

## Diversity of isopods (Crustacea): new data from the Arctic and Atlantic Oceans

JÖRUNDUR SVAVARSSON

*Institute of Biology, University of Iceland, Grensásvegi 12, 108 Reykjavik, Iceland and Sandgerði Marine Center, Garðvegi 1, 245 Sandgerði, Iceland*

Received 25 January 1997; accepted 7 March 1997

New data on the diversity pattern of isopods (Crustacea) from the northern most part of the North Atlantic and the Arctic Oceans is presented. The pattern of diversity with depth is similar at depths < 1000 m, but differs considerably below about 1000 m. In the Arctic the diversity of isopods (expressed both as numbers of species per sled and expected number of species) increased with increased depth to a maximum at depths of about 320 to 1100 m, but then declined towards deeper waters. There was a significant increase in numbers per sled and in the expected number of species with increased depth in the northernmost part of the North Atlantic Ocean. Additionally, changes occurred in the relative composition of the shallow and deep water fauna, with asellote isopods being relatively larger part of the isopod fauna in the Arctic than in the northern most part of the North Atlantic. This indicates major faunistic changes occurring at the Greenland-Iceland-Faeroe Ridge, possibly caused by rapid changes in the temperature. Furthermore, that the low diversity of the Arctic deep-sea is a regional phenomenon, and not a part of a large scale latitudinal pattern in the North Atlantic.

*Keywords:* diversity; deep sea; isopods; Atlantic Ocean; Arctic Ocean.

### Introduction

Isopods (Arthropoda, Crustacea) have been used to illustrate a highly diverse deep sea since the pioneering work of Hessler and Sanders (1967), based mainly on material from the Gay Head–Bermuda transect. Apart from a single earlier publication (Hessler and Sanders, 1967) and some citations to unpublished data (see for instance Menzies *et al.*, 1973), only recently have additional papers on isopod diversity been published (see Hessler *et al.*, 1979; Hessler and Wilson, 1983; Svavarsson *et al.*, 1990; Rex *et al.*, 1993; Brandt, 1993; Poore and Wilson, 1993; Poore *et al.*, 1994). These papers have focused mainly on the pattern of isopod diversity within the deep sea. Deep-sea isopod diversity has been shown to be regionally high (Poore *et al.*, 1994) or low (Svavarsson *et al.*, 1990), and a clear latitudinal gradient in diversity has been shown to occur in the North Atlantic Ocean, while in the South Atlantic a strong inter-regional variation uncorrelated to latitude was found (Hessler and Wilson, 1983; Rex *et al.*, 1993).

New data is presented here on isopod diversity from the Arctic Ocean and the North Atlantic Ocean. The diversity pattern was studied at a region where the North Atlantic Ocean meets the Arctic Ocean and where one would expect to find a latitudinal gradient in diversity. The relative proportion of the isopod suborders at each side of the Greenland-Iceland-Faeroe Ridge was also evaluated.

## Methods

Material from the North Atlantic Ocean and the Arctic Ocean was collected during cruises with the Norwegian RV *Håkon Mosby* during the years 1982 to 1994, the Icelandic RV *Bjarni Saemundsson* from 1992 to 1994 and the RV *Magnus Heinason* from the Faeroe Islands in 1993. Cruises from 1991 to 1994 were part of the ongoing international BIOICE project (Benthic Invertebrates of Icelandic waters; 1991).

Samples were taken with a modified Rothlisberg–Pearcy epibenthic sled (RP sled; Rothlisberg and Pearcy, 1976; Brattegard and Fosså, 1991). This sled is towed over the bottom and collects animals lifted in turbulence in front of the sled. The sled has 0.5 mm mesh in the cod end. A closing mechanism ensures that the sled opens only on the bottom and so reduces loss of material on retrieval. The replicability of this sled has been evaluated (Brattegard and Fosså, 1991) and is reasonable for the hyperbenthos.

