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Bathymetric distribution of Mysidacea in fjords of western Norway

Jan Helge Fosså, Torleiv Brattegard

Department of Marine Biology, University of Bergen, N-5065 Blomsterdalen, Norway

ABSTRACT: Depth distributions of 20 mysid species sampled between 32 and 1260 m are presented. A total of 113 sledge samples from 67 stations are evaluated. A change in the mysid fauna correlated to depth was found from the shallowest station and down to about 350 m. Below 350 m, fauna differences between fjords were greater than depth-related variations within fjords. Epibenthic species of *Erythrops* were found throughout the whole bathymetric range and of *Pseudomma* from 166 to 1260 m. Shallower than 100 m *Schistomysis ornata* and *Leptomysis gracilis* dominated by number, while deeper *Boreomysis megalops* and *B. arctica* dominated. Possible effects of the fjord sills on the faunal distribution are discussed. Bathymetric species groups containing all known mysid species from the studied area are proposed: 0 to 50 m containing 13 species, 30 to 100 m containing 5 species, 100 to 350 m containing 5 species, > 250 m containing 9 species.

INTRODUCTION

In recent years knowledge on the biology and behaviour of hyperbenthic mysids living in Norwegian fjords has increased. Autecological studies have been performed on *Boreomysis arctica* by Jakupsstovu (1970), *Lophogaster typicus* by Bjerkestrand (1979) and *Praunus flexuosus* by Attramadal (1980). Ecological and behavioural studies have been performed on various species (Matthews & Bakke 1977, Attramadal et al. 1985, Fosså 1985, 1986, Kaartvedt 1985, 1989) and biochemical aspects primarily on *B. arctica* by Brattelid & Matthews (1978) and Båmstedt (1978, 1981). Mattson (1981) analyzed the importance of mysids as food for fish on prawn trawl grounds. However, much basic knowledge about the mysid species is still not available, including depth distributions of species in the fjords.

There are many observations on the depth occurrences of mysids (e.g. Tattersall & Tattersall 1951), but few investigations describe continuous distributions, and those which do (e.g. Hargreaves 1985a, b, Murano 1975, 1976, 1977) are often concentrated on pelagic oceanic species.

Information on the bathymetric distribution of deep-living hyperbenthic species found in Norwegian waters has been gained in other areas (e.g. Mauchline 1982, 1986, Astthorsson 1984, 1985). However, indirect methods, such as information obtained from stomach content analyses of fish from different depths, have often been used.

The present paper presents results on the bathymetric distribution of species, number of species, and number of individuals of primarily hyperbenthic mysids on level bottoms in west Norwegian fjords. The depth range covered by sampling was 32 to 1260 m. Bathymetric species groups are proposed and an overview is presented of all species known from the area.

STUDY AREA

Several of the main fjord systems of western Norway, including the deepest threshold fjord known, Sognefjorden (maximum depth 1308 m), were studied (Fig. 1). The fjords in the northern area (Stns 1 to 10) have sill depths between 126 and 200 m. Sognefjorden has an outer sill of 164 m depth while the tributary fjords have no sills. The fjords in the Bergen area have sill depths of 200 m, Hardangerfjorden 150 m, and the inner sills of the fjords of Ryfylke 100 to 120 m.

While watermasses above sill depth in a fjord have free exchange with coastal water outside the fjord, exchange processes in the basin water below sill depth are hampered by the sill. Exchange occurs only when sufficiently dense water appears outside and above the sill. Renewal of the basin water may be partial, or all the old basin water may be flushed out of the fjord. In some

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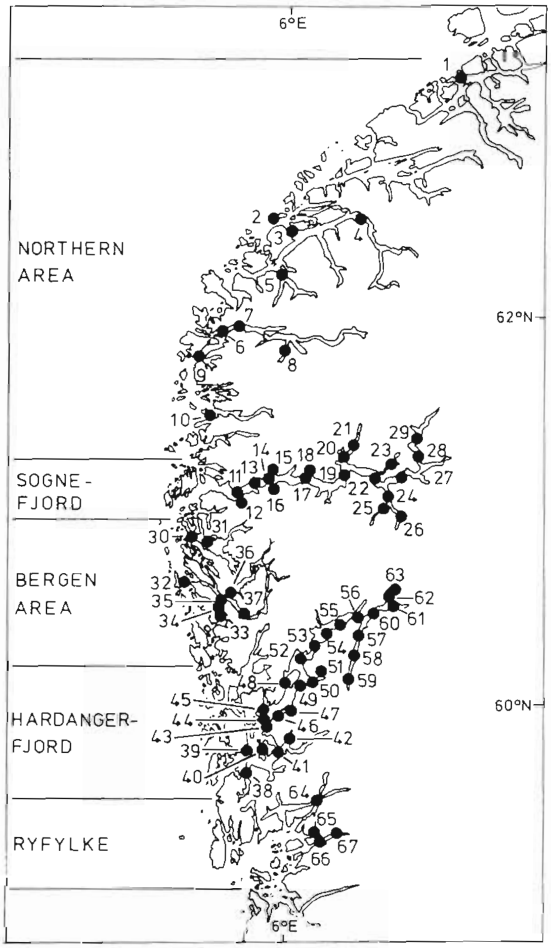

Fig. 1. Sampling stations in fjords of western Norway. (Names indicated for sub-regions are only valid for this investigation)

fjords renewal of the basin water may occur at intervals of several years, for instance about 10 yr in Sognefjorden and Nordfjord (Stns 6 to 8). In some fjords with shallow sill depth and small watermasses a stagnant period may lead to low oxygen levels due to biological respiration and chemical oxygen demand (Aure & Stigebrandt 1989). It is not known whether any of the stations in the present investigation have had seriously low oxygen levels, i.e. below 2 mg l^{-1} (= 1.4 ml l^{-1}) (Rosenberg 1980). In Sognefjorden, for instance, the lowest oxygen level recorded in the period 1919 to 1970 at 800 to 1200 m was 4.9 ml l^{-1} (72 % saturation) (Hermansen 1974). In Nordfjord, which was studied during the period 1931 to 1954, the lowest oxygen content at 400 m was 2.9 l^{-1} (45 % saturation) (Sælen 1967).

