria	9	26.47
Corophium crassicorne	8	23.53
Cheirocratus sundevallii	7	20.59
Bathyporeia elegans	7	20.59
B. guilliamsoniona	7	20.59
Perioculodes longimanus	7	20.59
Metaphoxus fultoni	7	20.59
Ampelisca tenuicornis	6	17.65
A. diadema	5	14.71
A. typica	5	14.71
Leucothoe lilljeborgi	5	14.71
Stenothoe marina	5	14.71
Apherusa bispinosa	5	14.71
Phtisica marina	5	14.71

TABLE III

Percentage dominance (> 1 % of total number of individuals)

	Dominance ranking	% of individuals
Bathyporeia guilliamsoniana	1	15.94
Corophium crassicorne	2	11.77
Metaphoxus fultoni	3	10.01
Bathyporeia elegans	4	8.61
Leptocheirus pectinatus	5	6.79
Perioculodes longimanus	6	6.36
Bathyporeia pilosa	7	6.13
Harpinia antennaria	8	3.88
Bathyporeia pelagica	9	3.86
Ampelisca tenuicornis	10	2.48
Aora gracilis	11	2.44
Ampelisca diadema	12	1.89
A. brevicornis	13	1.76
Tryphosella sarsi	14	1.42
Lysianassa plumosa	15	1.40
Synchelidium haplocheles	16	1.38
Guernea coalita	17	1.10
Cheirocratus sundevallii	18	1.08
Phtisica marina	19	1.01
Total		89.31

Table III shows the ranking of the 19 dominant species which make up 89 % of the total number, each accounting for more than 1 %.

The overall dominant species, *Bathyporeia guilliamsoniana*, represented almost 16 % of all specimens recorded, which, along with *Corophium crassicorne, Metaphoxus fultoni* and *Bathyporeia elegans* (the next high ranking species), accounted for more than 46 % of the total.

The three families, Pontoporeiidae, Phoxocephalidae and Corophiidae taken collectively, accounted for more than 60 % of all the specimens taken at Loch Ewe.

A comparison of the frequency of occurrence of the amphipod species in the sampled stations and the dominance ranking (Tables II and III) shows that the most abundant species were not necessarily those which were most widely distributed. Thus, by numerical ranking, the top four most abundant species were found in less than a quarter of all the sampled stations.

Multivariate Analysis

A preliminary ordination indicated that one station (29) was markedly different from the rest. This shallow subtidal station contained only 16 *Hyale nilssoni* - a species which was absent from all other stations. In order to remove the influence of station 29 and lessen the influence of uncommon species at other stations, a second ordination was performed omitting station 29 and selecting the downweighting option for the DECORANA analysis.

A plot of axis 1 (eigenvalue = 0.948) against axis 2 (eigenvalue = 0.590) shows that intertidal sites (stations 27, 28 & 30 to 34) tend to have low axis 1 and axis 2 scores and are faunistically similar to several of the shallower stations (21 to 23) in the 21 to 26 subtidal group (Fig. 3).

Most of the stations in the central transect (stations 15 to 20 ; Fig. 1) are faunistically similar and are grouped towards the middle of axis l and the bottom of axis 2. Correlations between axes scores and the measured environmental variables show that organic carbon is highly correlated with axis 1 ($P<0.001$), whilst none of the other axes was correlated with any measured environmental variable (Table IV). However, by placing stations into bathymetric classes using charted depth contours (Fig. 2a), a correlation was also found between axis 1 and depth ($P<0.05$).

Thus, the major determinants of amphipod assemblages in Loch Ewe would appear to be sediment organic carbon and depth which are likely to be intercorrelated.

Axis 2 was not associated with any measured environmental variable and its identity remains unclear. Axes 3 and 4 also had relatively high eigenvalues (0.395 and 0.209, respectively), but again these were not correlated with any measured environmental variable. Chlorophyll *a* was not correlated with the distribution of amphipods, but was correlated with depth (Table IV).

The TWINSPAN analysis complements the ordination in that the first dichotomy separated stations into intertidal/shallow subtidal sites and deeper sites. Intertidal and shallow water

TABLE IV

Spearman's rank correlation matrix between axes scores and environmental data. (* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$)

	Axis 1	Axis 2	Axis 3	Axis 4	Median diameter	Organic carbon	Chlorophyll *a*
Median diameter	-0.280	0.014	0.086	0.240			
Organic carbon	0.590***	0.197	-0.056	0.005	-0.489**		
Chlorophill *a*	-0.092	-0.179	0.135	-0.212	-0.338	0.132	
Depth	0.419*	-0.038	0.071	-0.036	-0.132	0.023	-0.616***

sites were characterized by *Bathyporeia* species, *Corophium crassicorne* and *Perioculodes longimanus* (11 stations), while deeper sites were characterized by *Synchelidium haplocheles* and *Harpinia antennaria*.