Data from 59 localities in the Arctic Ocean and 38 localities in the North Atlantic Ocean are presented, the former from a depth range of 19 to 3894 m, while the samples from the North Atlantic were collected within a range of 63 to 1407 m. The samples from the Arctic Ocean were taken in the area to the north and east of Iceland (Iceland Sea, Norwegian Sea), while the samples in the Atlantic Ocean were taken to the southwest, south and southeast of Iceland (exact localities can be obtained from the author). There is a rapid decline in near-bottom temperature with increased depth in the Arctic. In quite shallow waters (near-shore surface) the temperature ranges from about 2° (winter) to 8° (summer) (Ingólfsson, 1996), while the near-bottom temperatures at 400–500 m reach below 0°C. In the North Atlantic (off southern Iceland) temperatures declines steadily from about 6° (winter) to 11°C (summer, both near-shore surface) in shallow water to about 3.1° to 3.4°C (near-bottom) at considerable depths (1500 to 2000 m).

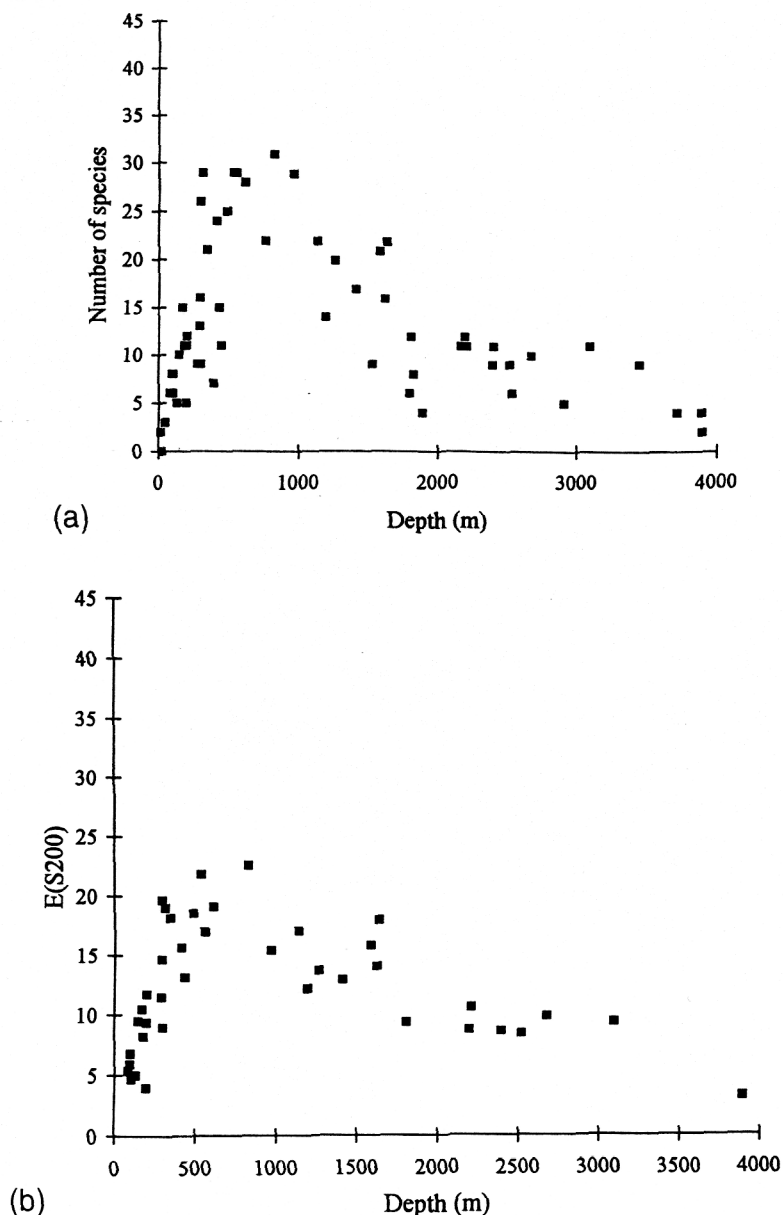
In addition 47 samples of isopods taken with the Woods Hole epibenthic sled (WHOI sled) in the North Atlantic Ocean collected by Dr. R.R. Hessler and coworkers have been included. These were sorted and identified in the laboratory of Dr. R.R. Hessler and the data kindly provided by Dr. G.D.F. Wilson.