MATERIAL AND METHODS

Sampling. Samples were collected at 67 different stations in the major fjord systems in western Norway between 1978 and 1985 (Fig. 1, Table 1). Some of the mysids, especially those living shallower than about 300 m, are known to undertake diurnal vertical migrations (Kaartvedt 1985, 1989, Fosså 1986). As a consequence, the number of individuals caught during night and day may differ considerably. To avoid this effect we analyzed only daytime hauls from 0 to 300 m but both daytime and night-time hauls from deeper than 300 m. A total of 113 samples were used in this work.

Sampling was performed with a slightly modified Rothlisberg and Pearcy epibenthic sledge (Rothlisberg & Pearcy 1977, Buhl-Jensen 1986, Brattegard & Fosså unpubl.). The 1 m wide opening of the 0.5 mm meshed net samples from 26 to 59 cm above the sediment when the sledge is in contact with the bottom. When the sledge leaves the bottom the net is closed and precludes pelagic contamination. Most hauls lasted about 20 min at a mean velocity of about 1 knot, which gives a sampled distance of maximally 617 m or an area of 617 m^2. Numbers of individuals in each haul were standardized to a 1000 m long haul. One sample (1978) was made from RV 'August Brinkmann d.e.', the rest from RV 'Håkon Mosby'.

Numerical methods. The entire bathymetric range covered was divided into 12 depth zones of 100 m, except for the shallowest and deepest zones which were 68 and 160 m, respectively. Pooling of data from different stations into bathymetric zones will obscure between-station variance but depth gradients will be more easily recognized. This effect was, however, desirable in this study. The range of 100 m was chosen because a finer partitioning would have resulted in too few samples within some of the bathymetric zones while a coarser partitioning would be less sensitive.

Middle depth (Md) calculated for a species was defined as:

$$Md = \sum_{i=1}^{n} \frac{N_i\, i}{N}$$

where N_i = number of the species in one haul at depth i; N = total number of individuals of the species in all samples; n = number of samples. The average number of individuals per haul within each bathymetric zone was used when calculating Md.

The sampling intensity was different in the different zones, and rarefaction curves were calculated according to Hurlbert (1971) in order to detect undersampling (Heck et al. 1975, Haila 1983). For this, the number of new species obtained per sample as a function of sample number was plotted.

Affinities between stations and species were analyzed by means of Detrended Correspondence Analysis (DCA) where detrending by polynomials was used. This procedure is superior to detrending by segments

Table 1. Samples using RP-sledge from fjords of western Norway between July 1978 and February 1985

Stn	Depth (m)	Fjord	Date	Time (h)	Latitude N	Longitude E
1	326	Talgsjøen	9 Jun 81	18:40	63° 08.4′	07° 52.8′
2	258	Breisund	10 Jun 81	06:05	62° 28.1′	05° 50.2′
2	258	Breisund	12 Aug 81	13:20	62° 28.4′	05° 47.7′
3	450	Sulafjorden	19 Mar 81	02:05	62° 24.9′	06° 02.7′
3	450	Sulafjorden	19 Mar 81	13:10	62° 25.0′	06° 02.3′
3	446	Sulafjorden	10 Jun 81	07:40	62° 25.1′	06° 01.0′
3	445	Sulafjorden	12 Aug 81	07:35	62° 25.3′	06° 01.6′
3	447	Sulafjorden	13 Aug 82	17:00	62° 23.5′	06° 04.2′
3	450	Sulafjorden	14 Oct 84	13:15	62° 24.2′	06° 03.3′
4	679	Storfjorden	12 Aug 81	04:10	62° 26.7′	06° 50.3′
5	700	Voldafjorden	10 Jun 81	18:15	62° 10.4′	05° 57.7′
5	695	Voldafjorden	11 Aug 81	19:25	62° 10.2′	05° 59.7′
5	699	Voldafjorden	14 Oct 84	16:45	62° 10.3′	05° 58.7′
6	490	Nordfjorden	11 Jun 81	23:50	61° 54.1′	05° 19.0′
7	584	Nordfjorden	11 Aug 81	13:25	61° 55.4′	05° 26.7′
7	580	Nordfjorden	13 Aug 82	07:00	61° 55.5′	05° 28.1′
7	580	Nordfjorden	27 Nov 82	20:30	61° 55.4′	05° 25.3′
7	578	Nordfjorden	18 Jun 83	17:15	61° 55.4′	05° 25.3′
7	586	Nordfjorden	12 Oct 84	06:20	61° 55.4′	05° 27.0′
8	142	Hyenfjorden	12 Oct 84	14:10	61° 46.8′	05° 57.9′
9	382	Frøysjøen	11 Jun 81	05:10	61° 47.3′	05° 02.3′
9	366	Frøysjøen	11 Aug 81	07:35	61° 47.6′	05° 02.8′
10	419	Stavfjorden	11 Aug 81	03:25	61° 28.0′	05° 07.0′
10	418	Stavfjorden	12 Aug 82	19:40	61° 28.1′	05° 07.3′
10	420	Stavfjorden	28 Nov 82	12:05	61° 28.1′	05° 07.2′
11	1250	Sognefjorden	22 Nov 80	03:15	61° 03.0′	05° 25.0′
11	1250	Sognefjorden	13 Mar 81	00:00	61° 01.4′	05° 20.2′
11	1250	Sognefjorden	11 Jun 81	12:20	61° 02.8′	05° 25.0′
11	1256	Sognefjorden	10 Aug 81	21:35	61° 02.8′	05° 25.0′
11	1252	Sognefjorden	24 Aug 82	00:45	62° 02.9′	05° 24.9′
11	1250	Sognefjorden	28 Nov 82	17:45	61° 03.4′	05° 22.5′
11	1250	Sognefjorden	9 Oct 84	00:20	61° 03.1′	05° 24.5′
12	135	Risnefjorden	17 Jan 82	08:50	61° 01.6′	05° 28.7′
12	116	Risnefjorden	16 Jun 83	12:40	61° 01.5′	05° 29.1′
12	100	Risnefjorden	23 Nov 84	14:00	61° 01.3′	05° 28.6′
13	1257	Sognefjorden	24 Mar 85	07:25	61° 06.6′	05° 36.0′
14	1260	Sognefjorden	17 Jan 82	00:25	61° 08.6′	05° 46.1′
15	230	Vadheimsfjorden	17 Jan 82	12:20	61° 11.1′	05° 48.5′
15	233	Vadheimsfjorden	10 Oct 84	09:10	61° 11.3′	05° 48.5′
16	144	Fuglesetfjorden	17 Jan 82	10:55	61° 05.6′	05° 49.9′
16	147	Fuglesetfjorden	23 Nov 84	08:40	61° 05.5′	05° 50.0′
17	1235	Sognefjorden	17 Jan 82	17:00	61° 08.3′	06° 09.1′
18	40	Lånefjorden	22 Nov 84	15:05	61° 10.9′	06° 14.2′
19	1100	Sognefjorden	24 Nov 80	07:30	61° 10.6′	06° 33.1′
19	1106	Sognefjorden	18 Jan 82	04:50	61° 09.2′	06° 35.7′
19	1091	Sognefjorden	10 Oct 84	12:45	61° 10.2′	06° 35.9′
19	1040	Sognefjorden	18 Jan 82	00:05	61° 10.4′	06° 41.4′
20	296	Fjærlandsfjorden	18 Jan 82	11:15	61° 13.7′	06° 34.3′
21	217	Fjærlandsfjorden	18 Jan 82	09:40	61° 18.6′	06° 40.9′
22	860	Sognefjorden	19 Jan 82	05:10	61° 07.4′	06° 54.2′
23	260	Sogndalsfjorden	18 Jan 82	14:10	61° 12.5′	07° 06.0′
24	506	Aurlandsfjorden	18 Jan 82	21:10	61° 00.9′	07° 02.8′
24	504	Aurlandsfjorden	11 Oct 84	13:45	61° 00.8′	07° 02.8′
25	32	Nærøyfjorden	11 Oct 84	11:25	60° 55.7′	06° 52.7′
26	410	Aurlandsfjorden	18 Jan 82	17:00	60° 56.7′	07° 09.3′
26	412	Aurlandsfjorden	11 Oct 84	08:00	60° 56.9′	07° 09.2′
27	935	Sognefjorden	19 Jan 82	10:15	61° 07.7′	07° 08.9′
28	648	Lusterfjorden	20 Jan 82	00:10	61° 14.7′	07° 21.7′
29	373	Lusterfjorden	19 Jan 82	19:30	61° 20.7′	07° 22.0′
30	470	Fensfjorden	24 Nov 80	20:30	60° 50.7′	04° 52.4′
30	470	Fensfjorden	11 Jun 81	20:00	60° 50.7′	04° 52.4′

