THE SHELL-BEARING, BENTHIC GASTROPODS ON THE SOUTHERN PART OF THE CONTINENTAL SLOPE OFF NORWAY

TORE HØISÆTER

Department of Biology, University of Bergen, PO Box 7800, N-5020 Bergen, Norway

Correspondence: T. Høisæter; e-mail: tore.hoisater@bio.uib.no

(Received 29 October 2009; accepted 12 January 2010)

ABSTRACT

The fauna of benthic shell-bearing gastropods on the continental slope off western Norway is described, based on material collected during the 1980s. Almost 3,000 specimens belonging to 96 species have been studied. The existence of a specific gastropod fauna restricted to the upper slope is documented, and the fauna is compared with that of the shelf, the 'lower' slope and the abyssal (below *c*. 2,000 m) depths of the Norwegian Sea. Possible dependence of the slope fauna on the negative temperature of the Norwegian Sea water and on internal waves in the region of the thermocline is discussed. Some species found on the upper slope are illustrated.

INTRODUCTION

The deep-water fauna of the Norwegian Sea was first described in several reports from the Norwegian North Atlantic Expedition, 1876–1878. The voluminous material of benthic animals from this expedition, carried out during three successive summers on the steamer *Vøringen*, was described taxonomically by several experts during the following decades. However a final, biogeographic summary was never published. All new or little known mollusc species was described by Friele (1877, 1882, 1886), and Friele & Grieg (1901) published a species-by-species account of all the molluscs found, together with their horizontal and vertical distribution.

Little has been published on the molluscs from the bathyal depths of this region since then. Friele (1903) reported on a small collection of molluscs from the first *Michael Sars* Expedition in the Norwegian Sea. Some material accidentally caught in a plankton net at two stations just west of Tampen (at 62°10′N and 62°15′N, respectively), during the first cruise of the research vessel *Armauer Hansen* in 1914, was worked up by Grieg (1915). Finally the French/Swedish NORBI expedition in 1976 covered the eastern and northern parts of the Norwegian Sea, from 2,500 to 3,800 m. Bouchet & Warén (1979) worked up the molluscan material from this expedition, and concluded that the benthic fauna of the abyssal (deeper than *c*. 2,500 m) is comparatively species poor, but highly endemic, sharing only a few species with similar depth zones in the North Atlantic south of the Iceland-Faroe Ridge, or the mollusc fauna on the slope shallower than *c*. 2,000 m.

In recent years reports based on material from BIOFAR and BIOICE, parts of the material from the *Ingolf* Expedition, and accumulated material from the waters north and east of Iceland, have contributed to a better understanding of the bathyal mollusc fauna in this area (Bouchet & Warén 1979, 1980, 1985, 1986, 1993; Warén 1989, 1991, 1993, 1996; Sneli *et al*. 2005). The valuable works of Bouchet and Warén are in fact revisions of most of the groups found in this area, making it possible to identify the majority of specimens encountered. Building on these revisions, Witbaard *et al*. (2005) looked at the mollusc fauna along a depth transect in the Faroe-Shetland Channel.

During the 1980s, 29 cruises in the Norwegian Sea with R/V *Håkon Mosby* were organized and carried out by Torleiv Brattegard, University of Bergen. These cruises resulted in a large amount of benthic animals from all depth zones of the Norwegian Sea west and north of Norway, as well as material from the Faroe-Shetland Channel, the Iceland-Faroe Ridge and the area around Jan Mayen Island. The majority of the material was sampled by a modified Rothlisberg–Pearcy sledge (Brattegard & Fosså, 1991), designed for collecting hyperbenthic fauna, but well suited also for sampling the smaller and lighter epibenthos. Recently a large part of this material has been made available to specialists, due to sorting efforts at a number of workshops, and by staff at the Zoological Museum in Bergen (where the material is deposited).

In this article an attempt is made, based on the material of benthic gastropods from some of these samples, to describe the faunal composition in the various depth zones of the slope in the southeastern part of the Norwegian Sea, and in the Norwegian Basin. For comparison, material from a few stations from the Norwegian shelf and the Iceland-Faroe Ridge has been included. To my knowledge this is the first study to document the gastropod fauna for a complete depth transect, from the shelf-break to the maximum depth, of the Norwegian Sea. This work leans heavily on the revisions by Bouchet and Warén mentioned above, but in some cases I have suggested further taxonomic revisions (see also Høisæter, 2009b)