The BIOICE samples were decanted over a 0.5 mm sieve and the residuals later sieved over a series of sieves (8, 4, 2, 1, 0.5 mm). Isopods were sorted in the Sandgerði Marine Center, Sandgerði, and identified to family, genus or species.

Species diversity was compared between samples by using the index of expected number of species (Hurlbert, 1971).

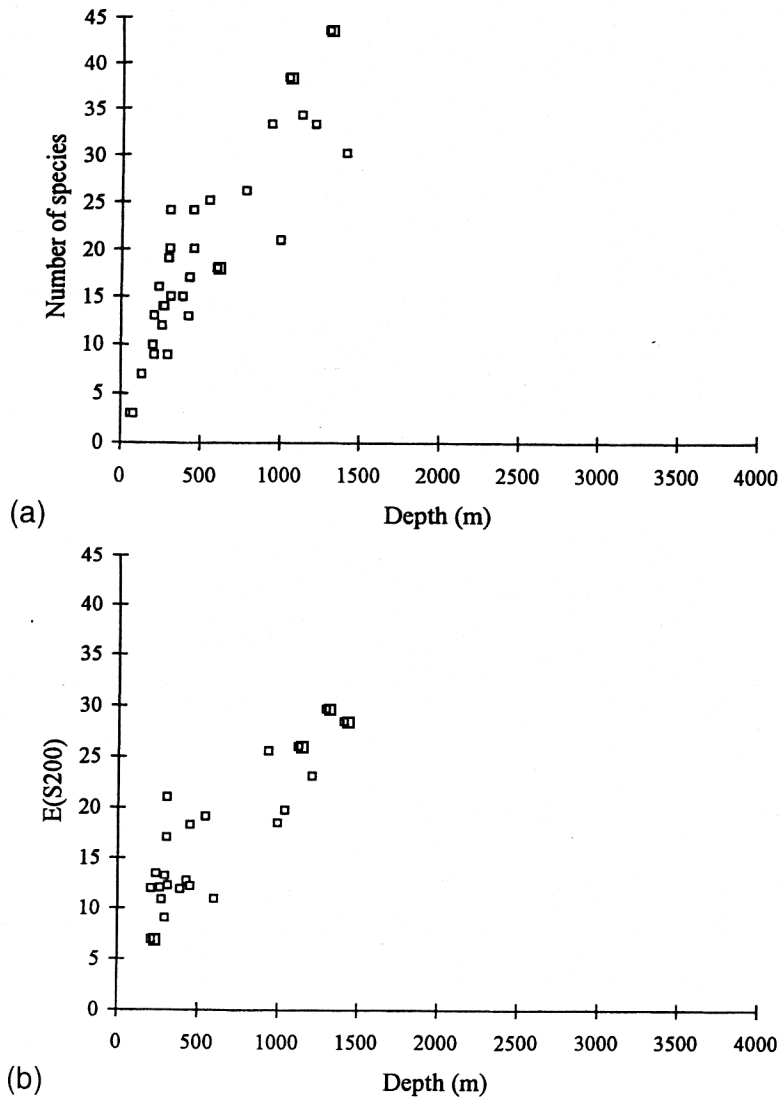
## Results

The number of species per sled (RP sled) in the Arctic Ocean was low in shallow waters (< 250 m) but increased with increased depth (Fig. 1a). The number of species were highest at 320–1100 m but became again low (often  $\approx$  10 species) in deeper parts of the Arctic Ocean. The maximum species numbers were thus found in areas where the temperature was < 0°C. The overall pattern of number of species per RP sled was different in the northernmost part of the North Atlantic Ocean (area southwest, south and southeast of Iceland). Species number increased significantly with depth (Spearman rank correlation coefficient,  $r = 0.897$ ,  $P < 0.001$ ) (BIOICE data, Fig. 2a) within the studied depth range (0–1500 m). There was not as rapid increase in number of species with depths in the shallowest water as in the Arctic.