Table 1 (continued)

Stn	Depth (m)	Fjord	Date	Time (h)	Latitude N	Longitude E
30	460	Fensfjorden	10 Aug 81	18:15	60° 50.7′	04° 52.4′
30	460	Fensfjorden	15 Nov 82	16:35	60° 51.5′	04° 55.5′
30	461	Fensfjorden	9 Oct 84	15:35	60° 50.9′	04° 55.2′
31	544	Fensfjorden	11 Jun 81	22:00	60° 49.8′	05° 03.2′
32	260	Hjeltefjorden	4 Jul 78	14:00	61° 35.0′	04° 55.0′
33	310	Byfjorden	17 Nov 83	01:00	60° 25.4′	05° 16.5′
34	315	Byfjorden	16 Nov 83	23:45	60° 29.1′	05° 14.2′
35	522	Byfjorden	16 Nov 83	19:25	60° 30.7′	05° 15.6′
36	591	Osterfjorden	16 Nov 83	14:45	60° 34.3′	05° 23.7′
37	218	Sørfjorden	16 Nov 83	12:35	60° 27.4′	05° 28.6′
38	454	Ålfjorden	1 Feb 83	19:20	59° 39.5′	05° 33.1′
39	366	Klosterfjorden	1 Feb 83	21:10	59° 45.6′	05° 35.4′
39	365	Klosterfjorden	2 Feb 85	21:40	59° 45.3′	05° 34.9′
39	368	Klosterfjorden	3 Feb 85	09:25	59° 45.3′	05° 35.3′
40	74	Eidsvik	31 Jan 85	14:20	59° 48.4′	05° 41.9′
41	335	Skåneviksfjorden	31 Jan 83	22:10	59° 48.9′	05° 53.0′
42	285	Matrefjorden	1 Feb 83	12:25	59° 48.5′	05° 58.2′
42	283	Matrefjorden	2 Feb 85	14:15	59° 48.3′	05° 58.0′
43	350	Husnesfjorden	31 Jan 85	21:15	59° 53.1′	05° 44.9′
43	320	Husnesfjorden	1 Feb 85	12:30	59° 53.9′	05° 44.4′
44	511	Husnesfjorden	31 Jan 83	16:45	59° 54.1′	05° 43.6′
44	509	Husnesfjorden	1 Feb 85	13:30	59° 54.4′	05° 44.4′
45	125	Onarheimfjorden	1 Feb 85	14:40	59° 57.1′	05° 41.4′
46	166	Onarheimfjorden	31 Jan 83	14:25	59° 57.2′	05° 52.9′
46	164	Onarheimfjorden	1 Feb 85	10:10	59° 57.2′	05° 53.1′
47	223	Onarheimfjorden	31 Jan 83	13:20	59° 58.2′	05° 58.7′
47	217	Onarheimfjorden	1 Feb 85	09:10	59° 58.2′	05° 59.2′
48	482	Øynefjorden	28 Jan 83	17:20	60° 07.2′	05° 55.9′
49	663	Sildafjorden	31 Jan 83	03:20	60° 06.2′	06° 05.9′
49	660	Sildafjorden	1 Feb 85	22:25	60° 06.5′	06° 06.6′
49	662	Sildafjorden	2 Feb 85	10:40	60° 06.8′	06° 06.3′
50	274	Maurangerfjorden	2 Feb 85	09:15	60° 07.2′	06° 14.2′
51	197	Maurangerfjorden	31 Jan 83	09:15	60° 08.5′	06° 16.4′
52	641	Hissfjorden	28 Jan 83	19:40	60° 14.1′	06° 05.6′
53	835	Samlafjorden	31 Jan 83	00:30	60° 17.9′	06° 12.4′
54	854	Samlafjorden	30 Jan 83	20:20	60° 21.6′	06° 18.6′
55	856	Samlafjorden	30 Jan 83	17:45	60° 25.0′	06° 26.6′
56	712	Utnefjorden	29 Jan 83	18:45	60° 24.8′	06° 41.1′
57	302	Sørfjorden	30 Jan 83	08:00	60° 21.8′	06° 39.2′
58	386	Sørfjorden	30 Jan 83	12:40	60° 14.7′	06° 35.6′
59	296	Sørfjorden	30 Jan 83	10:55	60° 10.0′	06° 33.7′
60	524	Eidfjorden	29 Jan 83	17:10	60° 27.7′	06° 46.9′
61	386	Eidfjorden	29 Jan 83	13:00	60° 29.8′	07° 00.1′
62	254	Osafjorden	29 Jan 83	09:55	60° 32.3′	06° 57.1′
63	137	Osafjorden	29 Jan 83	08:05	60° 34.3′	07° 00.0′
63	131	Osafjorden	29 Jan 83	08:55	60° 34.3′	07° 00.2′
64	404	Sandsfjorden	8 Nov 83	09:30	59° 30.0′	06° 14.5′
64	420	Sandsfjorden	8 Nov 83	16:55	59° 30.0′	06° 14.5′
65	315	Erfjorden	8 Nov 83	19:45	59° 19.0′	06° 13.0′
65	309	Erfjorden	9 Nov 83	14:15	59° 19.0′	06° 13.5′
66	643	Jøsenfjorden	9 Nov 83	10:40	59° 17.4′	06° 18.7′
67	110	Jøsenfjorden	9 Nov 83	08:55	59° 19.1′	06° 26.5′