MATERIAL AND METHODS

Most of the material was taken with a Rothlisberg–Pearcy (RP) sledge. The samples are not quantitative, but the most successful ones contained enough bottom substrate for a reasonable comparison to be made between them as to species richness and abundance. Sampling procedure followed the method outlined in Brattegard & Fosså (1991). All samples were carefully sieved through graduated geological sieves (16, 8, 4, 2, 1 and 0.5 mm meshes) after having been elutriated in a 50-l container. The material was preserved in buffered formalin and later transferred to 80% ethanol. Much of the material was in excellent condition after 20–30 years' storage. Of the total of 500 samples taken during the period March 1981 to June 1987, material from some 80 samples from the slope and deep basin, supplemented by two from the Faroe-Shetland Channel, four from the Iceland-Faroe Ridge, 13 from the slope around Jan Mayen and one from the Norwegian shelf (Fig. 1, Table 1), has been analysed for this study. A few samples taken with a Sneli detritus sledge (Sneli, 1998) from some of the same cruises, and five samples from two cruises with R/V

Journal of Molluscan Studies (2010) ***76****: 234–244. Advance Access Publication: 22 April 2010* *doi:10.1093/mollus/eyq003*

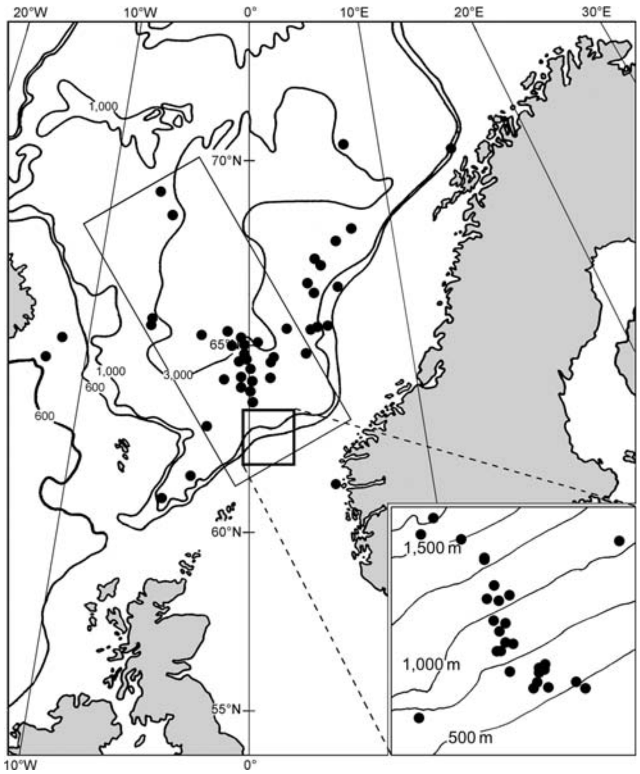

Figure 1. Map of the Norwegian Sea, with depth contours. Inset an enlargement of the intensely sampled area on the upper slope at the North Sea Fan. Most of the stations from the reduced data set are located within the rectangular area.

Johan Ruud from Tromsø, have also been included. These latter ones were from between 69°N and 71°N, while the majority of the RP material from the Norwegian slope was sampled between 62°N and 64°N. The samples were sorted under a stereo microscope by two of the scientific staff at Zoological Museum in Bergen (ZMBN).

This material is supplemented with information on the near bottom temperature for each sampling station (Fig. 2).

The total material is summarized in Table 1 (see also Supplementary material Table S1). Temperature data for additional stations as well as details not found in Supplementary material Table S1 are available electronically at ZMBN. To examine the effect of depth, 70 stations from an intensely sampled area in the southern part of the region (stations enclosed by rectangle in Fig. 1; Table 2, Supplementary material Table S2) were selected for more detailed analysis. These stations are mainly from the North Sea Fan, a large wedge of glacigenic sediments starting at the shelf break at roughly 460 m at the 'mouth' of the Norwegian Trench, and extending down to *c.* 3,600 m at 65°N in the Norwegian Basin.

The width at the upper part of the wedge is roughly 100 km, and the sea floor gradients are generally between 0.2° and 0.7° (Nygård *et al.*, 2004, 2007). Two 'control' stations were included, one from 471 m at 60°52′N, from a local depression in the Norwegian Trench outside Sognefjorden, and another from 400 m at the shallowest part of the Iceland-Faroe Ridge 64°26′N, 11°10′W.

The area of ocean traditionally called the Norwegian Sea has long been known to geophysicists as the 'Nordic Seas', in which the Norwegian Sea *sensu stricto* is just one of several ocean basins. For simplicity I use Norwegian Sea throughout as a collective for all basins in this area.

Similarity analyses based on Bray–Curtis similarity index for fourth-root transformed abundance data and presence/absence data were performed with Primer 6 (version 6-1-6). Group-average dendrograms and multi-dimensional scaling (MDS) analyses were made for both transformed data sets. In the multivariate analyses, all samples containing less than three species and/or three specimens have been weeded out. Two separate sets of analyses were performed, one with the two 'outgroups' (from the shelf and the Faroe-Iceland Ridge) and one without.

