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25

DISTRIBUTION AND HABITAT PREFERENCES OF SOME INTERTIDAL AMPHIPODS IN ICELAND

AGNAR INGÓLFSSON

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Distribution and habitat preferences of some intertidal amphipods in Iceland

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Abstract. A total of 801 samples of amphipods from 71 sampling stations on all coasts of Iceland were analysed. Results are presented for eleven species belonging to the families Gammaridae and Talitridae. Three species have a limited distribution around the coasts of Iceland, while the remaining species are found more or less commonly on all coasts where suitable shores exist. The distributional patterns observed were compared to those shown by the same species on the western and eastern coasts of the Atlantic. It is concluded that temperature is an important factor controlling the distribution of these amphipods.

Habitat partitioning was analysed by use of 41 habitat categories under eleven main headings. Each of the eleven species was found to have a habitat distribution different from that of the other species, with the possible exception of one species pair. Spatially successional series of species could be distinguished along environmental gradients found from sheltered shores with luxuriant fucoid vegetation to exposed shores without fucoids, from high to low tidal levels on rocky seashores, from upper to lower reaches of estuaries and from high-salinity to low-salinity ponds and lagoons. It is probable that habitat partitioning among the species results from differences in adaptations to several interacting physical factors, of which salinity, humidity, temperature, and oxygen level can be reasonably identified. Interspecific competition may reduce habitat overlap among species but the data are inconclusive.

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INTRODUCTION

Intertidal amphipods of the families Gammaridae and Talitridae in the North Atlantic region have been the subject of many ecological studies in recent years (e.g. Goodhart 1941, Spooner 1947, Jones 1948, Steen 1951, Den Hartog 1963, 1964, Vader 1965, Rygg 1972, Dennert 1973, Steele and Steele 1975c, Van Maren 1975). Habitat partitioning among species has been dealt with in many of these studies, although there is a lack of quantitative data on this aspect, and general statements are the rule. The present study was undertaken in an attempt to place habitat selection of these amphipods on a more quantitative basis than had been done previously. There is in addition a unique assemblage of species found on Icelandic seashores, the study of which could be expected to yield particularily interesting information on niche partitioning among related sympatric species.

A second aim of this study was to delimit the range of the intertidal species. As the species in question are largely confined to the intertidal zone and therefore have an almost linear distribution it was thought possible to delimit the range of each species rather accurately and thus facilitate a consideration of environmental factors controlling distribution. Most studies of distributional patterns of marine animals around Iceland have been marred by a very irregular sampling effort and there was clearly a need for a study based on samples distributed evenly around the coasts of Iceland.

METHODS

Collection of data

Amphipod samples were obtained from all coasts of Iceland. Samples were taken during low spring-tides along transects worked down seashores and along estuaries. Generally 5–7 samples were taken along each transect from as high up as amphipods were found down to the sublittoral. Additional samples were obtained from a variety of habitats whenever these were encountered. The zonation pattern of each transect was described with reference to dominant organisms, and on each sampling site the substrate was described, cover of species of algae estimated, presence of other animals noted, and where appropriate, temperature and salinity measured, the latter by use of a hydrometer with an accuracy of 0.2‰. The size of the sampling sites varied, but was almost always less than 5 m^2. The area searched at each sampling site was reasonably homogenous. A number of samples from southwestern Iceland were obtained from sampling sites 800 cm^2 in area so that densities could be determined, but otherwise the aim was to obtain at least 100 amphipods in each sample, but this was frequently not possible. Tidal levels of many sampling sites in southwestern Iceland were measured with surveying instruments and with reference to the tidal gauge of Reykjavík harbor. The amphipods were picked up from under stones or between algae with forceps. The algae were shaken in order to dislodge the animals. Sampling from under water was aided by use of hand nets (mesh-size about 1.5 mm) and on tidal flats the substrate down to a depth of 10 cm was sieved (mesh-size 1.5 mm). Almost all samples were obtained from May to August in 1974 and 1975.

Additional unpublished data have been used when appropriate, but separately from those of the general survey. The relevant information is contained in a number of reports compiled by the author and other staff members and students at the Institute of Biology, University of Iceland.

Analysis of data

In analysing habitat preferences 41 habitat categories under 11 main headings were established. The categories were defined prior to sampling but somewhat revised after sampling was completed. Definitions are given in Table 1. Habitats of categories 1—4 are characterized by low and often fluctuating salinities. The lagoons and coastal ponds (habitat category 1) are of several different types, but can be roughly grouped into two groups, 1.1 and 1.2, the former receiving salt water through underground seepage from the sea or via sea-spray, the latter connecting with the sea through a narrow channel. Estuaries (habitat category 3) in Iceland are usually very short, and pronounced salinity changes are confined to a small area around the mouth of the river. The term esturary will here be used to include the river channel itself traversing the intertidal region, as well as the intertidal area to each side of the channel if there are no tidal flats, while tidal flats are placed in a separate category (10). The rocky seashore is divided into four types, habitat categories 5—8, often referred to hereafter as shore types 5—8. The distinguishing feature of these types is the species composition of fucoid algae, and they represent a series from sheltered shores with stable substrate (type 5) to exposed shores where considerable movement of substrate occurs (type 8). Tidal flats (habitat category 10) are of several different types depending on substrate and fresh-water influence, but as few samples were obtained from this habitat, the category was not subdivided further. A few samples that could not be placed in a habitat category as defined were placed in category 12 (undefined).

The amphipods of each sample were identified and counted under a dissecting microscope. Descriptions and keys by Segerstråle (1947), Sexton (1942), Sexton and Spooner (1940), Stephensen (1928, 1935—1942) and Stock (1967) were the chief aids used in identification together with a

Table 1

Designations and definitions of habitat categories, and number of samples examined from each category from southern + western and from northern + eastern Iceland.

Category	Number of samples S + W		Number of samples N + E	
1. Lagoons and coastal ponds	31		31	
1.1. Little or no tidal change, salinities usually lower than 12‰				
1.1.1. Above water level		7		3
1.1.2. Below water level		11		19
1.2. Tidal range noticable, salinities fluctuating but rarely exceeding 25%				
1.2.1. Upper shore		3		4
1.2.2. Lower shore		3		5
1.2.3. Below water level at low tide		7		0
2. Tidepools	6		18	
2.1. Upper shore, above fucoids when these present		1		7
2.2. Middle shore, between uppermost fucoids and uppermost Fucus distichus L. when present		4		9
2.3. Lower shore, below uppermost F. distichus when this species present		1		2
3. Estuaries	11		73	
3.1. Upper tidal reaches, in river channel		4		22
3.2. Upper tidal reaches, above river channel		2		11
3.3. Lower tidal reaches, in river channel		2		21
3.4. Lower tidal reaches, above river channel		1		19

	Number of samples			
	S + W		N + E	
4. Small streams traversing shore	5		13	
4.1. Upper shore, above fucoids when these present		3		6
4.2. Middle shore, between uppermost fucoids and uppermost F. distichus when present		2		4
4.3. Lower shore, below uppermost F. distichus when this species present		0		3
5. General seashore where Ascophyllum nodosum (L.) Le Jol., Fucus vesiculosus L., F. distichus (and/or F. serratus L.) present	261		90	
5.1. Above fucoids				
5.1.1. Shores with Fucus spiralis L. (with or without Pelvetia canaliculata (L.) Decne et Thur.)		9		5
5.1.2. Shores without F. spiralis and P. canaliculata		3		7
5.2. P. canaliculata/F. spiralis zone		62		10
5.3. Upper third of F. vesiculosus/A. nodosum zone		57		23
5.4. Middle third of F. vesiculosus/A. nodosum zone		60		14
5.5. Lower third of F. vesiculosus/A. nodosum zone and boundary area with F. distichus (and/or F. serratus) zone		38		14
5.6. Main part of F. distichus (and/or F. serratus) zone		18		16
5.7. Zone between F. distichus (and/or F. serratus) and Laminaria (and/or Alaria) zones		14		1
6. General seashore where F. vesiculosus, F. distichus (and/or F. serratus) present, A. nodosum absent	18		73	
6.1. Above fucoids				
6.1.1. Shores with F. spiralis (with or without P. canaliculata)		1		1
6.1.2. Shores without F. spiralis and P. canaliculata		0		12
6.2. P. canaliculata/F. spiralis zone		2		2
6.3. Main part of F. vesiculosus zone		4		21
6.4. Lower third of F. vesiculosus zone and boundary area with F. distichus (and/or F. serratus) zone		5		10
6.5. Main part of F. distichus (and/or F. serratus) zone		6		25
6.6. Zone between F. distichus (and/or F. serratus) and Laminaria (and/or Alaria) zones		0		2
7. General seashore where F. distichus only fucoid present (except F. spiralis occasionally)	9		41	
7.1. Above F. distichus		5		11
7.2. Upper third of F. distichus zone		2		14
7.3. Middle third of F. distichus zone		0		4
7.4. Lower third of F. distichus zone		2		11
7.5. Zone between F. distichus and Laminaria (and/or Alaria) zones		0		1
8. Boulder or gravel shores without fucoids	5		38	
8.1. Upper third of shore		1		11
8.2. Middle third of shore		2		16
8.3. Lower third of shore		2		11
9. Area immediately below LWS, usually with Laminaria and/or Alaria	0		52	
10. Tidal sand- or mudflats	14		3	
11. Puccinellia maritima (Huds.) salt marshes	3		1	
12. Unclassifiable samples	2		3	

mimeographed key by Dr. W. Vader, Tromsö Museum, Norway. No attempt was made to identify juveniles smaller than 2.5 mm (excluding antennae). The percentage composition of identified specimens was calculated for each sample. All samples containing less than 5 amphipods were omitted from analysis.

For further analysis the samples were divided geographically into two groups on the basis of distribution and abundance of amphipod species (Fig. 1):

1. Samples from northwestern, northern, northeastern and eastern Iceland, i.e. the area north of the bay of Breidafjördur in the west to and including Hornafjördur in the southeast.