(ter Braak 1987a). A computer program by ter Braak (1987b) was used. Correspondence analysis (CA) constructs the theoretical variable that best explains the species data. The method does so by choosing the best values for the sites, i.e. values that maximize the dispersion of the species scores. The next axes also maximize the dispersion but subject to the constraint of being uncorrelated with previous axes. This ensures that new information is expressed on the later axes (ter Braak 1987a). The ordination axes (= eigenvectors) denote a point in a multidimensional space and the eigenvalues are equal to the dispersion of species scores. DCA was performed on all 67 stations without pooling into depth intervals.

The related TWINSPAN analysis (Two-way Indicator Species Analysis), which is a dichotomized ordination method based on the partitioning of the first axis of basic CA (Hill 1979, Gauch & Whittaker 1981) was used to separate (1) species groups and (2) groups of bathymetric zones along ordination axis 1. Six pseudospecies cut levels were used (0, 2, 10, 50, 100, 400) (which gives a crude scale of 5 abundance levels used in the analysis; see Hill [1979] for explanation of terms). TWINSPAN first classifies the samples (depth intervals) and then uses this classification to obtain a classification of the species. The result from a (D)CA-ordination is usually plotted in a system of axes and the ordination space partitions are imposed subjectively (drawn on the figure by hand) whereas TWINSPAN partitions are 'objective' and automatic (Gauch 1982).

Table 2. Number of hauls, mean number of individuals of mysids per haul, and total number of species in the different bathymetric zones in all fjords. N: number of species having their upper N(u) and lower N(l) limits in the defined bathymetric zones

Bathymetric zone (m)	Hauls	Ind. haul^{-1}	Species	N(u)	N(l)
32– 100	3	4977	9	9	2
100– 200	12	1389	11	4	2
200– 300	16	372	14	5	1
300– 400	18	279	15	1	1
400– 500	21	324	13		1
500– 600	13	193	11		2
600– 700	7	259	9		2
700– 800	4	133	7		3
800– 900	4	122	6		1
900–1000	1	352	5		
1000–1100	4	94	4		1
1100–1260	10	201	3		3

RESULTS

Number of species and individuals in depth zones

The average numbers of individuals per haul were relatively high, 4977 and 1389, in the 2 zones shallower than 200 m (Tables 2 and 3). *Schistomysis ornata* and *Leptomysis gracilis* were the most abundant species, but *Lophogaster typicus, Erythrops serrata* and *Boreomysis megalops* were also found in high numbers. Below 200 m the range of average number of individuals per haul in the depth zones was 94 to 372. The numbers per haul were slightly higher in the upper part of the bathymetric range.

A total of 20 mysid species were found in the geographic and bathymetric range covered. *Boreomysis*

Table 3. Depth intervals (m) and species ordered according to TWINSPAN results performed on mean abundance data of species in defined depth intervals. Minimum (Min) and maximum (Max) depth of occurrence, and middle depth (Md) based on data from all stations. (Full species names are given in Table 4)

	Species	Min	Md	Max	Mean abundance											
					Group I		Group II			Group III			Group IV			
					32–100	100–200	200–300	300–400	400–500	500–600	600–700	700–800	800–900	900–1000	1000–1100	1100–1260
1	*S. norvegica*	40	45	74	13											
	M. angusta	32	43	74	4											
	E. elegans	32	40	100	20	1										
	S. ornata	32	66	350	2846	8	1	1								
	L. gracilis	32	89	166	1256	481										
	L. typicus	32	88	296	489	167	2									
	E. serrata	40	113	490	326	136	32	23	1							
2	*B. megalops*	74	176	663	5	485	159	2	1	1	1					
	M. didelphys	40	194	700	18	22	3	6	2	4	1	1				
3	*M. typica*	100	175	663		82	12	6	1		1					
	P. obesa	135	287	509		3	3	6	1	1						
4	*P. affine*	166	345	585		1	33	9	27	1						
	M. insignis	110	487	1100		3	13	10	7	4	4	5	3	3	2	
5	*H. abyssicola*	254	438	700			1	41	9	19	6	1				
	E. microps	200	481	935			1	30	18	3	2	1	1	7		
	E. abyssorum	254	639	856			23	30	20	21	76	97	56			
6	*A. abbreviata*	254	570	1260			77	33	51	18	4	6	4	25	4	36
	B. arctica	254	774	1260			12	60	149	113	164	22	50	231	73	129
	P. roseum	320	838	1260				22	37	8			8	86	15	36

tridens was only recorded at Stn 1 and is only included in the DCA analysis in the following. The number of species increased from 9 in the shallowest zone to a maximum of 15 in the 300 to 400 m zone, and decreased to 3 species in the 1100 to 1260 m zone (Table 2). A steady decrease in species richness with depth of about 2 species per 100 m was found below 400 m and no species were added to the mysid fauna below 400 m.