The identifications of all species encountered (Supplementary material Table S3) are according to Høisæter (2009a). The depth zones are named in a way diverging somewhat from the global norm, and adapted to this particular study. Thus the shelf is defined by its fauna and partly by the temperature, as extending down to 490 m, the upper slope to 750 m, the middle slope to 1,000 m, the lower slope to 2,000 m and the abyssal basin from 2,000 to *c.* 4,000 m (maximum depth in the Norwegian Sea).

RESULTS

Overview

All the material included is presented in Supplementary material Table S1. As summarized in Table 1, 2,959 specimens (in addition to a few empty shells) belonging to at least 96 species were identified. Table 1 also shows the results of a first attempt to organize the 99 samples studied into six depth zones and two geographic areas (the Faroe-Shetland Channel, and the Iceland-Faroe Ridge).

The data from the reduced data set of 70 stations are summarized in Table 2 (complete data set in Supplementary material Table S2), and while the number of stations are reduced from 99 to 70, and the number of individuals from 2,959 to 2,547, the number of species is reduced only by seven, to 89.

Bathymetric patterns in the abundance and diversity of gastropods

Figure 3 shows the species richness and abundance in each sample, based on the material presented in Supplementary material Table S2. The different samples are identified by their depth, as this (with the exception of two stations from 804 m) identifies each station unambiguously.

Table 1. The total number of samples, species and specimens in each depth zone.

	Shelf	Faroe-Iceland Ridge	'Shelf break'	Upper slope	Middle slope	Lower slope	Faroe-Shetland Channel	Abyssal basins	Sum
Depth zones (m)	471	400	470–502	543–708	750–984	996–1,942	1,220–1,338	2,019–3,892	
No. of samples	1	1	4	12	17	33	2	29	99
No. of species	12	28	14	54	43	31	21	14	96
No. of specimens	25	139	155	816	414	419	96	893	2,959

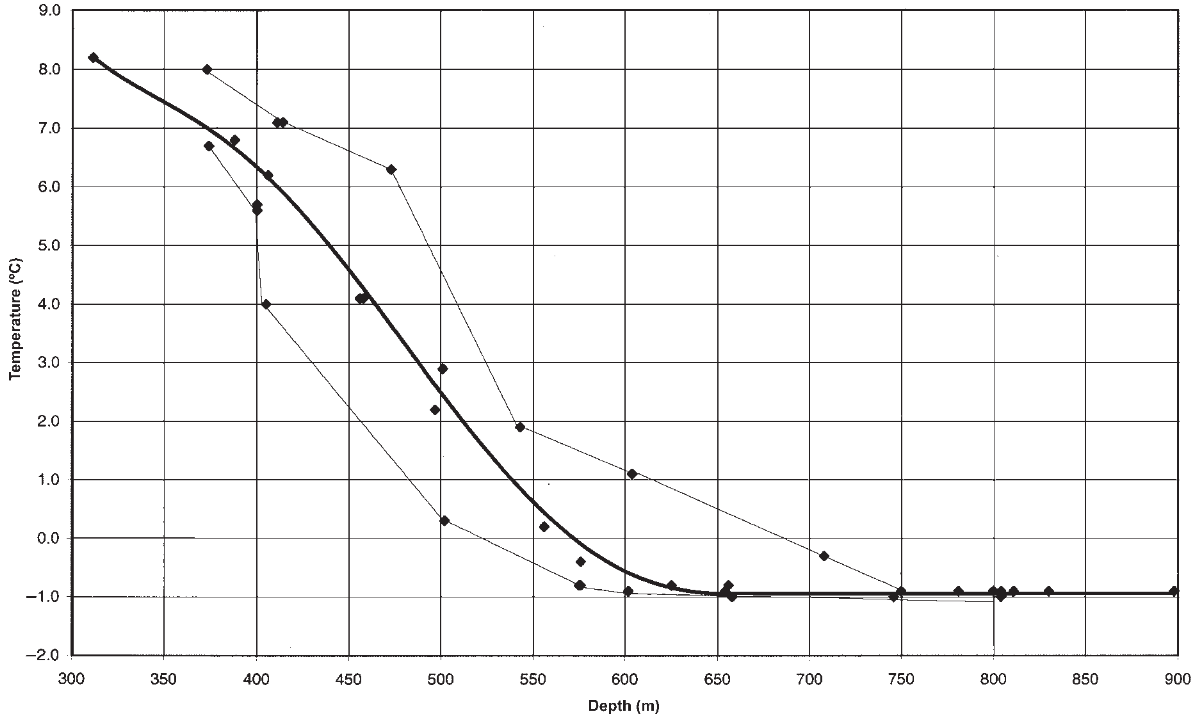

Figure 2. Plot of (near) bottom water temperature against depth. Data from field journal of *Håkon Mosby* cruises 1981–1987; complete data set between 61°30′N and 63°10′N and between 300 and 900 m, altogether 36 measurements. Trend line and maximum–minimum temperature lines included.