At the second dichotomy, the deeper group of sites can be further divided into stations with relatively high organic carbon content and characterized by *Leucothoe lilljeborgi* and *Ampelisca brevicornis*, and those characterized by the species *Synchelidium haplocheles*, *Harpinia antennaria*, *Ampelisca tenuicornis* and *Cheirocratus sundevallii*.

DISCUSSION

The amphipod fauna of Loch Ewe differs little from that of more southern areas such as the Irish Sea (Fincham, 1969) and the northern Irish loughs (Strangford Lough, Fincham, 1973 ; Belfast Lough, Parker, 1984). In the Irish Sea (Fincham, 1969), 19 species (out of 27) and 15 families (out of 17) were found to be in common with the fauna of Loch Ewe. In Strangford Lough (Fincham, 1973) 13 species (out of 22) and 13 families (out of 15) were common in the two areas. While in Belfast Lough (Parker, 1984), faunal overlap was more obvious at the family level (14 families in common out of 16) than at the species level (14 species out of 36).

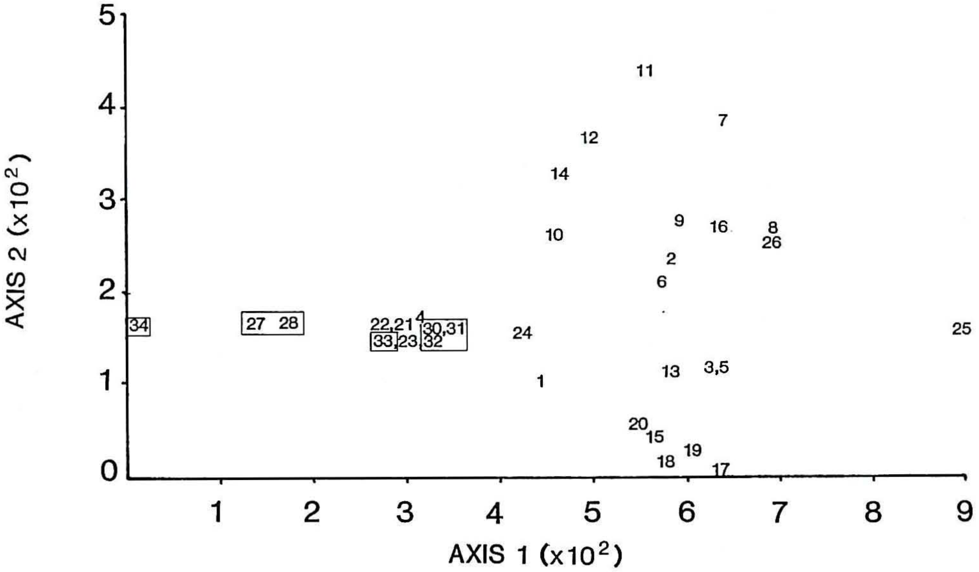

Fig. 3 : Ordination of amphipod assemblages from Loch Ewe stations (DECORANA). Intertidal stations outlined.

The above situation is not entirely unexpected since within a zoogeographical area, it is likely that similar physical environments will contain similar faunas (Jones, 1950). Given that the sediments of the shallow continental shelf are mainly sandy with variable amounts of silt and that the physical parameters along the west coast of Britain do not show marked differences, the observed similarity is therefore understandable.

Using Lincoln's grouping of the species into geographic elements (Lincoln, 1979), species could be separated into four categories : arctic boreal, cold temperate, temperate and warm temperate. Table V shows the predominance of the temperate species with the presence of an important cold temperate element. The presence of the additional arctic boreal species *Paraphoxus oculatus* and *Calliopius laeviusculus,* and the warm temperate species *Metaphoxus fultoni* and *Megaluropus agilis* indicates the infuence of faunas with centres of distribution outside British latitudes, which extends their southerly and northerly boundaries into this area.

Further comparison of the faunal data obtained from this survey with previous records from Loch Ewe (McIntyre & Eleftheriou, 1968 ; Eleftheriou, 1979) and various localities at the west coast of Scotland (Scott, 1896 ; Raitt, 1937 ; Reid, 1941) indicates a degree of overlap with these records and thus extends the range of distribution of these amphipod species. Moreover, certain species such as the Phoxocephalids *Metaphoxus fultoni* and *Paraphoxus oculatus* and the Aorid *Leptocheirus pectinatus* constitute new records for the Minch, while the Melitid *Cheirocratus intermedius* is the first record from the west Scottish coast, having already been found in the east Scottish coast by Raitt (1937).