2. Samples from southern, southwestern and western Iceland, i.e. the area west of Hornafjördur in the southeast to and including the northern shores of the bay of Breidafjördur in the west.

The results are presented mostly in the form of frequencies of occurrance of species in samples from a specific habitat category (or a combination of these). Utilization of percentage composition and densities (where available) adds comparatively little further information, as there is a fair positive correlation between the frequency of a species in a habitat on one hand and the average percentage of amphipods which it constitutes and its densities in that habitat on the other. There are some exceptions from this, notably in habitats situated at high tidal levels. Amphipods are scarce at these levels, and a species occurring in many samples from this region may not at all be common there.

To analyse geographical distribution samples taken within a radius of 5—8 km were combined. This resulted in 71 sampling stations spaced evenly around the coast (Fig. 2), except that there were few stations along the south coast, where the shore is unsuitable for macroscopic animals over wide stretches due to surf and moving substrate.

Non-parametric statistics have been used throughout, either the chi-square test or the Mann-Whitney U test.

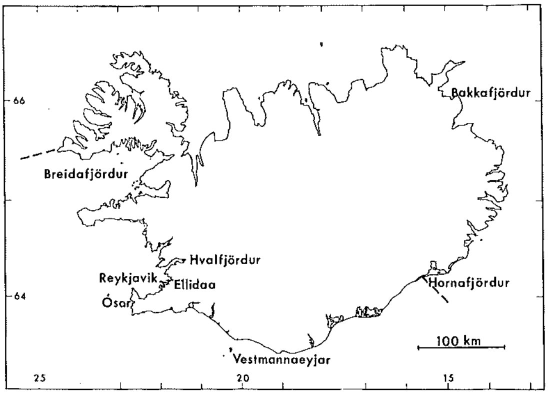

Figure 1. Outline map of Iceland with chief localities mentioned in the text. Also shown are boundaries as used in this paper between northern and eastern coasts and southern and western coasts.

RESULTS

Altogether 801 samples of amphipods were obtained from 71 sampling stations, representing some 44.000 identified specimens. Although all identified amphipods were included in the analysis, only the results for 11 intertidal species belonging to the families Gammaridae and Talitridae will be discussed here. Other species obtained were rarely abundant in the intertidal zone. They constituted about 13% of the identified amphipods, but about 85% of these were obtained from the subtidal region (habitat category 9).

Gammarus oceanicus Segerstråle

This is the most common and widespread of the intertidal amphipods of Iceland, occurring commonly on all coasts except the south (Fig. 2), where over wide stretches the only habitats suitable for amphipods are low-salinity lagoons. This is the species that Stephensen (1940) refers to as *Gammarus locusta* (Linné) sens. str. (see Spooner 1951) and is the only species treated in his synopsis of Icelandic amphipods that is so well represented in collections that individual localities are not listed. In the present survey it was found in about half the samples and it constituted almost 30% of the amphipods identified.

This species occurs under a wide range of conditions (Table 2). It is most characteristic of the moderately exposed rocky shores of types 6 and 7, especially the latter (Fig. 4), although the difference in frequency on these two types of shores does not quite reach significant proportions ($0.1 > P > 0.05$ for whole island). On both types of shores it is the commonest amphipod present, and although it is also quite common on the more sheltered shores of type 5 and the exposed shores of type 8, it is here overshadowed by other species (Table 2). *G. oceanicus* is rather evenly distributed vertically on general seashore, althoug it does show a tendency to increase in abundance downwards (Fig. 5). On shores of types 5 and 6 considered together it occurs less often in habitats 5.3 and 6.3 and those above than in habitats 5.4 and 6.4 and those below ($0.05 > P > 0.01$ for whole island). The same trend is also seen on shores of type 8 (nonsignificant), while it is hardly present on shores of type 7. The species occurs subtidally (habitat category 9) much more abundantly than any other species here considered (Table 2).

In estuaries (habitat category 3) the species is quite common in the lower reaches, and occurs here both in the river channel itself (and thus surrounded by virtually fresh water at low tide) and in the intertidal area on each side of the channel (habitats 3.3 and 3.4, Table 3). A special study was made of the distribution of amphipods in the Ellidaar estuary in Reykjavik, southwestern Iceland (Fig. 1), and the data thus obtained, which have been kept separate from those of the general survey, show well the typical distributional patterns of amphipods in Icelandic estuaries. The tidal reaches of the Ellidaar estuary are about 500 m long. Samples were obtained along transects run perpendicular to the river channel at 8 stations, station 1 being most upriver. The vertical interval between sampling sites along the transects was 50 cm. Samples were grouped together into tidal intervals at each station, as shown in Table 4. *G. oceanicus* is seen to be common in the lower reaches, replacing *G. duebeni* seawards at all but the highest tidal levels and also in the river channel itself. In the MTL-MHWN tidal interval *G. oceanicus* becomes the dominant species at station 7, but in MLWN-MTL interval this occurs slightly more upriver, at station 6. It is the dominant species in the MLWN-MLWS interval at all stations where the interval occurs. In the river channel it replaces *G. duebeni* at a tidal level around MLWN and shows here a broad overlap with *G. zaddachi*.

Few samples from tidal flats were obtained during the survey, but considerable information on the amphipod fauna of tidal flats has been obtained during ecological investigations of several localities in recent years (Table 5). *G. oceanicus* is everywhere the most common amphipod, except on flats characterized by the polychaete *Nereis diversicolor*, which are more estuarine in character than are the other types.

G. oceanicus is found rarely in coastal ponds and lagoons (habitat category 1, Table 2) and in all investigated cases salinities reach at least 10‰ on a tidal cycle in these habitats, although measurements as low as 3.2‰ have been obtained. In tidepools and small streams (habitat categories 2 and 4) it is never found above the fucoid zone.

The species is much more frequent on type 5 shores in northern and eastern Iceland than on southern and western coasts (Table 2, $P < 0.001$), but it appeared equally common in other habitat groups in the two areas. This is probably due to type 5 shores of southern and western Iceland being on the average more sheltered and with more luxuriant fucoid vegetation than those in northern and eastern parts.

The habitat preferences of the species outside Iceland appear to be rather similar to what is reported here, although quantitative data are scant (Bousfield 1973, Brattergård 1966, Dennert 1973, Segerstråle 1959, Steele and Steele 1972, Steen 1951, Tzvetkova 1968). It is reported from all tidal levels, but seems to prefer the lower part of the shore and is frequently encountered subtidally, even to a considerable depth. It enters the lower reaches of estuaries and has been recorded at salinities lower than 1‰ (Dennert 1973) although it is unclear how permanent these conditions were.

Gammarus locusta (Linné)

As mentioned above, *Gammarus locusta* (Linné) of Stephensen (1940) was in fact *G. oceanicus*. The only previous acceptable record of true *G. locusta* from Iceland is that mentioned by Segerstråle (1947) from Bakkafjördur, northeastern Iceland. According to the present survey the species is rare in the intertidal zone of Iceland, and there are no records from the east coast south of Bakkafjördur (Fig. 2). In all it was only found in 7 samples, i.e. in one sample from each of the following habitats (see Table 1): 5.6, 6.5, 6.6, 8.2 and 8.3, and in two samples from habitat 9. These habitats are all located low on the shore or subtidally. Uniquely the species has been found in abundance subtidally on sandy and muddy bottom at the small inlet of Osar, southwestern Iceland (Fig. 1) (H. Gudmundsson, unpup. manuscr.), where the species also occurs intertidally, but not a single specimen has been found during several additional surveys of sandy or muddy subtidal areas in Iceland.

Outside Iceland the species is found in the lowest part of the intertidal as well as subtidally, often on soft bottoms (Brattegård 1966, Goodhart 1941, Den Hartog 1964, Jones 1948, Segerstråle 1959, Spooner 1957, Steen 1951).

Gammarus setosus Dementieva

Stephensen (1940) records this species from all coasts of Iceland except the southern coast. In the present survey *G. setosus* was found to be common on shores in northwestern, northern and eastern Iceland (Fig. 2). It is also found in western Iceland south of the northern shore of the bay of Breidafjördur, but is much less common and more local here.

In northern and eastern Iceland this species is most common on the exposed boulder shores of type 8, and it is the dominant amphipod of these shores (Table 2, Fig. 4). It is also common on the more sheltered shores of type 7 (difference in frequency on these two types nonsignificant), but here it is overshadowed by *G. oceanicus*. It is considerably less common on the still more sheltered shores of types 5 and 6. In low-salinity habitats it is found rather sparingly. In estuaries (Table 3) it occurs especially in the lower reaches, both in the river channel itself and above it, as does *G. oceanicus*. In two lagoons where the species was found salinities were 10‰ and 11‰ (single measurements), while in a third, four measurements done at various stages of the tidal cycle ranged from 3–16‰.

G. setosus has a tendency to be most common rather high on the shore, usually above the main occurrance of *G. oceanicus*. This tendency does not reach significant proportions on shores of type 8, but on type 7 shores, the species occurs significantly more often in samples from habitats 7.1+7.2 than from habitats 7.3+7.4+7.5 ($0.05 > P > 0.01$), being especially frequent in the 7.1 samples. On shores of types 5 and 6 considered together (Fig. 5) it is also more frequent in samples from habitats 5.3+6.3 and those higher up than in samples from habitats 5.4+6.4 and those lower down ($P \sim 0.05$). The species is rarely encountered subtidally.