Table 2. The number of samples, species and specimens in each depth zone selected for the multivariate analyses.

	Shelf	'Ridge'	'Shelf break'	Upper slope	Middle slope	Lower slope	Abyssal basins	Sum
Depth zones (m)	471	400	497–502	543–708	750–984	996–1,751	2,019–3,892	
No. of samples	1	1	3	10	10	20	25	70
No. of species	12	28	13	54	37	26	14	89
No. of specimens	25	139	154	813	353	201	861	2,547

The number of species and number of individuals each exhibit depth-related patterns. Both graphs show a trend of gradual increase from 497 m to a peak at 602 m, and a gradual decrease with depth down to a steady, low level from 984 to 2,150 m. The number of species remains at this low level, but the abundance increases from 2,150 to 3,000 m. This increase is mostly due to a very few dominant species. Samples from the lower slope (Table 2) contained an average of only 10 specimens per sample compared with 81 on the upper slope (and 34 below 2,000 m), and a total of 26 species as against 54 on the upper slope (and 14 species below 2,000 m). These are not very precise measures, but indicate that the most diverse and abundant gastropod fauna in this part of the Norwegian Sea is found on the upper slope.

The multivariate analyses (only those based on fourth-root transformed data, and the data set without the two outgroups, shown, Fig. 4) indicate that except for the clear discontinuity at around 500 m, there is a gradual turnover in fauna with depth, although the 17 stations below 2,000 m cluster closely together. Fourteen species are found in this group, and the individual samples contains between four and eight species. These stations are dominated by six abyssal species (see below).

I feel that some further grouping can be justified, if the diagrams are interpreted broadly. The shelf group (here represented by the 471 m station, not included in Fig. 4, but see Supplementary material Table S2) is very different from all the deeper stations, with at most three species in common with any other sample. This is in agreement with results from earlier investigations on the shelf fauna, which is well studied on this part of the Norwegian shelf. The other 'outgroup' station from 400 m on the Iceland-Faroe Ridge (64°26′N, 11°10′W, not included in Fig. 4) has a somewhat higher content of slope species, although its relationship to other stations is low, having at most seven species in common with any station. In the multivariate analyses (not shown) it falls out as an intermediate station between the one from 471 m and the deeper slope stations.

The eight stations from 543 m down to 708 m constitute an upper-slope group. The samples from these stations, with a few exceptions, are also those with the highest species diversity and abundance. As will be further discussed below, this group is characterized by a number of species not found above and scarcely if at all below this depth zone.

The three species-poor stations from around 500 m (497, 501 and 502 m in Fig. 4) differ from all other stations. They lack many of the species characteristic of the upper slope, but include a couple of species known from the upper slope north of Iceland, but not found in any other group (Fig. 4).

Taxonomic composition

Among the 96 species identified, at least six species are undescribed (*Skenea* n. sp. A, *Skenea* aff. *proxima*, *Eumetula* n. sp., *Alvania* aff. *moerchi*, *Velutina* n. sp. E and *Admete* n. sp.), while another two (*Cerithiella danielsseni* and *Admete contabulata*) are resurrected after having earlier been synonymized with shelf species. The family-level taxonomic composition is shown in Figure 5, based on the material from deeper than 490 m, but excluding two species of *Alvania* found only in a single sample at 870 m at 70°N. These are found far north of the area of primary interest, and probably belong to a specialized fauna (see Discussion).

The Buccinidae dominate the species composition with 15 species in the material, but the Rissoidae (Supplementary material Table S3), with only four species have only slightly fewer specimens. In both of these families the high abundance is due to a single species, *Mohnia mohni* and *Alvania wyvillethomsoni*, respectively. The third most abundant family is the Philinidae, with five species and 451 specimens, of which 338 belong to *Laona finmarchica*. Both Conidae (traditionally referred to as Turridae) and Turbinidae are also high in numbers of species and specimens (Supplementary material Table S3). At the other extreme the otherwise very species-rich family Pyramidellidae is represented by a single, not very common species.