Quantitative assessment of the amphipod densities in these earlier works is not possible, as some are merely faunistic records (Scott, 1896 ; Reid, 1941) while others provide insufficient information and therefore are not easily interpretable.

Eleftheriou (1979), in his quantitative survey of Firemore Bay in Loch Ewe, showed that densities of the species found in common with the present survey were consistently higher in the shallow sandy sediments of the Bay. The exceptions were those species which were found predominantly in the siltier sediments of the deeper stations, such as *Ampelisca tenuicornis* or those such as *Gitana sarsi*, *Apherusa bispinosa* and *Podalirius typicus* whose distribution was influenced by the inconsistent presence of algal debris.

It should be noted that the special conditions prevailing at sea lochs (circulation regime, terrestrial inputs, sedimentation etc.) strongly influence the type and composition of the fauna, particularly in relation to the faunal association of the adjacent open sea location (Fincham, 1973 ; Parker, 1984). In this context we note the restricted distribution and low abundance of the amphipod fauna in the main body of the loch and the more varied and abundant fauna in the shallow periphery.

Both the analyses run by the DECORANA and TWINSPAN programmes suggest that the primary determinants of amphipod assemblages in Loch Ewe are depth and sediment organic carbon. These assemblages are characterized by indicator species, the distribution of which is consistent with the literature. Close examination of the indicator species distributions suggests that the first TWINSPAN division separates intertidal/shallow subtidal stations from deeper stations. *Bathyporeia elegans* and *B. guillamsoniana* are found both intertidal-

TABLE V

Geographical distribution (after Lincoln, 1979) and previous records of the Loch Ewe amphipod fauna.

	Geographic element	Prévious records			
Acidostoma obesum	T		B		D
Hippomedon denticulatus	T		B		D
Lysianassa plumosa	T	A			
Tryphosella horingi	CT	A			
T. sarsi	CT		B'		
Ampelisca brevicornis	T		B		D
A. diadema	T	A	B		D
A. tenuicornis	T		B		D
A. typica	T		B'	C	D
Iphimedia minuta	T				D
Gitana sarsi	T			C	D
Leucothoe lilljeborgi	T	A			
Stenothoe marina	T				D
Hyale nilssoni	CT			C	D
H. pontica	T				D
Gammarus locusta	T	A		C	D
Cheirocratus intermedius	CT				
C. sundevallii	T	A	B	C	
Maera othonis	T		B		D
Bathyporeia elegans	T				D
B. guilliamsoniana	T			C	D
B. pelagica	T		B		D
B. pilosa	CT				D
Urothoe elegans	T		B'	C	
Argissa hamatipes	CT				D
Monoculodes carinatus	T		B'		D
Perioculodes longimanus	T				D
Pontocrates altamarinus	CT				D
Synchelidium haplocheles	T				D
Westwoodilla caecula	CT		B		
Harpinia antennaria	CT	A	B	C	
H. crenulata	T			C	
Metaphoxus fultoni	WT				
Paraphoxus oculatus	AB				
Megaluropus agilis	WT				D
Apherusa bispinosa	T	A			D
A. jurinei	T				D
Calliopius laeviusculus	AB				D
Atylus falcatus	CT		B'		D
A. swammerdami	T	A	B'		D
A. vedlomensis	CT	A	B'		D
Dexamine spinosa	T	A	B'	C	D
D. thea	T				D
Guernea coalita	T				D
Sunamphitoe pelagica	T			C	D
Aora gracilis	T			C	D
Lembos longipes	CT				D
Leptocheirus pectinatus	T				
Microprotopus maculatus	T			C	D
Corophium crassicorne	T		B'	C	D
Siphonoecetes kroyeranus	CT		B'	C	D
Phtisica marina	T	A	B		D
Podalirius typicus	T				D

T = temperature
CT = Cold temperature
WT = Warm temperature
AB = Artic boreal

A = Scott (1896)
B = Raitt (1937)
B = West coast Scotland
B' = North coast Scotland, Orkney, Shetland, east Atlantic
C = Reid (1941)
D = Eleftheriou (1979)

ly and sublittorally and the two species are generally associated with finer sediments ; both are considered to be indicator species of Fincham's shallow water community (Fincham, 1969). The subdivision of the *Bathyporeia* group into subgroups based upon *B. elegans* and *B. guilliamsoniana* (Fig. 4) cannot be related to any measured environmental parameter. In addition, *Corophium crassicorne* and *Perioculodes longimanus* were found both intertidally and in the shallow sublittoral in association with finer sediments. *Perioculodes longimanus* is considered to be an accessory species of the shallow sand community (Eleftheriou, 1979).