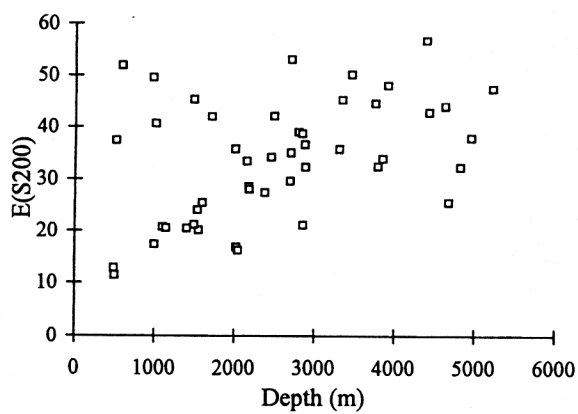


**Figure 1.** Number of isopod species per RP sled (a) and expected number of species ( $E(S_{200})$ ) (b) at different depths in the Arctic Ocean.

Sled samples are not quantitative and the number of individuals caught can differ widely. The problem concerned with different numbers of individuals has commonly been dealt with using Hurlbert's expected number of species, which allows comparison of samples with different numbers of individuals. This practice involves rejection of samples with only a few specimens (most often samples with  $< 50$ ,  $100$ , or  $200$  individuals per sample are omitted). Similar pattern was observed for the isopods in the Arctic when  $E(S_{200})$  was applied as when numbers per sled were used (Fig. 1b). Main difference lies in less pronounced differences in diversity between the deeper and shallower Arctic fauna. A significant increase occurred in the number of species with increased depth in the North



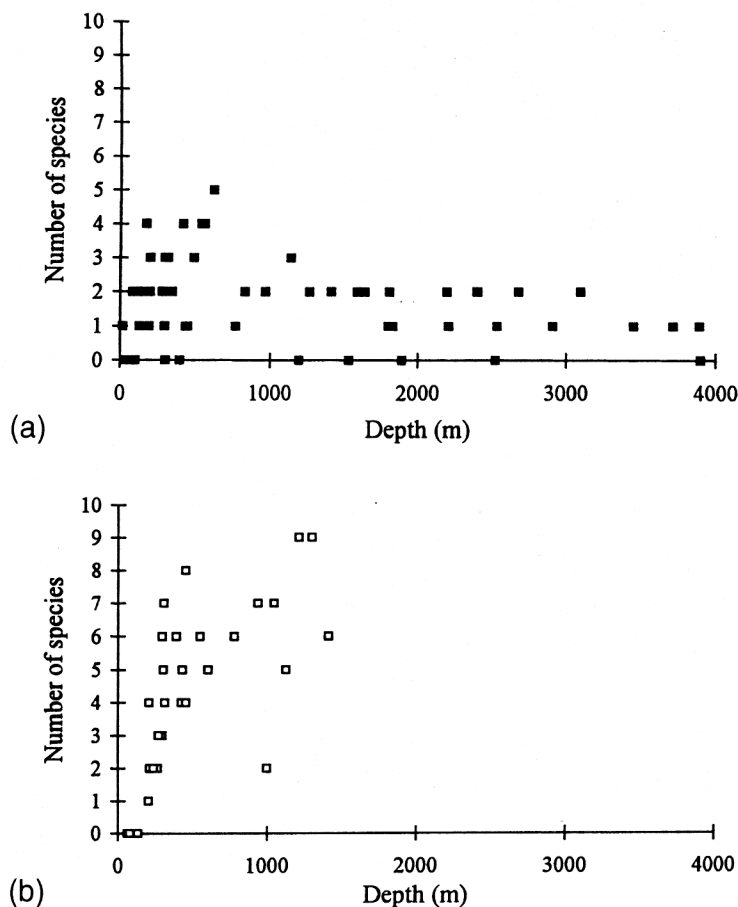
**Figure 2.** Number of isopod species per RP sled (a) and expected number of species ( $E(S_{200})$ ) (b) at different depths in the most northern part of the North Atlantic Ocean.