In southern and western Iceland *G. setosus* behaves in a rather different fashion from that described above. It is here almost totally lacking from the sheltered and semi-exposed shores of types 5–7. Shores of type 8 are infrequent in this area, but it is significant that *G. setosus* was found to be the dominant species in samples from the single transect worked on this type of shore. Otherwise the chief habitat of the species in southern and western Iceland are coastal ponds and high-level tidepools (habitats 1.1 and 2.2), but it is not a common species here. Salinities in these ponds and pools generally ranged from 2–10‰ but they may fluctuate considerably on a tidal cycle. In one pool where salinities were usually below 5‰ measurement of 24‰ was obtained on one occasion. *G. setosus* is usually accompanied by *G. duebeni* in these ponds and pools, less often by other species.

There is scant information on the habitat preferences of *G. setosus* in other areas, although it has frequently been recorded from the intertidal zone of arctic waters. On the western coast of the Atlantic it is found on the general seashore, in tidepools, stream outflows and beach seeps, and in brackish regions of brooks and rivers down to salinities of about 3‰ (Bousefield 1973, V. J. Steele and D. H. Steele 1970). South of Newfoundland the species is only found in the outlets of cool fresh-water streams in summer (Steele and Steele l.c.). In the White Sea it inhabits all horizons of the intertidal area (Tzvetkova 1968), but on the western coast of the Atlantic it occurs slightly higher on the shore than *G. oceanicus* (Steele and Steele 1974).

Gammarus zaddachi Sexton

This species has not previously been reported from Iceland, perhaps due to confusion with other species. In the survey it was found to be abundant in estuaries and lagoons around the coast of Iceland (Fig. 2). There are, however, only a few records from northeastern Iceland, probably due to scarcity of suitable habitats there.

The species occurs in a restricted range of low-salinity habitats (Table 2). It is above all characteristic of estuaries, where it is primarily found in the river channel itself, thus remaining submerged at low tide (habitats 3.1 and 3.3, Table 3). Its distribution in the Ellidaar estuary appears typical (Table 4). Here it occurs throughout the channel and overlaps broadly with *G. duebeni* in the upper reaches and with *G. oceanicus* in the lower. It does not always extend as high up the channel as *G. duebeni* does, although this is the case in the Ellidaar estuary, and it is sometimes found subtidally in front of mouths of large rivers. It is found in small numbers in the intertidal region on each side of the river channel, especially close to the channel. On tidal flats characterized by *Nereis diversicolor*, which are under considerable fresh-water influence, *G. zaddachi* is the dominant amphipod, and is here often accompanied by the amphipod *Pseudalibrotus littoralis* (Table 5).

G. zaddachi is also common in lagoons and coastal ponds (habitat category 1). Salinities where the species was found ranged from less than 0.5‰ to about 17‰, and were frequently found to vary within a tidal cycle. In these habitats the species is usually accompanied by *G. duebeni*, but unlike that species it is almost confined to regions that are continuously submerged. *G. zaddachi* is, however, absent from many small coastal ponds where *G. duebeni* is present, although salinities were frequently found to be similar to those of ponds also containing *G. zaddachi*. It does not occur in tidepools. It is found occasionally in small streams running over the shore, but apparently less often than *G. duebeni*, but data on this habitat are rather scant.

Den Hartog (1964) summarizes what was known of the habitat of this species outside Iceland, and the present observations are in good agreement with his conclusions. It is often regarded as a sublittoral species because it is largely confined to the river channel of esturaries and usually occurs continuously submerged in lagoons, but some workers have also recorded it from areas that become exposed at low tide (Vader 1972, Brattegård 1966). As in Iceland, it is not found in small tidepools (Dennert 1973).

Gammarus duebeni Lilljeborg

Stephensen (1940) records this species from several localities in Iceland, chiefly from the western coast. In the present survey it was found to be abundant on all coasts of Iceland where suitable habitats existed (Fig. 2).

The species prefers low-salinity habitats (Table 2). It is particularily characteristic of coastal ponds and lagoons (habitat category 1), occurring here both where continously submerged as well as in the intertidal area (where tidal changes present) or just above water level (where there are no tidal changes). In the coastal ponds (1.1) salinities ranged from 0.15—12‰, but where frequently around 2‰. Only small fluctuations of salinities were found were repeated measurements were made. Salinities fluctuate more in the lagoons (1.2). Three examples of these fluctuations on a single tidal cycle are as

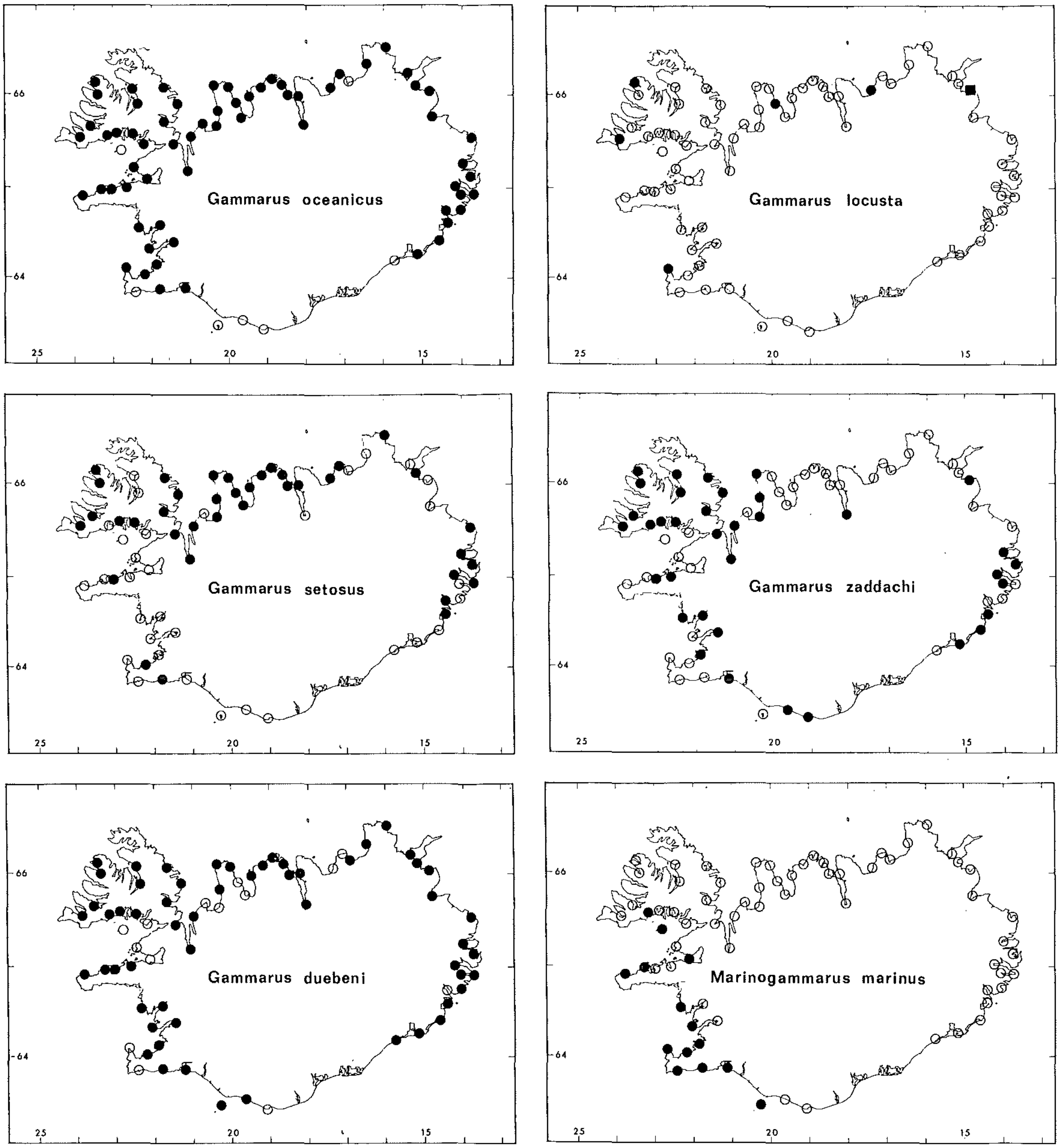

Figure 2. Distribution of *Gammarus* spp. and of *Marinogammarus marinus* in Iceland according to present survey. ● positive sampling stations. ○ negative sampling stations. Segerstråle's (1947) record of *G. locusta* is also shown (■).