There was a high correlation between number of species caught and the number of hauls within each bathymetric zone ($r = 0.79$, $p = 0.005$). To determine if this was a coincidence or a real interdependence, rarefaction curves were calculated (Fig. 2). Most of the curves level off against an asymptotic value indicating sufficient sampling. The curves for the 600 to 700 m and 700 to 800 m bathymetric zones end rather steeply, thus indicating undersampling of species. The curve for the 32 to 100 m bathymetric zone also levels off. This was rather unexpected because only 3 stations were sampled. However, the theoretical model for the distribution of species among individuals suggests that this zone was sufficiently sampled. Plots of cumulative number of species versus number of samples (not shown) indicated, as the rarefaction-curves did, undersampling between 600 and 800 m, but also for the 32 to 100 m zone.

Multivariate analyses

DCA was performed on $\ln(x+1)$ transformed mean abundance data from the 67 stations (Figs. 3 and 4). The eigenvalues for the 4 first axes were 0.756, 0.250, 0.169 and 0.132, respectively, indicating that the plots in Figs. 3 and 4 depict about 77 % of the variation in the species data. Ordination axis 1 was significantly correlated with depth ($r = -0.68$, $p < 0.001$) indicating that this axis in essence is describing variance ascribable to depth. Sample scores on axis 1 were plotted against depth (Fig. 5) and clearly showed a steep gradient with depth down to about 350 m. Below 350 m there was little change related to depth. The ordination plot of samples (Fig. 4) shows that below 350 m the samples spread out along axis 2. This effect was mainly due to *Erythrops abyssorum* and *Pseudomma roseum* having the highest and lowest scores on axis 2, respectively (Fig. 3). *E. abyssorum* was found at deep stations in all areas except in Sognefjorden and had a frequent and wide distribution in Hardangerfjorden. *P. roseum* was found in every haul deeper than 860 m in Sognefjorden (corresponds to the cluster of stations down to the left in Fig. 4), and only sparsely at a limited depth range (335 to 510 m) in Hardangerfjorden.

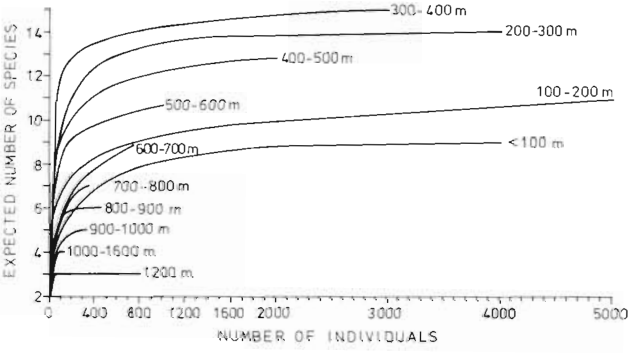

Fig. 2. Rarefaction curves for 12 defined bathymetric zones

TWINSPAN classified the bathymetric zones into 4 groups (Table 3). The main division (the first division) occurred at 200 m, and then 2 further divisions occurred at 500 and 800 m, respectively. The species were classified into 6 groups. The first division separated species with main abundance above and below 200 m. Below we summarize the characteristics of the groups.

Species group 1. All species in the group had their only or highest abundance in the 32 to 100 m zone.

The upper limit of the bathymetric distribution for the 7 species in this group could not be established because no samples were taken above 32 m. The lower

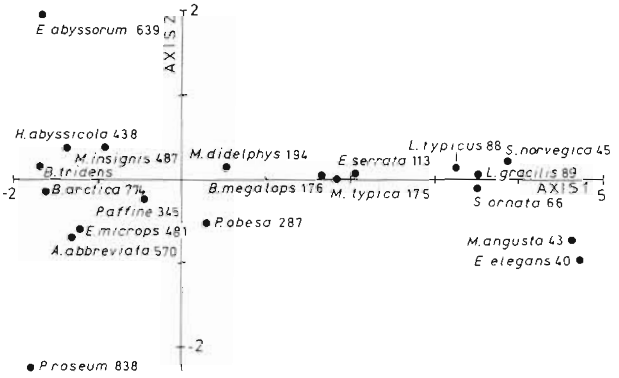

Fig. 3. Correspondence ordination of the 20 mysid species along axes 1 and 2. The middle depth (m) is given together with the species name

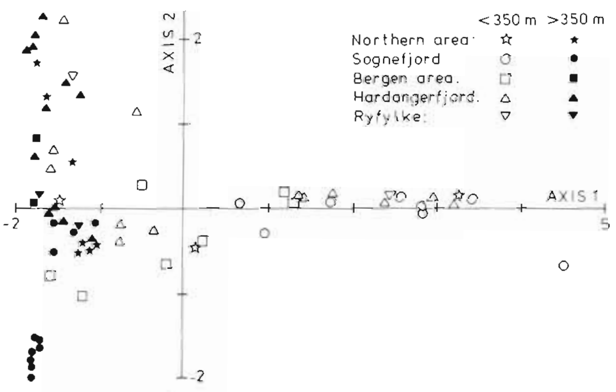

Fig. 4. Correspondence ordination of 67 stations from fjords in western Norway. Open symbols: stations shallower than 350 m; filled symbols: deeper stations. Five sub-regions (defined in Fig. 1) are separated using different symbols

limits of the species are well defined because of the comprehensive sampling in the depth range of their deepest distribution (Fig. 6, Table 2).

Siriella norvegica, *Mysidopsis angusta* and *Erythrops elegans* had the shallowest distributions, with lower depth limits at 74, 74, and 100 m, respectively. The other species in this group (Table 3) were also common between 100 and 200 m and even if the abundances were low they showed a quite high frequency of occurrence in this zone. *E. serrata* was recorded down to 490 m.