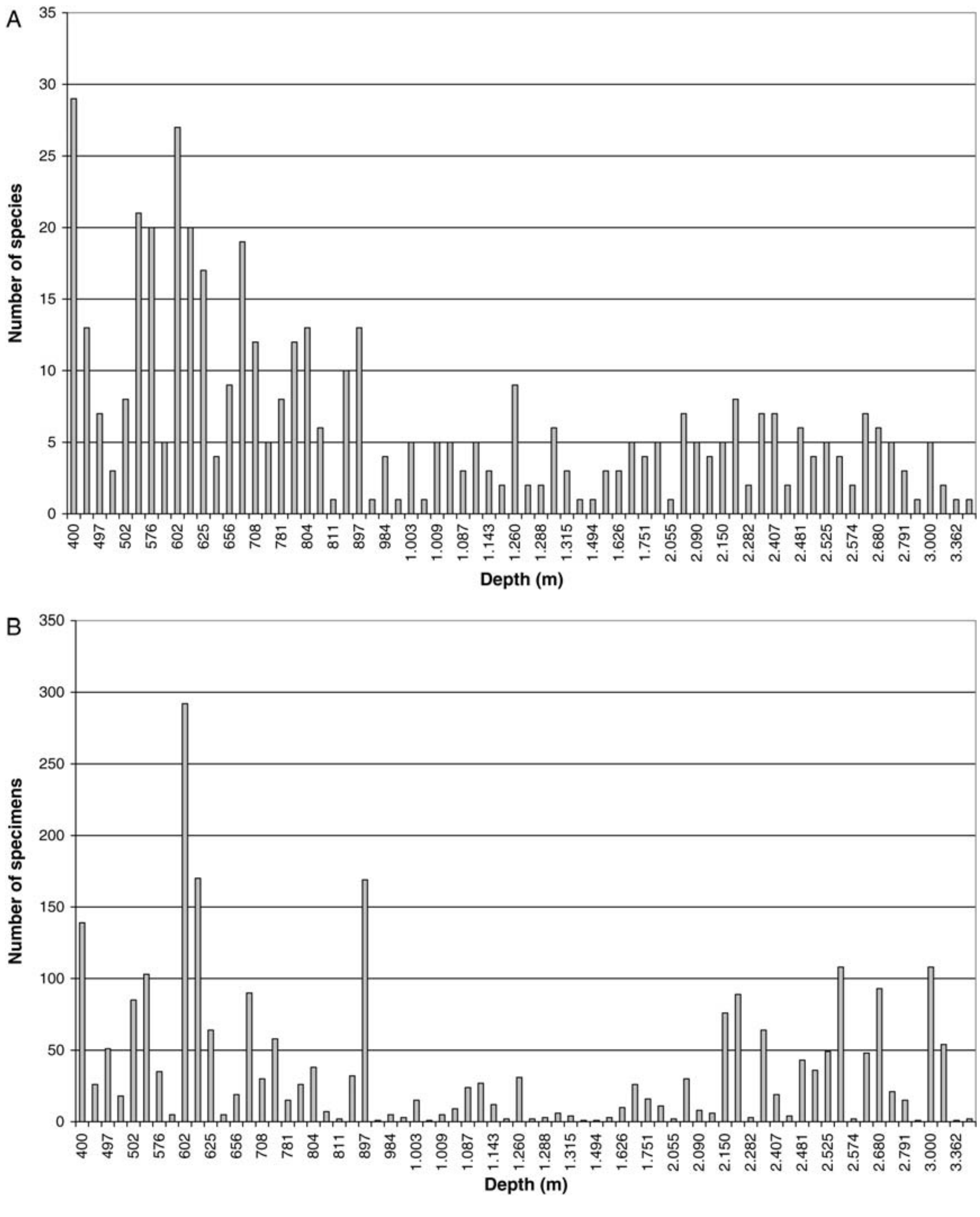

Figure 3. A. Number of species in each sample (reduced data set of 70 stations). **B.** Number of specimens in each sample. Sampling depth used as sample identifier. Due to lack of space, only every second sample identified. For further details see Supplementary material Table S2.

A number of species are found both on the shelf and on the upper to middle slope. This category is composed of about 30 species (Table 3, Supplementary material Table S2). Some of these are sufficiently morphologically distinct on shelf and slope that future studies might show them to be separate species. (e.g. Høisæter, 2009b, for discussion of the distinction between shelf species *Cerithiella metula* and its slope counterpart *C. danielsseni*).

The remaining species have so far only been reported from below 500 m, in sub-zero temperatures, or on the Arctic shelf. These species can, based on this investigation, be subdivided into slope species, abyssal species and an important hitherto unreported group, which I call the 'ecotone' group. This last group is composed of species primarily living on the upper slope, where the bottom water temperature fluctuates between negative and positive values on a diurnal basis, as a result of internal waves. Based on available information this depth zone (Fig. 2) extends roughly from 500 m down to 700 m, although it may have different upper and/or lower limits on other parts of the slope. The 15 species I have included in this group (Table 3) have either been found exclusively in this depth zone, or occur only as scattered specimens further down the slope. At least four of these species are so far undescribed, and another three are here reported from the Norwegian part of the slope for the first time. Photographs of 11 of these species together with six shelf and one slope species with high abundances in the 'ecotone' samples are presented in Figures 6 and 7. *Skenea* n. sp. A (Fig. 6E), *Alvania moerchi* (new to the