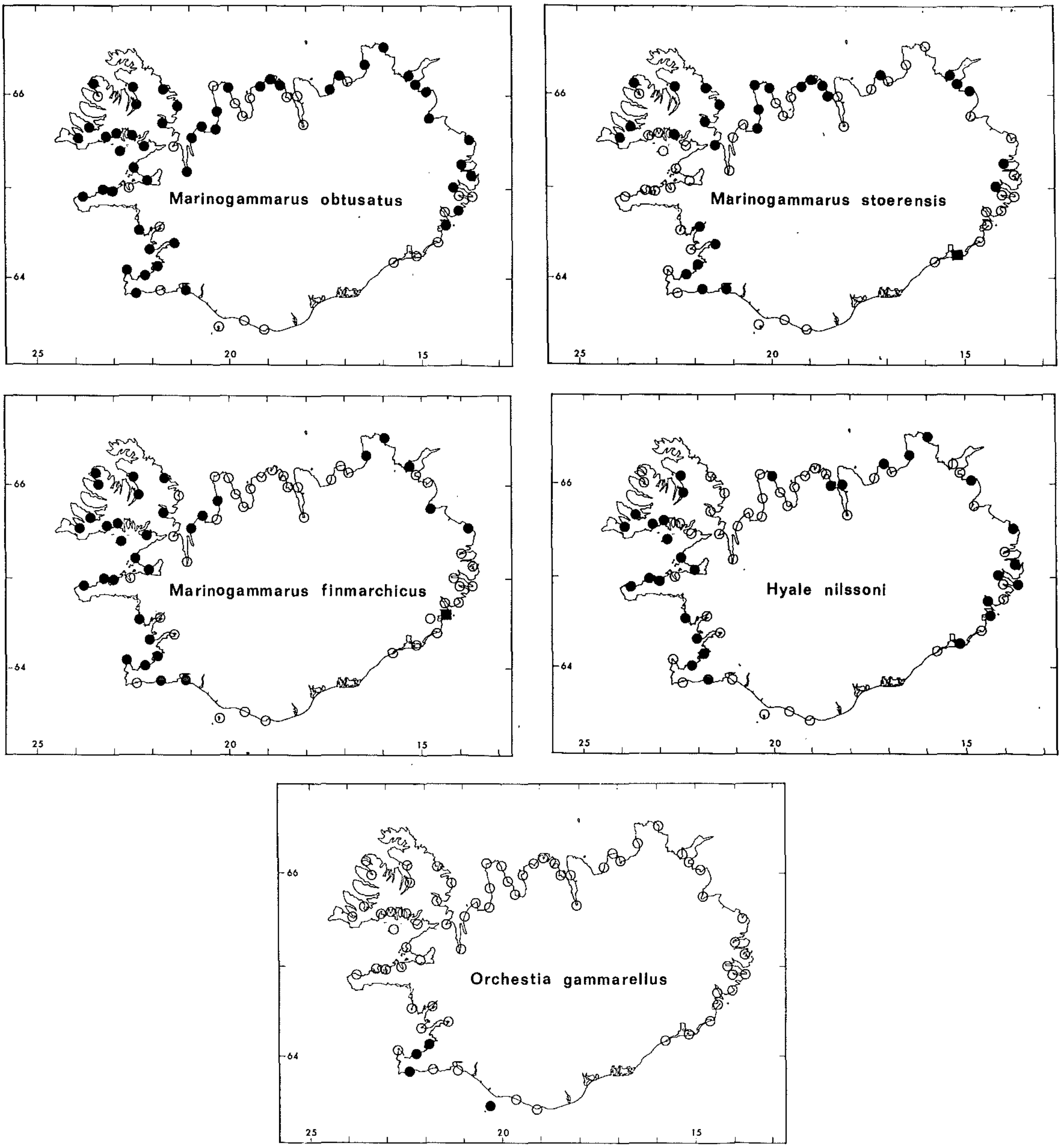

Figure 3. Distribution of *Marinogammarus* spp., *Hyale nilssoni* and *Orchestia gammarellus* in Iceland according to present survey. Symbols as in Fig. 2. Records from Stephensen (1940) that extent the distributional area of *M. finmarchicus* and *M. stoerensis* are also shown (■).

Table 2

The occurrance of the 9 most common species of intertidal amphipods in samples from southern + western and northern + eastern coasts of Iceland. See Table 1 for definitions of habitat categories. A = percentage of samples in which a species occurs. B = average percentage of amphipods which a species constitutes in those samples where it occurs, when occurring in 5 or more samples.

Habitat category	Area	Number of samples	Average number per sample	G. ocean.		G. set.		G. zadd.		G. dueb.		M. obtus.		M. finm.		M. mar.		M. stoer.		H. nils.	
				A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
1	S+W	31	40	6		19	32	13		90	92	0		0		13		0		0	
	N+E	31	29	6		10		35	62	77	86	0		0		0		0		0	
2	S+W	6	27	33		50		0		50		0		33		0		0		0	
	N+E	18	25	33	80	11		0		56	93	6		0		0		0		17	
3	S+W	11	24	18		0		64	69	64	73	0		0		0		0		0	
	N+E	73	27	27	30	22	46	64	81	40	62	0		3		0		7	30	0	
4	S+W	5	15	15		0		40		100	65	0		0		0		0		0	
	N+E	13	21	31		31		8		69	91	0		0		0		0		0	
5	S+W	261	35	20	52	1		0		9	55	62	66	19	42	27	45	2	36	34	55
	N+E	90	75	56	55	31	24	0		14	75	60	66	23	24	0		14	8	17	19
6	S+W	18	36	67	54	0		0		6		39	58	33	19	28	25	0		39	46
	N+E	73	68	73	64	22	15	0		21	72	34	63	8	17	0		18	21	12	18
7	S+W	9	145	89	96	0		0		0		11		0		11		0		22	
	N+E	41	68	85	71	54	29	0		2		12	46	2		0		31	27	0	
8	S+W	5	37	40		100	97	0		0		20		0		0		0		0	
	N+E	38	82	63	53	68	70	0		8		5		5		0		11		0	
9	S+W	0	—	—		—		—		—		—		—		—		—		—	
	N+E	52	117	65	25	8		0		0		2		0		0		2		0	
10	S+W	14	58	43	65	0		0		14		43	33	36	28	21		0		0	
	N+E	3	44	100		0		50		0		33		33		0		0		0	
11	S+W	3	18	0		0		0		67		0		0		0		0		0	
	N+E	1	24	0		0		0		100		0		0		0		0		0	
12	S+W	2	35	50		0		0		0		0		0		50		0		0	
	N+E	3	63	67		0		0		33		0		0		0		0		0	

Table 3

Percentage of samples from different parts of estuaries (habitat group 3) in which species of amphipods occur. See Table 1 for definitions of habitats 3.1. — 3.4.

Habitat	Number of samples	G. duebeni	G. zaddachi	G. oceanicus	G. setosus	M. stoerensis	M. finmarchicus
3.1.	26	56	74	4	7	4	0
3.2.	13	85	23	15	15	0	0
3.3.	23	13	65	43	30	9	9
3.4.	20	30	75	45	25	10	0

follows: 0.4—15‰, 6—25‰, 3—16‰. The species is often accompanied by *G. zaddachi* in these habitats, more rarely by other species, but frequently it is the only species present. *G. duebeni* was once found in a warm spring a few hundred meters from the shore. The temperature was 18.3—19.0 °C, and the water was slightly saline (0.5—1.0‰). It was the only amphipod present and was abundant. There is one previous record of this species from a warm spring in Iceland (Schwabe 1936), also situated close to the shore (temperatures 10—20°C).

In small tidepools located above the fucoid zone or at a comparative tidal level (habitat 2.1) *G. duebeni* is usually the only amphipod present,

Table 4

The distribution of amphipods in the Ellidaar estuary, Reykjavik, southwestern Iceland, based on pooled data obtained on 11 October 1972, 27 September 1973 and 3 October 1974. Figures in the main body of the table show percentage composition of pooled samples grouped together according to tidal intervals. Heigh levels are given in m above chart datum

	Station							
	1	2	3	4	5	6	7	8
	Height of water level in river channel at low tide							
	3.6	3.4	2.1	1.6	1.2	1.1	1.0	0.7
MHWN – MHWS (2.87 – 3.94)	N=0	N=50 Gd 64 Gz 32	N=120 Gd 88 Gz 11 Go 1	N=83 Gd 80 Gz 20	N=36 Gd 97 Go 3	N=30 Gd 100	N=45 Gd 89 Gz 9 Go 2	N=0
MTL – MHWN (2.07 – 2.87)	–	–	N=107 Gd 93 Gz 6 Go 1	N=115 Gd 84 Gz 14 Go 2	N=120 Gd 61 Gz 20 Go 19	N=42 Gd 48 Gz 7 Go 45	N=114 Gd 4 Go 96 Ms 1	N=41 Gz 3 Go 97
MLWN – MTL (1.30 – 2.07)	–	–	N=37 Gd 92 Gz 8	N=63 Gd 73 Gz 27	N=55 Gd 53 Gz 11 Go 36	N=35 Gd 3 Gz 6 Go 91	N=60 Go 97 Ms 3	N=90 Go 91 Mf 9
MLWS – MLWN (0.12 – 1.30)	–	–	–	–	–	N=37 Gz 19 Go 78 Ms 3	N=40 Gz 10 Go 90	N=41 Go 95 Mf 5
River channel (low tide)	N=12 Gz 100	N=69 Gd 29 Gz 71	N=79 Gd 56 Gz 43 Go 1	N=83 Gd 54 Gz 46	N=82 Gd 5 Gz 66 Go 29	N=35 Gz 51 Go 49	N=48 Gz 40 Go 60	N=29 Go 96 Mf 4

Abbreviations: Gd = Gammarus duebeni; Gz = G. zaddachi; Go = G. oceanicus; Ms = Marinogammarus stoerensis; Mf = M. finmarchicus; N = Number of specimens

although occasionally accompanied by *G. setosus*. Salinities of these pools are extremely variable, but they apparently never become hypersaline in Iceland. In tidepools further down on the shore *G. duebeni* becomes scarcer and is replaced by several other species.

In estuaries *G. duebeni* is chiefly found in the upper reaches (habitats 3.1 and 3.2, Table 3) and

Table 5

The dominant amphipods of three different types of tidal flats in Iceland, based on the result of ecological surveys performed by staff and students of the Institute of Biology, University of Iceland. Species are listed in order of dominance, and those species that were common only on some of the tidal flats investigated are placed in parenthesis.

Tidal flats dominated by Nereis diversicolor O. F. Müller (3 localities)	Tidal flats dominated by Mytilus edulis L. (4 localities)	Tidal flats dominated by Arenicola marina (L.) (6 localities)
Gammarus zaddachi Pseudalibrotus littoralis (Kröyer) (G. oceanicus) (G. duebeni)	G. oceanicus (Marinogammarus stoerensis) (P. littoralis) (Pontoporeia femorata Kröyer)	G. oceanicus P. femorata (Anonyx nugax (Phipps))

its distribution in the Ellidaar estuary appears typical (Table 4). It occurs both in the river channel itself and in the intertidal area to each side of the channel. In the Ellidaar estuary the species is common in the river channel down to a tidal level near MLWN. To the side of the channel it is prominent at all stations in the uppermost tidal interval (MHWN-MHWS), but at lower tidal levels it decreases gradually seawards, and this decrease starts sooner the lower the tidal level. It is accompanied by *G. zaddachi* almost everywhere, but is replaced seawards by *G. oceanicus* at all except the highest tidal levels. The species is not found in rivers above the level of tidal influence.