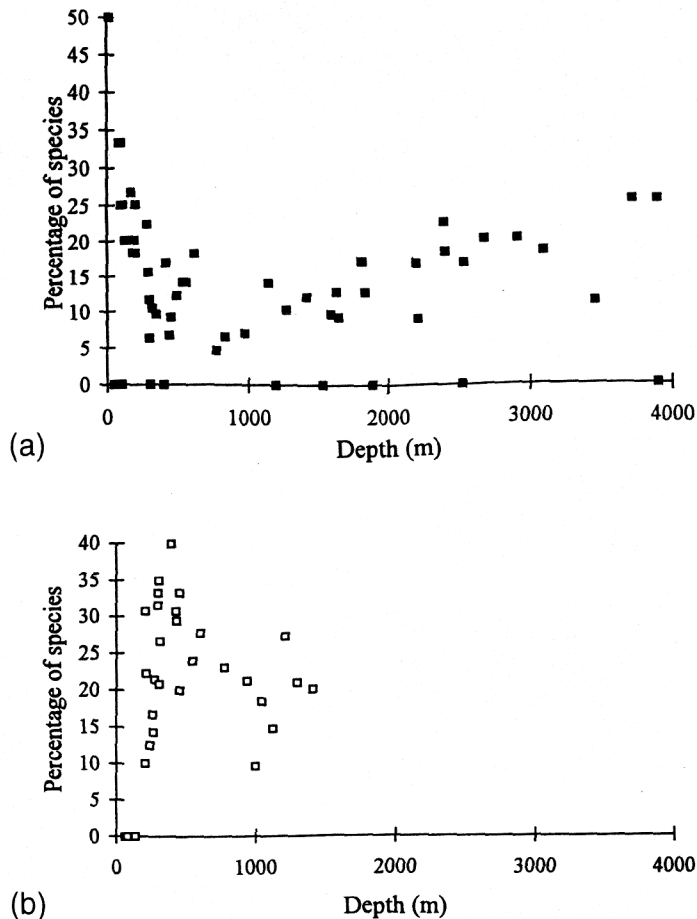
**Figure 3.** Expected number of species ( $E(S_{200})$ ) for samples taken by the WHOI sled in the North Atlantic Ocean.

Atlantic when  $E(S_{200})$  was used (Fig. 2b). The data collected by the WHOI sled have been presented elsewhere (see Rex *et al.*, 1993). The number of species increased significantly with increased depth (Spearman rank,  $r = 0.41$ ;  $P < 0.01$ ) in the North Atlantic Ocean (Fig. 3), despite the fact that these samples were taken over a large part of the North Atlantic Ocean (localities can be seen in Rex *et al.*, 1993).  $E(S_{200})$  of the WHOI dataset varied, however, considerably within regions and at similar depths.

When only asellote isopods were considered, the pattern found was similar to which was seen for all species, both in the Arctic and in the North Atlantic (data not shown). Furthermore a similar pattern was found when all non-asellote species (flabelliferans, gnathiids, valviferans, anthurideans) were considered (Fig. 4a, b). Non-asellote species were looked upon as a percentage of the total number of species and here the pattern was different between the Arctic Ocean and the North Atlantic (Fig. 5a, b). In the Arctic the proportion was high at shallowest depths and decreased towards a minimum at 800–1000 m, but then increased at greatest depths. In the North Atlantic the proportion of non-asellotes was highest at depths shallower than 500 m.



**Figure 4.** Number of species per RP sled of non-asellote isopods in the Arctic Ocean (a) and the northernmost part of the North Atlantic (b).



**Figure 5.** Non-asellote species as a percentage of the whole isopod number of species in each sample taken by the Rothlisberg–Pearcy sled in the Arctic Ocean (a) and the northernmost part of the North Atlantic Ocean (b).

## Discussion

Isopods have been considered highly diverse in the deep sea for a long time despite the fact that little data has been published on their diversity, except relatively recently (see Hessler and Wilson, 1983; Svavarsson *et al.*, 1990; Rex *et al.*, 1993; Brandt, 1993; Poore and Wilson, 1993; Poore *et al.*, 1994; Brandt *et al.*, 1996). What has been meant by high isopod diversity in the deep sea has not always been clear. The notion of high diversity may partly be based on diversity of new taxa found in the deep sea, i.e. researchers have been stunned by the number of new species seen in the deep-sea samples.