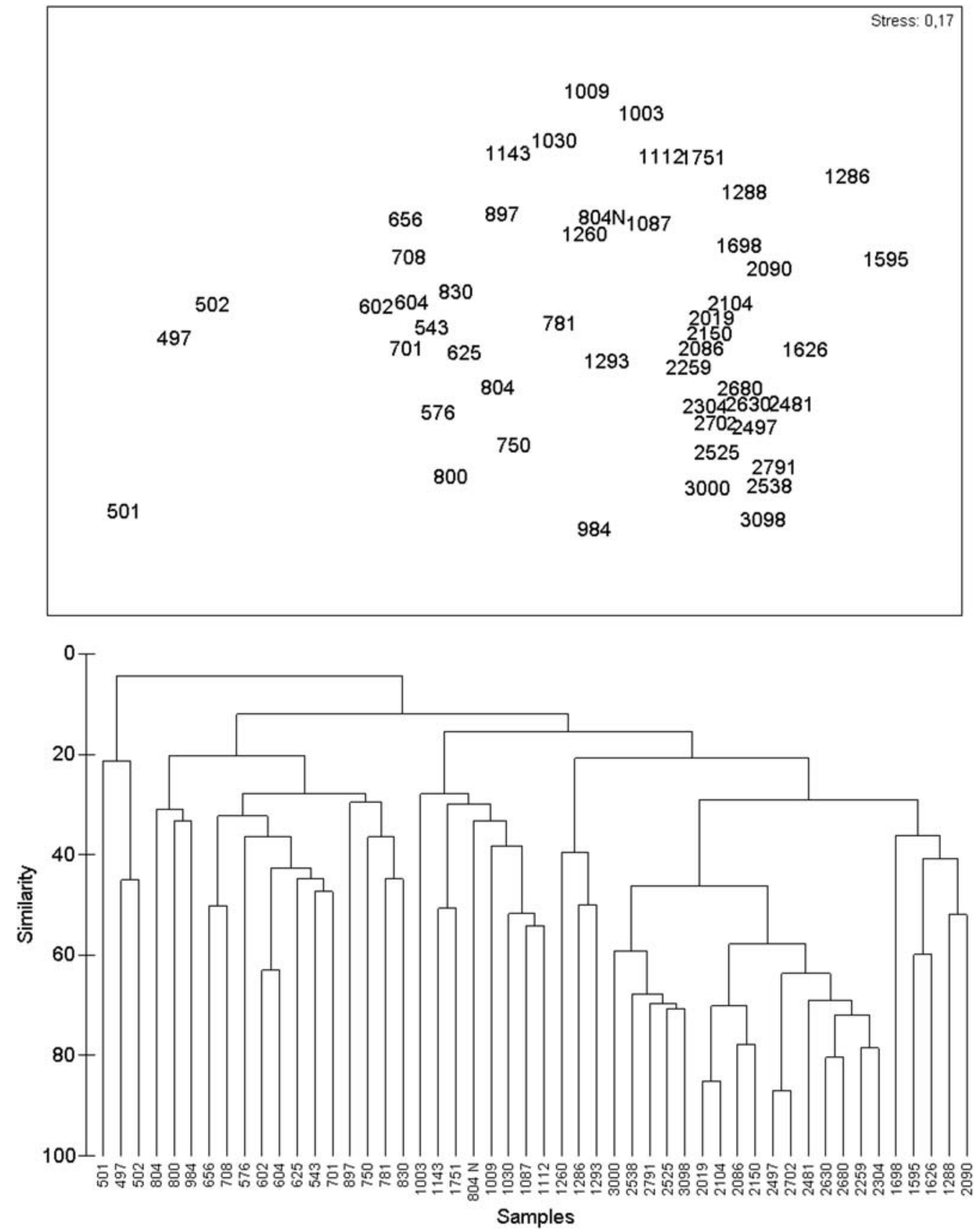

Figure 4. MDS and dendrogram based on Bray–Curtis similarity of fourth-root transformed abundance data for 50 stations from the area at the North Sea Fan and in the basin just to the north (Fig. 1).

'Norwegian' slope) (Fig. 6G), *Onoba islandica* (new to the 'Norwegian' slope) (Fig. 7A), *Velutina undata* (Fig. 7B), *Colus latericeus* (Fig. 7D) and *Admete* n.sp. (Fig. 7C) are all fairly common members of this 'ecotone' group, and together with the less common *Eumetula* n. sp. (Fig. 7F), and *Skenea* aff. *proxima* (Fig. 6D), serve to define the group. *Alvania wyvillethomsoni* (Fig. 6H) is by far the most common member of this 'ecotone' fauna, but since the species is found frequently down to 2,150 m in this region, it is classified as a slope species. The very common philinid, *Laona finmarchica* (if indeed it is a single species) is in the same category.