In small streams traversing the seashore (habitat category 4) *G. duebeni* is chiefly found at upper tidal levels. Above the fucoid zone or at a comparative tidal level (habitat 4.1) it is usually the only species present. Normally it does not extend above the *Verrucaria-Littorina* zone (supralittoral fringe) but in one case animals were found in a stream about 8 m higher than the uppermost part of the supralittoral, and in the most extreme case the vertical distance was about 20 m. The horizontal distances were roughly 5 and 15 m respectively.

G. duebeni is not uncommon on the general seashore, and here it occurs more frequently on the more sheltered shores of types 5+6 than on shores 7+8 ($0.05 > P > 0.01$ for whole island). On shores of types 5 and 6 it is virtually confined to habitats 5.3 and 6.3 and those above (Fig. 5) and in this region its frequency is higher in samples from immediately above the fucoids (5.1+6.1) than in samples from the uppermost part of the fucoid zone (5.2+5.3+6.2+6.3) ($P < 0.001$ for whole island), but amphiods are rather scarce at the former level. Similar, although nonsignificant trends are seen on shores of types 7 and 8.

The habitat preferences of *G. duebeni* in Iceland are on the whole similar to what is reported for the species in other regions (Bousfield 1973, Brattegård 1966, Dennert 1973, Den Hartog 1964, Jones 1948, Kinne 1959, Rygg 1972, Segerstråle 1946, Spooner 1957, Steele and Steele 1969, Tzvetkova 1968). In Iceland it is not, however, found in fresh water considerable distance from the shore as it is frequently in the Faroes (Poulsen 1928), parts of the British Isles (Hynes 1954, Sutcliffe 1967, 1974) and Brittany (Pinkster et al. 1970) and it is worth mentioning that the freshwater species *Gammarus pulex* (L.) and *G. lacustris*

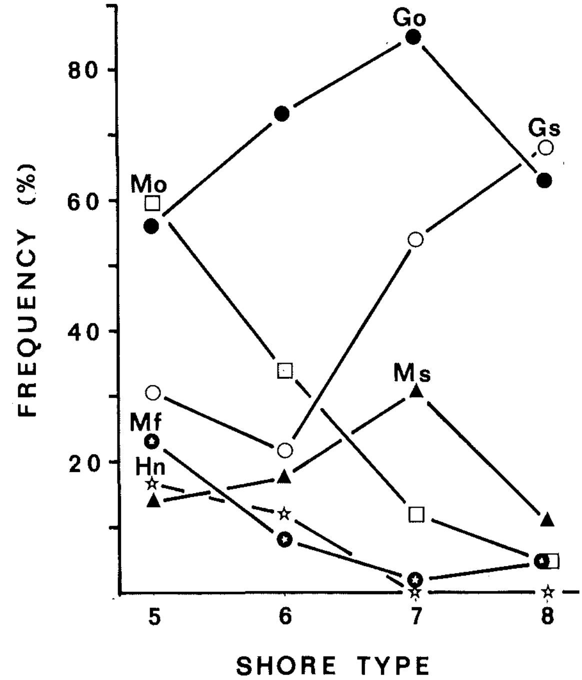

Figure 4. The frequency of six species of intertidal amphipods in samples from shores of types 5—8 (see Table 1) in northern and eastern Iceland. The species are: *Gammarus oceanicus* (Go), *G. setosus* (Gs), *Marinogammarus obtusatus* (Mo), *M. finmarchicus* (Mf), *M. stoerensis* (Ms), and *Hyale nilssoni* (Hn).

G. O. Sars have not been found in Iceland, although the latter certainly occurs under similar temperature conditions elsewhere (Ökland 1969).

Marinogammarus marinus (Leach)

This species is recorded from only one locality by Stephensen (1940), the Vestmannaeyjar Islands in southwestern Iceland. The present investigation showed it to be confined to the southwestern and western shores of Iceland, from the Vestmannaeyjar Islands in the south to the northern shore of the bay of Breidafjördur in the north (Fig. 2). It is abundant in suitable habitats north to the southern shore of this bay, but much less so further north.

The species is most frequent on sheltered shores of types 5 and 6 (Table 2). In other habitats it is infrequent but it has been found occasionally on tidal flats and in lagoons (habitat categories 10 and 1). Salinities in these lagoons have ranged from 5—30‰ and fluctuate widely on a tidal cycle.

The species has a rather restricted vertical distribution. It is not infrequent in samples from just above the fucoid zone (habitats 5.1 and 6.1), but reaches maximum frequencies in the uppermost part of the fucoid zone (habitats 5.2, 5.3, 6.2 and 6.3), and is clearly much less frequent below this (Fig. 5), although present in small numbers down to the sublittoral. *M. marinus* is the dominant Gammaridae in the *P. canaliculata/F. spiralis* zone (habitats 5.2 and 6.2), but is greatly outnumbered by *M. obtusatus* already in habitats 5.3 and 6.3. With reference to tidal levels *M. marinus* can be said to be common in the MHW-MTL region.

Elsewhere the species is also found to inhabit rather high tidal levels, usually above MTL (Jones 1948, Sexton and Spooner 1940, Spooner 1957). It may extend down to about MLWN (Goodhart 1941) but according to Den Hartog (1964) and Vader (1965) only when *M. obtusatus* is absent. Its upper limits appear usually to be around MHW. It is sometimes found in streams traversing the shore (Jones 1948) and extends some distances into estuaries (Den Hartog 1964, Spooner 1957). It has often been recorded from muddy substrates (Jones 1948, Vader 1965, Van Maren 1975).

Marinogammarus obtusatus (Dahl)

This is by far the commonest *Marinogammarus* species in Iceland, and Stephensen (1940) records it from several localities that are all in southwestern and western Iceland. In the present investigation the species was found to be common on all coasts, except for the south coast (Fig. 3), where lack of suitable habitats is undoubtedly responsible for its absence, as is true of many of the other amphipod species.

The species is expecially characteristic of the sheltered rocky shores of type 5, where it is usually the commonest amphipod (Table 2, Fig. 4). It also occurs frequently on the somewhat more

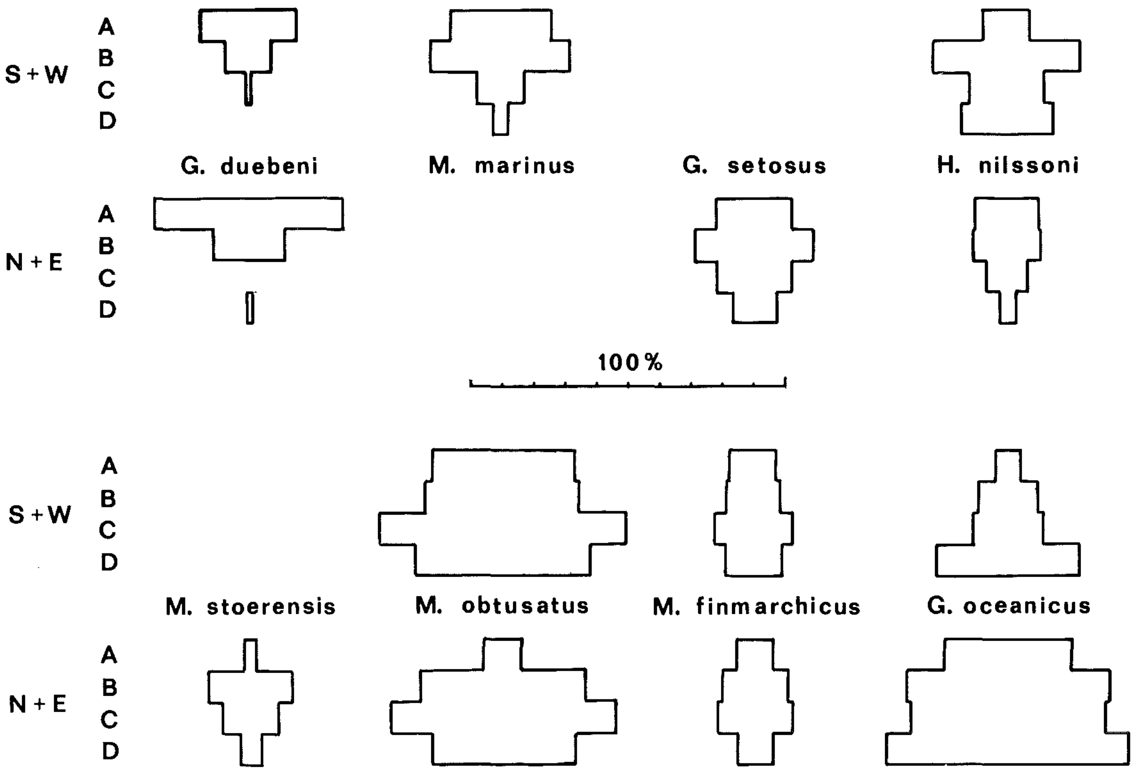

Figure 5. The frequency of eight species of intertidal amphipods in samples from different tidal levels on shores of types 5 and 6 in northern and eastern (N+E) and in southern and western (S+W) Iceland. A = habitats 5.1+6.1. B = habitats 5.2+5.3+6.2+6.3. C = habitats 5.4+5.5+6.4. D = habitats 5.6+5.7+6.5+6.6. See Table 1 for definitions of habitats.

exposed shores of type 6, although significantly less so ($0.01 > P > 0.001$ for northern and eastern Iceland). In other habitats it is less common, and although it was obtained in a rather high proportion of the few samples from tidal flats (habitat category 10), other data indicate that it is not a common species in such situations (Table 5). It is absent from low-salinity environments (habitats 1, 2.1, 3, 4).