The indicator species for the deeper group, *Synchelidium haplocheles* and *Harpinia antennaria*, are exclusively subtidal in Loch Ewe and are associated with sandy sediments ranging from fine to coarse.

In considering the subdivision of the deeper sites at TWINSPAN level 2, it should be noted that *Ampelisca brevicornis* is considered to be an important component of the offshore fine sand community (Jones, 1950) and is known to be associated with sediments containing a dominant fine fraction (Kaim Malka, 1969 ; Sheader, 1977). It has also been reported that this species requires the fine sediment fraction for successful feeding (Enequist, 1949 ; Salvat, 1967 ; Massé, 1971). We have no data or additional information regarding environmental or other factors which may account for these divisions with respect to the other indicator species in this group.

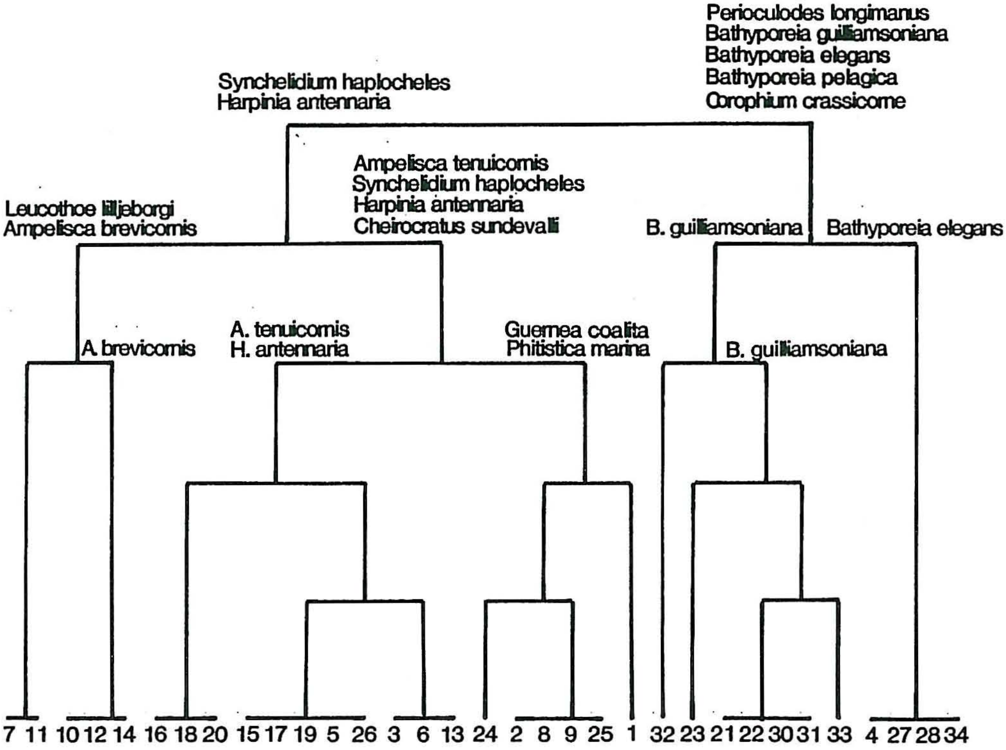

Fig. 4 : TWINSPAN dendrogram showing relatedness of amphipod assemblages in Loch Ewe, together with indicator species for the major TWINSPAN divisions.

The conclusion of the majority of previous studies (Fincham, 1973 ; Parker, 1984) has been that particle size is an important determinant of amphipod distribution. However, Buchanan (1963), in his work in the Northumberland coast, found no correlation between the density of *Haploops* and median diameter. In common with Buchanan, we find no correlation with sediment median diameter.

It should be noted that none of the previous studies present data relating amphipod distribution to organic carbon content or depth, the two principal determinants of amphipod assemblages found here.

At present, there are few data available to resolve this confusion and, in particular, the well documented tolerance of many amphipod genera and species to a range of sediment types emphasizes the difficulty in resolving such questions.

With this in mind, it is perhaps better, therefore, to view with caution the correlative approach adopted here and opt for detailed experimental studies of amphipod ecology to improve our understanding of amphipod assemblages.

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