In addition to the species mentioned above, *Skenea peterseni* (Fig. 6C), *Turrisipho lachesis* (Fig. 7E), *Colus holboelli* (not shown) and the shelf species *Anatoma crispata* (Fig. 6A), *Solariella obscura* (Fig. 6B), *Rugulina fragilis* (Fig. 6F) and the three common shelf *Oenopota* species (*O. bergensis* Fig. 7I; *O. tenuicostata* Fig. 7H and *O. violacea* Fig. 7G) are also common members of this 'ecotone' fauna.

Obtusella tumidula (*sensu* Warén, 1996) (Fig. 6I) was only found at the 497 m station. It may be confined to this depth zone at the upper edge of the ecotone, as all species found there (except *Skenea* n. sp. A) are well known shelf species, or it might belong to the group of shelf species occasionally occurring in negative temperatures.

Nineteen species are classified as slope species, based on their occurrence in high numbers both on the upper and lower slope, or on the lower slope only. Of these *Alvania wyvillethomsoni* is by far the most abundant. It is found in every depth zone, from the 543 m sample down to 2,150 m. *Laona finmarchica* seems to be common down to at least 1,000 m. Only scattered specimens are found at greater depths, with the four specimens from 2,304 m being the deepest. *Iphinopsis inflata* is a species with a well-