M. obtusatus is common at all tidal levels in the fucoid zone but is rare subtidally. It is also rather frequent in samples from immediately above the fucoid zone (habitats 5.1 and 6.1), but amphipods are scarce here. The species reaches maximum abundance rather low on the shore, around the boundary of the *A. nodosum*/*F. vesiculosus* and *F. distichus* zones (habitats 5.4, 5.5 and 6.4) (Fig. 5). It occurs significantly more often in sample from these habitats, taken as one, than in samples from above ($P < 0.001$) and below ($P < 0.001$) this on shores of types 5 + 6 (for whole island). In southwestern Iceland, where reference to actual tidal levels can be made, the species is seen to be common at all levels below about MHWN, while it reaches maximum abundance in the MLWN-MTL interval.

The habitat preferences of *M. obtusatus* in other regions appear similar. In Newfoundland it is, however, said to occur only on moderately exposed shores (D. H. Steele and V. J. Steele 1970), and generally it does not seem to occur higher on the shore than to MTL (Goodhart 1941, Den Hartog 1964, Jones 1948, Sexton and Spooner 1940, Spooner 1957, Vader 1965, Van Maren 1975). Most authors stress that it is essentially in intertidal species that is rare subtidally.

Marinogammarus stoerensis (Reid)

Stephensen (1940) records only a single specimen from Iceland, from Hornafjördur in the southeast. The present investigation showed it to occur around the coasts of Iceland (Fig. 3). It is however, absent from much of the south coast, undoubtedly due to lack of suitable habitats. It seems furthermore to be rather local, and was in all found at less than half the sampling stations. Due to the small size of this species it is less easily collected than other Gammaridae species and may therefore be more common than the data indicate.

The species appears to be most common on the moderately exposed shores of type 7 (Table 2, Fig. 4). It is significantly less common on shores of types 5 ($P < 0.001$ for whole island) and 8 ($0.05 > P > 0.01$ for northern and eastern Iceland), while the difference between shores of types 6 and 7 is nonsignificant. The data indicate little preference for a particular tidal level, but in northern and eastern Iceland it shows a slight but significant tendency to prefer middle levels of shores of types 5 and 6 considered together (i.e. habitats 5.2–5.5 and 6.2–6.4) rather than those above and below considered as one group ($0.01 > P > 0.001$) (Fig. 5). The species is occasionally met with subtidally, and there are a few records from the lower reaches of estuaries (Tables 3 and 4). It has not been found in other low-salinity habitats. Although not recorded from tidal flats in the general survey, the species was surprisingly found to be very abundant in beds of mussels (*Mytilus edulis*) during a survey of tidal flats in Hvalfjördur, southwestern Iceland (unpublished reports compiled by G.M. Gislason and S.S. Snorrason). The species was not recorded at all in two additional tidal flats investigated, where *Mytilus edulis* was the dominant animal.

The species is considerably less frequent on shores of type 5 in southern and western Iceland than in the north and east ($P < 0.001$). This may be due to an average differences between the two areas in shores classified as type 5 (cf. *G. oceanicus*, p. 7).

Outside Iceland the species is usually said to be strictly indertidal and largely confined to areas on the shore where there is considerable fresh-water influence (Bousfield 1973, Jones 1948, Sexton and Spooner 1940, Spooner 1957, Steele and Steele 1975a, Vader 1965). Preferred tidal levels are stated to be between MHWN and MLWN (Sexton and Spooner 1940, Vader 1965) and below MTL (Bousfield 1973). It has been found to penetrate short distances up estuaries (Sexton and Spooner 1940). These observations are in fair agreement with the present data, except that there is little indication that the species shows a preference for regions of the intertidal in Iceland with strong fresh-water influence, and it was never found in fresh-water streams traversing the shore (habitat category 4).

Marinogammarus finmarchius (Dahl)

Stephensen (1940) records this species from only one locality in Iceland, Djupivogur on the southeastern coast. In this survey it proved to be rather common on shores on the whole of the western coast, from the southwest to the westernmost part of the north coast (Fig. 3). It was also found on the northern and eastern coasts, but was decidedly more local here. This can probably be ascribed to a scarceness on northern and eastern coasts of the sheltered shores with rich fucoid vegetation preferred by this species. Its absence from southern shores is undoubtedly due to lack of suitable habitats there.

The habitat preferences of this species in Iceland appear almost identical to those of *M. obtusatus* but it is a much less common species. It is most common on the sheltered shores of type 5, and although not infrequent on shores of type 6 also (Table 2, Fig. 4) it occurs here significantly less often ($0.05 > P > 0.01$ for whole island). In other habitats it is much less common, but unlike *M. obtusatus* it has been found in a few samples from the lower reaches of estuaries (Tables 3 and 4).

M. finmarchicus is found at all tidal levels on shores of types 5 and 6, although it is scarce, as are other amphipods, above the fucoid zone (habitats 5.1 and 6.1) but as *M. obtusatus* it reaches maximum abundance rather low on the shore, in habitats 5.4, 5.5 and 6.4 (Fig. 5). Its frequency in samples from these habitats is, however, only significantly different from its frequency in samples from above and below this when samples from these two levels are pooled ($0.05 > P > 0.01$ for whole island).

On the western shores of the Atlantic *M. finmarchicus* is reported to occur on the average higher on the shore than *M. obtusatus* (Steele and Steele 1975b), but on the European coasts their preferred tidal levels appear to be similar (Brattegård 1966, Spooner 1957, Tzvetkova 1968) and the two are often said to occur together. Several authors mention a tendency for *M. finmarchicus* to occur in tidepools (Steen 1951, Jones 1948, Spooner 1957, Dennert 1973, Bousfield 1973). Bousfield (1973) even refers to it as being a dominant species of tidepools at about the level of MHW in New England. Tidepools at this level are in Iceland almost exclusively inhabited by *G. duebeni*, but *M. finmarchicus* has been found sparingly in tidepools lower on the shore.

Hyale nilssoni (Rathke)

Stephensen (1940) records this species from several localities, all except one (Djupivogur in southeastern Iceland) on southwestern coasts. I found the species to be quite common around the coasts of Iceland (excepting the south coast), although somewhat local on northern shores (Fig. 3). It seems to be most abundant in the southwest.

H. nilssoni is more difficult to collect than species of Gammaridae, because of its active behaviour, and may therefore be more common than the records indicate.

This species is almost totally confined to shores of types 5 and 6 with rich fucoid vegetation, and it is about equally common on both types (Table 2, Fig. 4). It has been found commonly at all tidal levels, but shows a clear preference for the upper part of the fucoid zone (Fig. 5). In particular it is common in the *P. canaliculata/F. spiralis* zone of these shores (habitats 5.2 and 6.2), being more frequent here than above the fucoids (habitats 5.1+6.1) ($P < 0.001$ for whole island) and immediately below (habitats 5.3+6.3) ($P < 0.001$ for whole island). This preferred level corresponds roughly with the area around MHWN on these shores. It is not found subtidally.

On both types of shores the species is much more frequent in samples from southern and western Iceland than in those from the north and east ($0.01 > P > 0.001$ for type 5 shores, $0.05 > P > 0.01$ for type 6 shores). In part this may be so because the algae from many sampling sites in southern and western Iceland were more thoroughly searched for amphipods (in the laboratory) than was possible for samples from other areas, and it was found that *H. nilssoni* constituted a much higher percentage of amphipods obtained from the algae than of amphipods collected by searching the sampling sites after the algae had been removed. In a number of samples from southwestern Iceland 70% of the 590 *H. nilssoni* obtained came from the algae, while for *M. marinus*, for example, the corresponding percentage was only 13% of the total of 129 animals. There was no apparent difference in this respect among the various Gammaridae species. This also shows that the microdistribution of *M. marinus* and *H. nilssoni* is clearly different, although they occur at similar levels on the same types of shores.

Habitats reported for the species elsewhere are on the whole similar (Bousfield 1973, Chevreux and Fage 1925, Goodhart 1941, Den Hartog 1963, Spooner 1957).

Orchestia gammarellus (Pallas)

This species was recorded from Iceland for the first time by Ingolfsson (1974). It has a very limited distribution, being confined to the extreme southwest, from the Vestmannaeyjar Islands to Reykjavik (Fig. 3). The species is quite common within its limited range.

In the survey the species occurred only in 4 samples, all taken from the *P. canaliculata/F. spiralis* zone (habitat 5.2) or *Puccinellia* salt marshes (habitat 11). In spring of 1975 much of the distributional area of the species was traversed on foot for the purpose of mapping the intertidal region. *O. gammarellus* was frequently encountered, specially under stones on *Puccinellia* salt marshes, which are at a slightly higher level than the uppermost *P. canaliculata*, but it was also found in the *P. canaliculata/F. spiralis* zone. In 1976 a survey of salt marsh animals by use of pitfall traps at Galgahraun near Reykjavik showed *O. gammarellus* to be abundant throughout the vertical extent of the marsh with a peak in the middle of the *Puccinellia* zone. The upper limit of the species appeared to the near the level of highest annual high water, considerably above the highest *Puccinellia* plants (Ingolfsson 1977).

These observations agree well with those from other regions (e.g. Den Hartog 1963).

Association of species

Association of species was tested by investigating by use of chi-square whether any two of the 9 most common species occurred more or less

Table 6

Chi-square tests of association among the 9 most common species of intertidal amphiods in northern and eastern Iceland (above diagonal, 436 samples) and in southern and western Iceland (below diagonal, 365 samples). Positive association is indicated by +, negative by –, and no association by O. Note: There are no tests involving *M. marinus* above diagonal and *M. stoerensis* below diagonal because of scarcity of these species.