The diversity of isopods has mostly been evaluated using sleds, although isopods collected in box corers have been used together with other benthic fauna to estimate local and global diversity (Grassle and Maciolek, 1992). Hessler and Sanders (1967) and Hessler and Wilson (1983) reported 27 to 53 species/sled while more than 100 species of isopods in samples have also been mentioned (Hessler *et al.*, 1979). Later papers have indicated a fairly large variation in the number of species per sled within regions (1–60 species of isopods per sled, Table 1 in Poore *et al.*, 1994; range from <10 to >50 species, E(s) for 200 individuals in the Argentine Basin of the South Atlantic Ocean, see Rex *et al.*, 1993).

This variability could indicate that (i) large spatial/regional variability in isopod diversity exists in the deep sea, with high-diversity localities and low-diversity sites, or (ii) that the replicability of the sled used, the WHOI sled, may be low due to the sleds behavior (differences in the areas sampled, sampling deep or shallow in the sediment, etc.).

Previous studies based on samples taken with the WHOI sled have suggested a high inter-regional variation in species diversity, not only confined to the isopods (Rex *et al.*, 1993). Hurlbert's expected number of species has widely been used on sled samples to make them comparable. Using Hurlbert's expected number of species on samples from sleds which have a low replicability and which may operate differently in each case (for instance collection of 2000 specimens over distance of 1 km vs. 2000 specimens over 0.1 km) may be questionable. The shape of the rarefaction curves depends upon the pattern of the relative abundance of the species (James and Rathbun, 1981), the latter may depend upon the operation of the sled. Further, a rejection of samples with less individuals than the number used for comparison (i.e. 50, 100, 200 or even 500 individuals) may result in unwarranted rejection of actual data from low diversity sites.

The present data using different sled types support the notion of generally high diversity of isopods in the open deep sea and further regional differences in isopod diversity (North Atlantic versus the Arctic). The scale of the diversity needs to be evaluated by using box corers along with the sleds. Furthermore, the regional diversity needs more attention as the local richness may be sensitive to regional richness (Cornell and Karlson, 1996). Despite numerous papers on the systematics of deep sea isopods, there are only a few dealing with the complete isopod fauna at numerous localities that would allow the evaluation of regional and local diversity. Poore *et al.* (1994) recorded a total of 359 species of isopods (regional diversity; 46 samples, of these 30 were WHOI sled samples) taken at the continental slope (200–3150 m) of southeastern Australia and here the maximum number of species per sled was 60. In the Arctic Ocean the entire asellote fauna had only 106 species (Svavarsson *et al.*, 1993a), while the local diversity estimated from sled samples (distance covered by the RP sled may be up to 1300 m) approached 29 species per sled. Hence, a single sled sample may contain one-sixth (southeastern Australia) or more than one-fourth (Arctic Ocean) of the regional fauna. The sleds (RP and WHOI sleds) therefore seem to be quite efficient in sampling isopods. The high numbers of species per sled may give a good estimation of the regional diversity, but the low replicability of the WHOI sled may give false impression of a variation of the inter-regional diversity.

Low diversity of the deep-sea isopod fauna of the Arctic Ocean has previously been explained in terms of isolation and young age of the area (Gurjanova, 1938; Dahl *et al.*, 1976; Svavarsson *et al.*, 1990; Svavarsson *et al.*, 1993). Other factors may also have contributed to low diversity, such as changes in the general circulation of the area and in the deep-water formation. Profound changes presumably occurred in the intermediate-water circulation of the North Atlantic during the last deglaciation (13 to 11,7 k years ago, Smith *et al.*, 1997). Recent studies have shown that temporal changes occurred in the diversity of Pliocene deep-sea ostracods in the North Atlantic, the diversity being low during glacial periods, but higher during interglacials (Cronin and Raymo, 1997). Highest diversity was observed here at similar depths to the sill depth of the Greenland-Iceland-Faeroe Ridge, which isolates the deep Arctic from the North Atlantic Ocean. Svavarsson *et al.* (1993) and Negoescu and Svavarsson (in press) suggested that this ridge and the complicated hydrographic condition were major obstacles for the entry of deep-sea species into the Arctic. The low diversity of the Arctic Ocean has suggested to be part of a