Species group 2. *Mysidopsis didelphys* and *Boreomysis megalops* were both present in the shallowest zone, had their highest abundance in the 100 to 200 m zone, and showed a wide depth distribution (Fig. 6). *M. didelphys* was not abundant. In the range 100 to 300 m, *B. megalops* had a high frequency of occurrence and was the most abundant mysid (Table 3).

Species group 3. *Mysidella typica* was caught at every station between 100 and 200 m and had its highest abundance in this range. *Parerythrops obesa* was both less frequent and less abundant and seemed to prefer deeper stations than *M. typica*. Neither species was recorded in the shallowest zone.

Species group 4. The 2 species *Pseudomma affine* and *Mysideis insignis* were recorded in the 100 to 200 m zone and had their main abundance between 200 and 500 m. *P. affine* seemed to be concentrated in the 200 to 500 m range but with 2 peaks. *M. insignis*, although not abundant, showed a remarkably high frequency of occurrence through its whole depth range (Fig. 6).

Species group 5. The 3 species did not occur shallower than 200 m and were not caught in the deepest part of Sognefjorden. They had a wide bathymetric distribution: *Erythrops microps* was distributed from 200 to 935 m, *E. abyssorum* from 254 to 856 m and *Hemimysis abyssicola* from 254 to 700 m with one peak at 300 to 400 m and another at 500 to 600 m.

Species group 6. *Amblyops abbreviata*, *Boreomysis arctica* and *Pseudomma roseum* were present at the deepest stations sampled but not recorded shallower than about 250 m. *A. abbreviata* and *B. arctica* had the same bathymetric range (254 to 1260 m), but differed in middle depth (Table 3). *A. abbreviata* was most abundant in the 200 to 300 m zone while *B. arctica* was more evenly distributed. The apparent peak between 900 and 1000 m for *B. arctica* was based on one single haul and could be coincidental. *B. arctica* was present in every haul deeper than 300 m and was the most frequent and abundant of all species in this depth range (Fig. 6). *P. roseum* had a bimodal distribution. In Sognefjorden it was only found at 860 m and deeper. In the other fjords it was only found between 320 and 544 m.

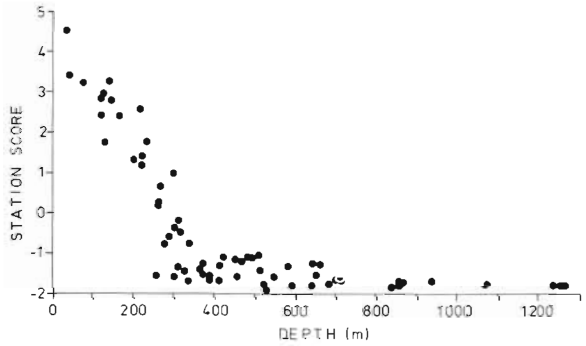

Fig. 5. Station scores on the first axis of the correspondence analysis plotted against the depth of each station

Congeneric species

The 4 species of *Erythrops* were clearly separated in depth distribution (Fig. 6) and along axis 1 of DCA they were separated by 2.8 to 3.7 SD units, except *E. microps* and *E. abyssorum* which separated along axis 2 by 2.6 SD units (Fig. 3). *Pseudomma affine* and *P. roseum* also had different depth distributions – the first typified the shallower species. Both species were absent at the deepest stations in Hardangerfjorden and *P. affine* was not recorded in Sognefjorden at all. *Boreomysis megalops* and *B. arctica*, and *Mysidopsis angusta* and *M. didelphys* also had different depth distributions with slight overlap.

DISCUSSION

General distributions of species

The sampling effort was not evenly distributed in the bathymetric range covered (Table 2). Relatively few samples were taken shallower than 100 m and between 600 and 1100 m, partly due to lack of suitable level bottoms for towing the RP-sledge. The high correlation between number of samples and species within the bathymetric zones may indicate a causal relationships with the sampling effort. The rarefaction curves (Fig. 2) and sample-species plot (not included) do indicate an undersampling in the 32 to 100, 600 to 700 and 700 to 800 m ranges. The peak in number of species in the 300 to 400 m zone might consequently be questioned. Especially in the 32 to 100 m range it is likely that some shallow water species were not caught. We are, however, convinced that the number of species shows a general pattern of decrease in species below about 400 m as no new species were found below 320 m which lies in the most intensively sampled depth range (Table 2).

The 2 multivariate methods, DCA and TWINSPAN, represent different approaches in analyzing the bathymetric distribution of the mysid fauna. DCA describes a continuous picture and TWINSPAN separates the species into distinct groups.