	G. zaddachi	G. duebeni	M. finmarchicus	M. obtusatus	M. marinus	M. stoerensis	G. setosus	G. oceancius	H. nilssoni
G. zaddachi		+	–	– – –		–	– –	– – –	–
G. duebeni	0		– –	– – –		– –	– –	– – –	0
M. finmarchicus	0	– – –		+ + +		0	–	0	0
M. obtusatus	– –	– – –	+ + +			+	–	0	+ + +
M. marinus	0	0	0	0					
M. stoerensis							+ + +	+ + +	+
G. setosus	0	+ +	0	– –	0			+ + +	0
G. oceanicus	0	– –	0	– –	0		+		0
H. nilssoni	0	– – –	– – –	– –	+ +		– –	0	

Levels of significance:		
	+ or –	$0.05 > P > 0.01$
	+ + or – –	$0.01 > P > 0.001$
	+ + + or – – –	$P < 0.001$

often together in samples than predicted by chance. Separate analyses were performed for samples from northern and eastern and for southern and western Iceland. An analysis of this type would reveal similarities and dissimilarities in habitat preferences among species indepentently of the subjective definitions of habitat categories. As the samples are not, however, taken randomly in all possible habitats of the amphipods in question, some care is needed in interpreting the results.

The results are seen in Table 6. It is possible to distinguish the following groupings of species, although they are not distinct:

(a) *G. zaddachi and G. duebeni*
(b) *M. obtusatus* and *M. finmarchicus*
(c) *M. marinus* and *H. nilssoni*
(d) *G. oceanicus, G. setosus* and *M. stoerensis*

All four groups are interlinked by some positive associations except groups (a) and (b) and groups (a) and (c). All possible combinations (pairs) of the 9 species occurred at least once, except that *G. zaddachi* and *M. finmarchicus* were never found together in a sample.

The results are in general agreement with those obtained by habitat analysis, and indicate that the habitat categories here used are meaningful units with respect to habitat preferences of amphipods. Clearly *G. zaddachi* and *G. duebeni* form a group because they occur in low-salinity environments much more frequently than other species. In addition *G. setosus* has in southern and western Iceland withdrawn from most high-salinity environments occupied in the north and east, and therefore forms a positive association with *G. duebeni* in the former but not in the latter area. *M. obtusatus* and *M. finmarchicus* both occur primarily on shores of type 5. The majority of the samples (72%) from southern and western Iceland come from this type of shore. Tests of associations in this area are therefore largely tests of associations within this type of shore. In spite of this *M. obtusatus* and *M. finmarchicus* remain positively associated, whereas *M. obtusatus* and *H. nilssoni*, which are positively associated in samples from northern and eastern Iceland, become negatively associated here because of the difference in preferred tidal levels. *H. nilssoni* and *M. marinus*, on the other hand, occupy similar levels and are therefore positively associated. Finally, *G. oceanicus*, *G. setosus* and *M. stoerensis* form a group as they are all common on moderately exposed shores.

DISCUSSION

Distribution

Much evidence points to temperature being an important factor controlling the geographical distribution of marine animals (e.g. Hedgpeth 1957, Briggs 1974).

The sea surface temperature during winter around the coast of Iceland is highest off the south coast, being lower off the west coast while temperatures are similar and lowest off the northern and eastern coasts (Fig. 6). In summer, the temperature is highest off southern and western coasts, lower off the northern and northeastern shores and lowest off the middle of the east coast. There is a sharp temperature boundary off the southeast coast, where temperatures may change for 4–5°C over a distance of some 90 km (Stefánsson 1969). The above temperatures are based on data collected some distance from the shore and thus give only a rough indication of the sea temperatures experienced by intertidal animals.

Several authours (e.g. Stephensen 1940, Thorson 1941, Einarsson 1948, Madsen 1949) have investigated distributional patterns of marine animals in Iceland. Briggs (1974) summarizes the results as follows (p. 261): "Examination of data on the local distribution of both fishes and invertebrates show a definite pattern. Both the purely boreal species and the eurythermic temperate forms tend to be confined to the south and west coasts, the arctic species are mainly restricted to the north and east, and the arctic-boreal animals are generally found all around the island". Consideration of marine

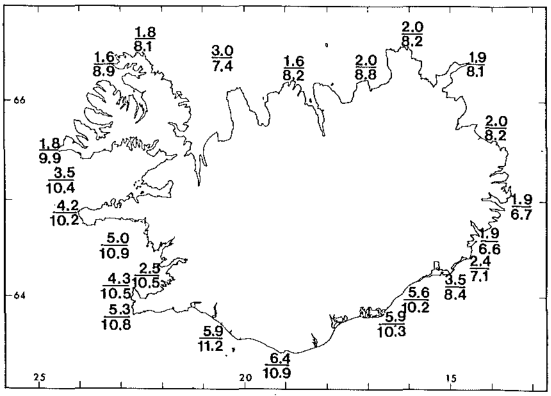

Figure 6. Mean surface temperatures at selected stations around the coast of Iceland in February (upper figures) and August (lower figures) based on data collected 1949 – 1966 (Stefansson 1969).

algae (J ó n s s o n 1912, A d e y 1968, M u n d a 1972, 1975) have yielded very similar results. The overall correspondence between distributional patterns and the temperature of the sea around the coasts of Iceland is therefore strong.

Few of the animals considered in the above surveys have been mainly intertidal in habits. For intertidal species both sea and air temperatures can be expected to be important, interacting in a complex manner (S o u t h w a r d 1958). In Iceland air temperatures at coastal stations generally decline from south to north (data in E y t h o r s s o n and S i g t r y g g s s o n 1971) on both western and eastern coasts. In summer, however, temperatures along the east coast are 1 – 2°C lower than at corresponding latitudes on the west coast and similar to temperatures of the north coasts. Based on average temperatures from 1931 – 1960, July temperatures range from a little more than 11°C in the extreme south to a little above 8°C in the north and east, while average January temperatures range from about 1 – 2°C in the extreme south to a little less than ÷2°C in the north. Sea temperatures exceed air temperatures during winter on all coasts, but the difference is smallest along the east coast (S t e f a n s s o n 1969). In summer, air temperatures usually exceed sea temperatures for some months, the difference being greatest along the east coast while on the south coast the difference is very small. On the whole air and sea temperatures around the coast of Iceland vary in a similar manner and it would be difficult to separate the effects of air and sea temperatures on distributional patterns of intertidal animals. Air temperatures probably somewhat reduce the difference in temperature regimes between the intertidal area of the east coast and that of other coasts, as compared with sublittoral habitats.

Of the 11 species of amphipods here considered, three have a limited distribution in Iceland. *O. gammarellus* is confined to the extreme southwest, while *M. marinus* is only found on southwestern and western shores. Both are therefore limited to the part of the Icelandic coasts where temperatures (both air and sea) are on the average highest. One species, *G. locusta*, seems to be lacking only from the east coast, where sea temperatures are on the average lower than elsewhere.

While *G. setosus* is found on all coasts, it is scarce on the warm southwestern coasts. The remaining species are found commonly on all coasts where suitable habitats exist.

All species considered occur in Norway. The first species to reach its northern limit here is *O. gammarellus* which has been recorded north to Væröy (67°40'N) (S t e p h e n s e n 1935 – 1942). The next is *M. marinus* for which the northernmost locality is Havöysund (71°00'N) (W . V a d e r pers. comm.). *G. locusta* occurs all the way to Vardö at the northeastern extremity of Norway (O l d e v i g 1959), and *M. stoerensis* extends slightly further eastwards into colder waters to Petsamo (S e g e r s t r å l e 1948). The remaining species extend still further eastwards. *H. nilssoni* does not appear to reach the White Sea, while *M. finmarchicus* and *M. obtusatus* do so (T z v e t k o v a 1968). Both *G. duebeni* and *G. zaddachi* reach still further eastwards. at least to the Kanin Peninsula (S e g e r s t r å l e 1948). Finally Both *G. setosus* and *G. oceanicus* extend to Spitsbergen and Novaya Zemlya (S t e e l e and S t e e l e 1974).

With the exception of *G. zaddachi*, *G. locusta* and *M. marinus* the above species also occur on the

Table 7

The order in which 11 species of intertidal amphipods occurring in Iceland reach distributional limits towards a colder temperature regime (see text for literature sources).

Europe	Iceland	America (east coast)
1. Orchestia gammarellus	1. O. gammarellus	1. M. stoerensis
2. Marinogammarus marinus	2. M. marinus	2—3. O. gammarellus
3. Gammarus locusta	3. G. locusta	M. finmarchicus
4. M. stoerensis		4. M. obtusatus
5. Hyale nilssoni		5. H. nilssoni
6— 7. M. obtusatus		6. G. duebeni
M. finmarchicus		7. G. oceanicus
8— 9. G. zaddachi		8. G. setosus
G. duebeni		
10—11. G. oceanicus		
G. setosus		

American shore of the Atlantic. Going northwards, *M. stoerensis* appears to reach its limit first, at Nova Scotia (Steele and Steele 1974). *O. gammarellus* and *M. finmarchicus* reach southern and eastern Newfoundland (Bousfield 1973, Steele and Steele 1974) while *M. obtusatus* extends to northern Newfoundland (Steele and Steele 1974). The ranges of *H. nilssoni* and *G. duebeni* extend to southern Labrador, while the latter species also occurs in Greenland (Bousfield 1973, Steele and Steele 1974). Finally *G. oceanicus* extends to northern Hudson Bay and western Greenland (ca 74°N) and *G. setosus* goes all the way to northern Ellesmere Island (ca 83°N) (Steele and Steele 1974).

On the whole the species drop out in the same order on both sides of the Atlantic as well as around Iceland as one moves into colder temperature regimes (Table 7). There appear to be two exceptions, if adequacy of distributional data can be assumed. The two talitrid species, *O. gammarellus* and *H. nilssoni*, extend considerably further into a cold temperature regime on the American side than on European coasts (including Iceland) relative to other species. This indicates that distributional limits of these two species are controlled in a fashion different from that of other species, and it may be significant that both species live under conditions where they may be more affected by air temperatures than other species here considered.