latitudinal trend in the whole of the North Atlantic and the Arctic Oceans (Rex *et al.*, 1993). The supposed decrease in species diversity towards north has been explained in part by more variable, though higher, input of energy at higher latitudes, while the effects of the last glaciation on marine life has also been suggested as an important factor (Rex *et al.*, 1993). It is evident from the data shown here that there are major changes occurring at the Greenland-Iceland-Faeroe Ridge, not only in species composition (Svavarsson *et al.*, 1993) but also in the general pattern of diversity.

Presence of large scale changes occurring over relatively short distances over the Greenland-Iceland-Faeroe Ridge (< 100 nautical miles) may partly be explained on basis of present environmental conditions. In this area there is an extremely rapid decline in temperature over short distance, being < 0°C at depths below 400 m to the north of the Greenland-Iceland-Faeroe Ridge, while at comparable depths south of the ridge the temperature is 4–7°C. This is due to the effects of the ridge holding cold (< 0°C) deep bottom water (Norwegian Sea Deep Water, see Stefánsson, 1962) in the Arctic Ocean, with some cold water spilling intermittently (overflow) over the ridge and into the North Atlantic Ocean. Both areas have highly seasonal input of energy, seen in seasonal sedimentation (Bathmann *et al.*, 1990; Gislason and Astthorsson, 1992) suggesting that the energy input is not an important factor in shaping diversity pattern in these shallow waters.

### Acknowledgements

I wish to thank Torleiv Brattegard (University of Bergen) for his hospitality on board RV *Håkon Mosby* during the BIOICE cruises, MRI in Reykjavík for providing ship-time on RV *Bjarni Saemundsson* and the Fiskirannsóknastofa of the Faeroe Islands for providing ship-time on RV *Magnus Heinason*, the staff of the Sandgerði Marine Center for sorting the specimens and Sigrún Haraldsdóttir, Brynhildur Davidsdóttir, Guðmundur Guðmundsson and Tómas Gislason for help with sorting or identifying species. I thank the Icelandic National Science Foundation and the Science Foundation of the University of Iceland for providing funds. I also wish to thank George D. F. Wilson (Australian Museum) for allowing me to use the data from the North Atlantic Ocean and his valuable comments and suggestions, Niel L. Bruce (Zoologisk Museum, University of Copenhagen) for his constructive comments and finally Professor Agnar Ingólfsson (University of Iceland) for his valuable comments and fruitful discussions over the years.

### References

- Bathmann, U.V., Peinert, R., Noji, T.T. and von Bodungen, B. (1990) Pelagic origin and fate of sedimenting particles in the Norwegian Sea. *Prog. Oceanogr.* **24**, 117–25.
- Brandt, A. (1993) Composition, abundance, and diversity of peracarid crustaceans on a transect of the Kolbeinsey Ridge, north of Iceland. *Polar Biol.* **13**, 565–76.
- Brandt, A., Vassilenko, S., Piepenburg, D. and Thurston, M. (1996) The species composition of the peracarid fauna (Crustacea, Malacostraca) of the Northeast Water Polynya (Greenland). *Meddelelser om Grønland, Bioscience* **44**, 1–30.
- Brattegard, T. and Fosså, J.H. (1991) Replicability of an epibenthic sampler. *J. Mar. Biol. Assoc. UK* **71**, 153–66.