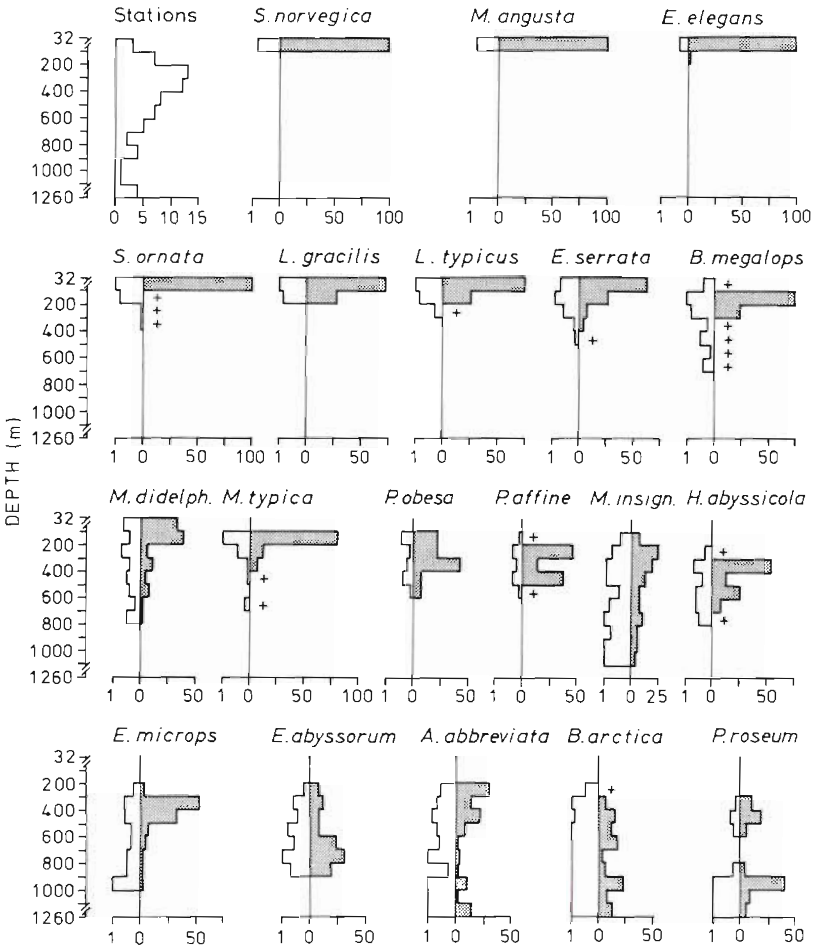

Fig. 6. Numbers of stations in the 12 defined bathymetric zones; frequency of occurrence (white bars) and percentage relative distribution of the species among the zones (shaded bars). (+) < 2 %

The DCA results (Figs. 3 and 4) suggested a continuous faunal change related to depth from the shallowest stations to about 350 m. Stations below this depth spread out along ordination axis 2 (Fig. 4). We interpret this as a result of larger faunal differences between fjords than faunal changes due to depth within fjords. TWINSPAN proposed the first division between the depth zones at 200 m and separated the most abundant shallow-living species from most of the deep-living species (Table 3). It is perhaps the effect of the sills, causing the isolation and stability of the basin water, that is operative around 200 m where TWINSPAN proposes the first division. Faunal gradients with depth have often been correlated with abiotic factors, for instance temperature, salinity and light intensity (Carney et al. 1983). In the fjords both salinity and temperature fluctuate much above the sill depths (maximum about 200 m), but are very stable below (e.g. Sælen 1962, Hermansen 1974). We do not know of any factors that could explain the break in the pattern at 350 m suggested by DCA. Unfortunately, no other datasets exist that present distributional information on animals from fjords and cover a comparable depth range.

Erythrops abyssorum and *Pseudomma roseum* spread the stations along ordination axis 2 (Fig. 3). *E. abyssorum* was not found in Sognefjorden, while it was widely distributed at appropriate depths south and north of Sognefjorden. Depth per se cannot be the decisive factor as *E. abyssorum* is widely distributed in the North Atlantic and is recorded down to 1100 m (Tattersall & Tattersall 1951). In Hardangerfjorden *P. roseum* was restricted to depths between 320 and 511 m in the outer area (Stns 39, 40, 44, 45) while *E. abyssorum* was found throughout the fjord at 254 to 856 m. Neither species was recorded shallower than about 250 m, which is well below sill depth in the fjords studied. Species of *Erythrops* and *Pseudomma* studied here are in general epibenthic (Mauchline 1968, Fosså 1986) One possible explanation for the distribution pattern is that, due to substrate preferences, the species are not likely to colonize all types of sedimentary substrates in fjords.

The most widespread and abundant species in the deep fjords is *Boreomysis arctica* (Table 3, Fig. 6). This species has a wide distribution in the North Atlantic (Tattersall & Tattersall 1951, Mauchline 1980). In the fjords it has both a hyperbenthic and a pelagic element in the populations (Matthews & Bakke 1977). Its distribution mainly below the sill depths may enhance population maintenance due to reduced advective loss from fjord basins.

The deep fjords also hold stocks of other widely distributed oceanic species, for instance the mesopelagic fishes *Maurolicus muelleri* and *Benthosema glaciale* (Gjøsaeter 1973, 1981a, b) and the bathypelagic scyphomedusan *Periphylla periphylla* (Fosshagen 1979). The fjord populations of these species are probably almost isolated from the oceanic populations. The oceanic radiolarian *Coeloplegma* sp. was present in Jøsenfjorden, Ryfylke, in 1973 to 1975 where it mainly occurred deeper than 275 m. It has not been found in any of the neighbouring fjords (Fosshagen 1979). According to Fosshagen this species is an example of an oceanic species that may have isolated self-sustaining populations in fjord basins. Pelagic copepods endemic to Sognefjorden and Hardangerfjorden are known. They have not been found in other fjords, e.g. in Ryfylke, even after extensive search (Fosshagen 1967, Fosshagen pers. commn). One common trait of the radiolarian and copepod species mentioned above is their distribution well below sill depth.

It seems that the individuality of a fjord is most likely to be found below sill depth. However, in the shallow brackish water too, planktonic species dominating in one fjord may not be recorded in adjacent fjords (Fosshagen 1980, Swanberg & Bjørklund 1987).

Bathymetric species groups

Based on results from the DCA and TWINSPAN, and our interpretations, we have defined the bathymetric groups in Table 4. In addition to the species of this study we have presented distributional information on

Table 4. All known mysid species of western Norway grouped into bathymetric groups after their main distribution. In the right column species known to occur in western Norway but not present in our samples are listed

This study	Other sources	
0 to about 50 m		
Siriella norvegica G. O. Sars	*Neomysis integer* (Leach)	(e)
Mysidopsis angusta G. O. Sars	*Praunus flexuosus* O. F. Müller	(b, e)
Erythrops elegans (G. O. Sars)	*Praunus inermis* (Rathke)	(b, e)
	Praunus neglectus (G. O. Sars)	(b, e)
	Hemimysis lamornae (Couch)	(a, e)
	Heteromysis formosa S. I. Smith	(a, e)
	Leptomysis lingvura (G. O. Sars)	(a, d)
	Michteimysis mixta (Lilljeborg)	(c)
	Mysidopsis gibbosa G. O. Sars	(a)
	Schistomysis spiritus (Norman)	(a)
30 to about 100 m		
Schistomysis ornata (G. O. Sars)	*Erythrops erythrophthalma* (Goes)	(a)
Leptomysis gracilis (G. O. Sars)		
Lophogaster typicus M. Sars		
Erythrops serrata (G. O. Sars)		
100 to about 350 m		
Boreomysis megalops G. O. Sars		
Mysidella typica G. O. Sars		
Mysidopsis didelphys (Norman)		
Parerythrops obesa (G. O. Sars)		
Pseudomma affine G. O. Sars		
>250 m		
Boreomysis tridens G. O. Sars	*Mysidella typhlops* G. O. Sars	(a)
Hemimysis abyssicola G. O. Sars		
Mysideis insignis (G. O. Sars)		
Erythrops microps (G. O. Sars)		
Amblyops abbreviata G. O. Sars		
Erythrops abyssorum G. O. Sars		
Boreomysis arctica (Krøyer)		
Pseudomma roseum G. O. Sars		