These considerations lead to the general conclusion that temperatures are somehow controlling the extension of the amphipods into cold temperature regimes. The way in which this is achieved is undoubtedly so complex (Southward 1958, Southward and Crisp 1954, Crisp and Southward 1958) that it may seem futile at this point to speculate further. It may be said, however, that in the present cases there seems to be a closer correspondence of distributional limits with summer sea temperatures (temperature data from Böhncke 1936 and Krauss 1958) rather than winter sea temperatures, although this corresspondance is certainly not very close for some species, and there is slight indication that sea temperatures are more important than air temperatures.

None of the species considered reach distributional limits towards a warmer temperature regime in Iceland, but *G. setosus* appears to come close to this. This is in agreement with its distribution elsewhere where its southern limit is further northward than that of the other species. In Norway the southernmost locality appears to be Röst (ca. 67½°N) (Stephensen 1935—1942), while in America its southern limit lies in Maine (Steele and Steele 1974).

On the basis of the distributional patterns of these amphipods, therefore, the temperature conditions in the intertidal region of Iceland appear to be similar to those found on the European Atlantic coast from about 67½°N north to a region near the border of Norway and the Soviet Union. The corresponding area on the western side of the Atlantic is more difficult to delimit, but appears to extend from Main north to Newfoundland.

The amphipod fauna of the intertidal zone of Iceland is clearly European in character rather than American. In Norway there are several species of intertidal amphipods of the families Gammaridae and Talitridae not found in Iceland. Among these, *Gammarus salinus* Spooner, *Marinogammarus pirloti* Sexton and Spooner, *Talitrus saltator* (Montagu) and *Talorchestia brito* Stebbing do not reach as far northwards as does *O. gammarellus* (Stephensen 1935–1942, Vader 1969, 1970, 1972). These species are therefore not to be expected in Iceland where *O. gammarellus* is only able to survive on the warmest coasts. *Hyale pontica* Rathke has on the other hand been found in Norway north to about 70°N (Vader 1971), i.e. considerably further north than *O. gammarellus* but not as far as *M. marinus*. The discovery of this species on the shores of southwestern Iceland is therefore to be expected in future studies.

Habitat preferences

The results show that each of the 11 species of intertidal amphipods here considered have their particular habitat distribution different from that of other species, with the exception of *M. obtusatus* and *M. finmarchicus* which appear very similar. All species show considerable overlap with at least one another species in habitat preferences, and few habitats are inhabited by only one species (mostly involving *G. duebeni*).

The habitat categories used in this study differ from each other in a number of recognizable ways. The four types of rocky seashores (habitat categories 5–8) differ in fucoid species composition, in fucoid cover, in total algal biomass, in degree of exposure to wave action, or possibly more relevantly, in degree of movement of the substrate, in amount of silt, and there are undoubtedly other unrecognized differences. The amphipods show a spatially successional series from sheltered shores with little movement of substrate and rich fucoid vegetation (type 5) to the exposed shores with considerable movement of substrate and no fucoids (type 8) as follows (Fig. 4): *M. obtusatus* and *M. finmarchicus* – *Hyale nilssoni* and *M. marinus* – *Gammarus oceanicus* and *M. stoerensis* – *G. setosus*. The overlap between adjacent species on this series is great and most species occur on all types of shores to some degree. It is not possible at the present time to correlate these differences among species with differences in their adaptations, and the elucidation of factors controlling habitat partitioning along this series will have to wait future studies.

Within each type of rocky shore the defined subhabitats differ in tidal levels, which in turn results in differences in species composition, biomass and cover of algae, in degree of exposure to air, fresh-water and sea-water, in temperature regimes, and in other ways. The amphipod species show more or less distinct preferences for particular tidal levels (Fig. 5), and they tend to occur in the following order, moving downwards on the shore: *O. gammarellus* – *G. duebeni* – *M. marinus* or *G. setosus* and *H. nilssoni* – *M. obtusatus* and *M. finmarchicus* – *G. oceanicus*. The vertical overlap between adjacent species is great. *G. duebeni* is known to be able to survive in saturated air better than *G. oceanicus* (Lagerspetz 1963) and *O. gammarellus* can survive considerable periods in saturated air (Williamson 1951), which agrees with the usual high position on general seashores of these two species. In addition it seems likely that the tolerance of *G. duebeni*, *G. setosus* and *M. marinus* to low salinities (see below) enables them to inhabit successfully high shore levels, where the effect of fresh-water run-off and precipitation can be expected to be considerable.

The habitats at different points in river channels in estuaries differ primarily in salinity regimes, and the amphipods tend to occur in the following order towards the sea, again with large overlap between adjacent species: *G. duebeni* – *G.*

zaddachi — *G. oceanicus* and *G. setosus*. In the intertidal region to each side of the river channel the difference among points at similar tidal levels along the estuary is presumably also primarily of salinity regimes, and here the order, going seawards, is usually as follows: *G. duebeni* — *G. oceanicus* and *G. setosus* — (*M. stoerensis* and *M. finmarchicus*). Experiments have shown (Beadle and Cragg 1940, Van Maren 1975, D. H. Steele and V. J. Steele 1970, V. J. Steele and D. H. Steele 1970, Sutcliffe 1968, Wernts 1963, and own unpublished data) that *G. duebeni* and *G. zaddachi* tolerate reduce salinities or fresh water better than other Gammaridae species here considered, *G. setosus* and *M. marinus* come next, while *G. oceanicus* and *M. finmarchicus* are considerably less tolerant. Finally *M. obtusatus* is relatively intolerant of low salinities, although still a euryhaline species (no information is available on *M. stoerensis*). The distribution of species in estuaries is in good agreement with the differences in adaptations to low salinities but other factors such as tolerance to desiccation are evidently involved also. In lagoons and coastal ponds species tend to occur in a similar order as in river channels, moving from lower to higher salinities. The absence of *G. zaddachi* from many small coastal ponds and from tidepools (p. 9.) is rather puzzling in view of its high tolerance to low salinities. It seems probable that low oxygen levels of these habitats, produced by rotting algae, are responsible for the absence of *G. zaddachi*. *G. duebeni* which thrives in these habitats is known to be considerably more resistant to low oxygen levels than *G. zaddachi* (Segerstråle 1946, Suomalainen 1958).

Temperature is clearly an important factor controlling macrodistributional patterns of intertidal amphipods but its role on a microdistributional scale is more difficult to evaluate. On the western coast of the Atlantic *G. setosus* withdraws to the outlets of cool fresh-water streams in summer towards it southern limit (V. J. Steele and D. H. Steele 1970), presumably because temperatures become too high for it elsewhere. In Iceland also, this arctic species occurs in a narrower range of habitats on the relatively warm southern and western coasts than in other parts. While the temperatures of the ponds and pools that the species especially inhabits in the south and west may become considerable higher than those of the sea on warm sunny days, the temperatures on the general seashore may be expected to become higher still under such conditions at low tide (Southward 1958), so as to make this habitat uninhabitable for the species. It is perhaps significant that *G. setosus* occurs on exposed shores in southern and western Iceland, where sea-spray may reduce the warming up of the shore at low tide in sunny weather, whereas it is almost totally lacking from sheltered shores here.

From the above it is clear that a number of interacting factors are controlling habitat selection of intertidal amphipods. Some of these factors can be identified, others not. Apart from physical factors, biotic factors can also be expected to be of importance, especially interspecific competition, which might enhance differences in habitat selection among species. There is, however, little evidence for this offered by the present data. In particular, the absence of *M. marinus* from northern and eastern coasts does not affect the vertical distribution of such species as *M. obtusatus*, *M. finmarchicus* and *G. oceanicus*. In the Netherlands *M. marinus* extends to lower levels on the shore when *M. obtusatus* is absent, while there is a sharp boundary between the two when both are present (Den Hartog 1964, Vader 1965). Den Hartog (1964) believes this to be due to interspecific competition. Goodhart (1941) also states that the two are never found together, although they may occur at similar tidal levels, while Brattegård (1966), Pinkster and Stock (1970), and Van Maren (1975) have often found the two together. Van Maren (1975) also found that *M. marinus* did not extend further down on the shore than usual south of the range of *M. obtusatus*, and she believes, as did Vader (1965), that habitat differences between the two where the result of preferences for different substrates, *M. marinus* preferring more muddy substrates than

M. obtusatus. No difference in this respect can be discerned in the Icelandic data (if anything, *M. obtusatus* has been recorded more often from mud than *M. marinus*) but neither is there an indication of strong competition between them there. Although the two prefer different tidal levels, the overlap is great. Of the total of 86 samples from Iceland containing *M. marinus, M. obtusatus* was thus present in no less than 40.

M. marinus and *G. setosus* occupy very similar levels on the shore in Iceland and may occur on similar shores (Fig. 5) but the two were only found together in two samples of the total of 95 containing either species from within the distributional area of *M. marinus*. As the temperature regime of the warm shores of southern and western Iceland is probably getting close to the limit that *G. setosus* can tolerate, it may not be able to withstand competition from *M. marinus* here and may only be able to succeed in habitats where the latter species is rare or absent (exposed shores, coastal ponds, tidepools). It is worth keeping in mind in this connection that the two species could possibly replace each other geographically as competitors of other species, and if so the effects of competition might be difficult to detect by comparisons of habitat partitioning among species within and outside the distributional area of *M. marinus*.

No significant differences were found between habitat preferences of *M. obtusatus* and *M. finmarchicus* in Iceland, and there is a high degree of positive correlation between their occurrances in samples. The two are known to differ in their tolerance to reduced salinities, and it seems likely that an investigation on a finer scale than here used would reveal differences between them, perhaps related to the microdistribution of salinities on the shore at low tide.

The shores of southern and western Iceland differ from those of northern and eastern Iceland in tidal range, this being about 3—4.5 m at spring tides in the former area and 1—2 m in the latter. The only recognizable effect of tidal range on amphipods is a reduction in the vertical range of preferred areas of each species on northern and eastern coasts as compared to what obtains elsewhere.

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