- Cornell, H. V. and Karlson, R.H. (1996) Species richness of reef-building corals determined by local and regional processes. *J. Anim. Ecol.* **65**, 233–41.
- Cronin, T.M. and Raymo, M.E. (1997) Orbital forcing of deep-sea benthic diversity. *Nature (London)* **385**, 624–7.
- Dahl, E., Laubier, L., Sibuet, M. and Strömberg, J.-O. (1976) Some quantitative results on benthic communities of the deep Norwegian Sea. *Astarte* **9**, 61–79.
- Gislason, A. and Astthorsson, O.S. (1992) Zooplankton collected by sediment trap moored in deep water south of Iceland. *Sarsia* **77**, 219–24.
- Grassle, J.F. and Maciolek, N.J. (1992) Deep-sea species richness: regional and local diversity estimates from quantitative bottom samples. *Amer. Nat.* **139**, 313–14.
- Gurjanova, E. (1938) On the question of the composition and origin of the abyssal fauna of the Polar Basin, *Comptes Rendus (Doklady) de 'Academie des Sciences de 'URSS* **20**(4), 333–6.
- Hessler, R.R., and Sanders, H.L. (1967) Faunal diversity in the deep sea. *Deep-Sea Res.* **14**, 65–78.
- Hessler, R.R., Wilson, G.D. & Thistle, D. (1979) The deep-sea isopods: A biogeographic and phylogenetic overview. *Sarsia* **64**: 67–75.
- Hessler, R.R., and Wilson, G.D.F. (1983) The origin and biogeography of malacostracan crustaceans in the deep sea. In *Evolution, Time and Space: The Emergence of the Biosphere* (R.W. Sims, J.H. Price and P.E.S. Whalley, eds) pp. 227–54. Systematic Association Special Volume 23, London: Academic Press.
- Hurlbert, S.H. (1971) The nonconcept of species diversity: a critique and alternative parameters. *Ecology* **52**, 577–586.
- Ingólfsson, A. (1996) The distribution of intertidal macrofauna on the coasts of Iceland in relation to temperature. *Sarsia* **81**, 29–44.
- James, F.C. and Rathbun, S. (1981) Rarefaction, relative abundance, and diversity of avian communities. *Auk* **98**, 785–800.
- Menzies, R.J., George, R.Y. and Rowe, G.T. (1973) *Abyssal environment and ecology of the world oceans*. New York: John Wiley & Sons.
- Negoescu, I. and Svavarsson, J. (in press). Anthurideans (Crustacea, Isopoda) from the North Atlantic and the Arctic Ocean. *Sarsia* **82**.
- Poore, G.C.B. and Wilson, G.D.F. (1993) Scientific correspondence: marine species richness (with reply to R.M. May). *Nature* **361**, 597–8.
- Poore, G.C.B., Just, J. and Cohen, B.F. (1994) Composition and diversity of Crustacea Isopoda of the southeastern Australian continental slope. *Deep-Sea Res.* **41**, 667–93.
- Rex, M.A., Stuart, C.T., Hessler, R. R., Allen, J.A., Sanders, H.L. and Wilson, G.D.F. (1993) Global-scale latitudinal pattern of species diversity in the deep-sea benthos. *Nature (London)* **365**, 636–9.
- Rothlisberg, P.C. and Percy, W.G. (1976) An epibenthic sampler used to study the ontogeny of vertical migration of *Pandalus jordani* (Decapoda, Caridea). *Fish. Bull.* **74**, 994–7.
- Smith, J.E., Risk, M.J., Schwarcz, H.P., and McConnaughey, T.A. (1997) Rapid climate change in the North Atlantic during the Younger Dryas recorded by deep-sea corals. *Nature (London)* **386**, 818–20.
- Stefánsson, U. (1962) North Icelandic waters. *Rit Fiskideildar* **3**, 1–269.
- Svavarsson, J., Brattegard, T. and Strömberg, J.-O. (1990) Distribution and diversity patterns of asellote isopods (Crustacea, Isopoda) in the deep Norwegian and Greenland Seas. *Progress in Oceanography* **24**, 297–310.
- Svavarsson, J., Strömberg, J.-O. and Brattegard, T. (1993) The deep-sea asellote (Isopoda, Crustacea) fauna of the Northern Seas: species composition, distributional patterns and origin. *J. Biogeog.* **20**, 537–55.