(a) Sars (1870–79); (b) Brattegard (1966); (c) Oug (1976); (d) Fosså (1984); (e) own obs.

all other species of Mysidacea known from western Norway, based on Sars (1870–79), Brattegard (1966), Oug (1976), Fosså (1984) and our own unpublished material.

Group 1 in Table 3 is rather heterogeneous and contains species with quite different bathymetric distributions. *Siriella norvegica, Mysidopsis angusta* and *Erythrops elegans* have shallow distributions compared to the others which were common down to 200 m and some even deeper. For these 3 species this study definitely does not describe a reliable depth distribution because the species are known to be distributed from a few metres depth, and the 2 latter species probably have their main occurrences shallower than the range studied here (Sars 1870–79, Tattersall & Tattersall 1951, Mauchline 1968, 1970a). For the 4 other species in group 1 (*Schistomysis ornata, Leptomysis gracilis, Lophogaster typicus* and *Erythrops serrata*) we have probably sampled the range of their main occurrence (Sars 1870–79, Tattersall & Tattersall 1951, Mauchline 1968, 1969, 1970b). These species were most abundant shallower than 100 m and frequent down to 200 m. *L. gracilis* was found by Sars (1879) at about 20 m, and the upper limit for the other species may also be shallower than the depths covered by this study. In general, we have too few samples from the 32 to 100 m depth range. Mauchline (1970b) states that *S. ornata* is associated with *E. serrata* and *L. gracilis* in Loch Etive, Scotland. In the Norwegian fjords it seems that *L. gracilis, L. typicus* and *E. serrata* occur in the same depth range (Fig. 6), while *S. ornata* seems to prefer more shallow water (Kaartvedt 1989, own obs.). Thus we have chosen to place the 7 species in 2 groups, 0 to 50 and 30 to 100 m. The shallowest interval, 0 to 50, is mainly outside the depths investigated here. Disregarding this shallowest interval, group 2 and 3 species have much in common and we suggest a single group for *Boreomysis megalops, Mysidella typica, Mysidopsis didelphys* and *Parerythrops obesa* together with *Pseudomma affine* from the next group.

Mysideis insignis was grouped together with *Pseudomma affine* because of its occurrence in the 100 to 200 m interval, but we feel that the very extensive depth range really places this species in a group of its own or that it is more naturally placed together with the deeper-living species.

Amblyops abbreviata, Boreomysis arctica and *Pseudomma roseum* have the capability to inhabit the deepest part of Sognefjorden and TWINSPAN separated them from the other deep-living species. However, lacking understanding why this separation exists, we have chosen to put all 7 species in one group together with *Mysideis insignis*.

The species not found by us belong, with 2 exceptions (*Erythrops erythrophthalma* and *Mysidella typhlops*), to the shallowest group. *Michtheimysis mixta* has the potential of going much deeper (e.g. Salemaa et al. 1986) but until now the species, which is not common in the area, has been found down to 30 to 40 m (Oug 1976). *Praunus* spp. are abundant in the phytal zone in the fjords except in wave-exposed areas. There is not much information about the other species but most probably they are distributed in the shallow parts of the fjords or, if deeper, in habitats not sampled by the sledge.

Erythrops erythrophthalma was found by Sars (1870) in western and southern Norway at depths between 60 and 110 m. *Mysidella typhlops* has never been recorded since Sars (1879) found it at about 375 m depth near Stn 57, and at similar depth between Stns 9 and 10. This species must either inhabit a habitat not sampled by us, or is very rare.

Mauchline (1980) gave a general bathymetric classification of species of mysids. Our 0 to 50 m corresponds to his 3 groups 'brackish water' (0 to 20 m), 'littoral' (0 to 10 m), and 'shallow shelf' (2 to 100 m). Our 30 to 100 m to his 'eurybathic shelf' (2 to 400 m), the 100 to 350 m to his 'deep shelf and upper slope' (100 to 400 m) and our deepest < 250 m to his 'slope' (200 to 700 m).

Congeneric species

TWINSPAN grouped *Erythrops elegans* and *E. serrata*, and *E. microps* and *E. abyssorum* together, but closer examination of Fig. 6 and Table 3 show that the species have quite different depth distributions. The same is the case for *Pseudomma* spp. A close examination of Fig. 6 shows that all 6 species of *Erythrops* and *Pseudomma* have peaks in abundances in different bathymetric intervals. The scores along the 2 first DCA axes are quite different, and the species are placed at the extremes of both axes, with exception of *E. microps* and *P. affine* which had similar scores.

Pseudomma roseum and *P. affine* were absent in the deepest zones in Hardangerfjorden even though they occur in much deeper habitats elsewhere (Tattersall & Tattersall 1951, Mauchline 1986, own obs.). One explanation could be that sediment properties are important. The species of *Erythrops* and *Pseudomma* have morphologically similar thoracalic extremities which suggests a similar behaviour at the sediment surface. They may occupy similar niches but at different depths to avoid competition.

Although every depth interval is occupied by typical epibenthic genera as *Erythrops* and *Pseudomma* it seems that below 100 m the most successful species in terms of numbers are *Boreomysis megalops* and *B. arctica*. They are not as closely associated with and dependent on the substrate as the epibenthic species

(Fosså 1986) and they are also to some extent pelagic (Matthews & Bakke 1977, Fosså 1985, Kaartvedt 1989). These species can thus utilize other habitats during their pelagic phase which may give them additional food resources.

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