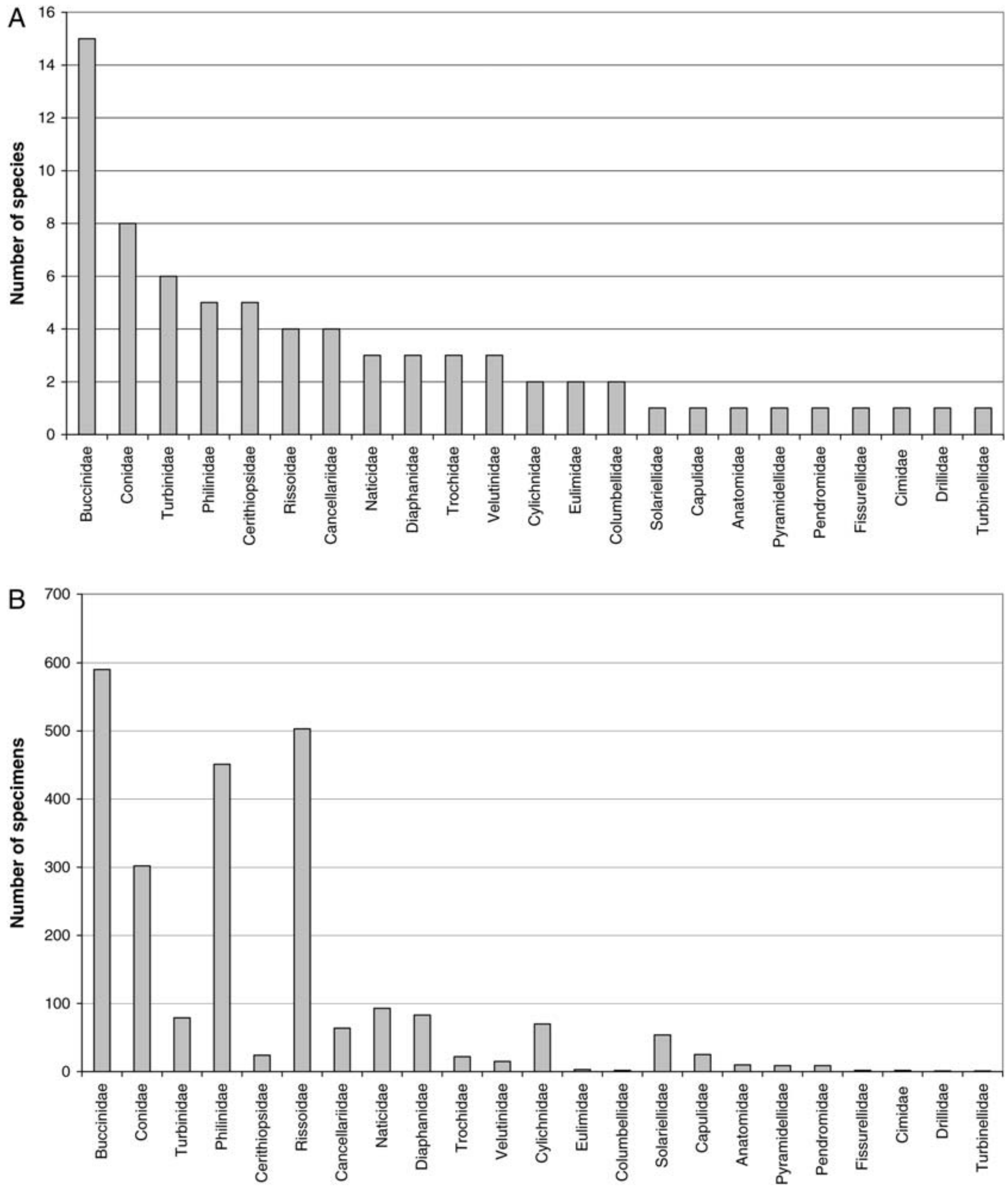

Figure 5. A. Number of species in each family, for stations below 490 m. **B.** Number of specimens in each family. The Conidae are usually referred to as family Turridae.

defined depth zonation, as 15 of the 16 specimens were found between 897 and 1,315 m. Other slope species, *Admete contabulata*, *Cerithiella danielsseni*, *Toledonia limnaeoides*, *Chrysallida sublustris* and *Cima* cf. *cuticulata*, occur in much lower numbers, but are more abundant on the lower slope than above 750 m. Two species *Colus holboelli* and *Buccinum hydrophanum* are placed in their categories with a question mark, as they are fairly common in both the ecotone and the slope zone. *Buccinum hydrophanum* is taxonomically problematic; the specimens I have identified belong to the form *elata* described by Friele (1882) from the slope. Whether this is cospecific with *B. hydrophanum* s. str. is unknown.

The material from the 25 stations deeper than 2,000 m largely supports the conclusions of earlier investigations, that the abyssal species in the Norwegian Sea constitute a well-defined group, with a number of endemics or near endemics. Thus *Mohnia mohni*, with 429 specimens (and only 14 from the slope above 2,000 m), is the second most abundant species (next to *Alvania wyvillethomsoni*) in the material. The 78 specimens of *Mohnia danielsseni* were all taken below 2,300 m. *Cryptonatica bathybii*, *Oenopota ovalis* and *Diaphana lactea* are other species mostly found below 2,000 m. The very small *Anekes undulisculpta* with four specimens in three samples from 2,090 to 2,481 m is most likely an abyssal endemic as well. Whether a faunistic discontinuity at around 2,200 m suggested by the multivariate analyses is real is doubtful. The only clear difference is that *Alvania wyvillethomsoni* has its deepest occurrence at 2,150 m, and *Mohnia danielsseni* has its shallowest at 2,304 m.

DISCUSSION

This is the first description of the gastropod fauna covering the depth range from 500 to 3,900 m from anywhere on the slope of the Norwegian Sea. As a result it is possible to describe the abundance, species diversity and faunistic composition throughout the complete depth range in a specific area of the slope off Norway. Whether the results are valid also for the slope further north along the continental margin or southwards into the Faroe-Shetland Channel is doubtful, because sediments, geological history, steepness of the slope and influence of internal waves, all differ appreciably.

The most unexpected result from this study is the discovery of a group of at least 15 gastropod species (here called the 'ecotone' group) more or less confined to the upper slope,

Table 3. The 73 species found on the slope and in the abyss of the Norwegian Sea, arranged into bathymetrical groups: (a) 490–750 m; (b) 750–2,000 m; (c) deeper than 2,000 m.

Shelf group	a	b	c	Ecotone group	a	b	Slope group	a	b	c	Abyssal group	a	b	c
Oenopota tenuicostata	37	18		*Skenea* n. sp. A	50	1	*Alvania wyvillethomsoni*	269	145	*28*	*Mohnia mohni*	4	10	415
Solariella obscura	46	8		*Onoba islandica*	38	1	*Laona finmarchica*	141	164	33	*Oenopota ovalis*		23	173
Diaphana hiemalis	2	23	6	*Admete* n. sp.	33		*Buccinum hydrophanum*	3	7		*Mohnia danielsseni*			78
Torellia delicata	19	5	1	*Turrisipho lachesis*	10	7	*Iphinopsis inflata*	1	15		*Cylichna lemchei*	13	1	48
Philine quadrata	9	13		*Skenea peterseni*	15	1	*Admete contabulata*	3	7		*Diaphana lactea*		6	41
Oenopota violacea	17	4		*Colus latericeus*	15	1	*Chrysallida sublustris*	4	5		*Cryptonatica bathybii*		10	28
Margarites costalis	20			*Alvania moerchi*	13		*Colus turgidulus*	3	5		*Anekes undulisculpta*			4
Cryptonatica affinis	2	18		*Velutina undata*	11		*Cerithiella danielsseni*	1	6		*Skenea turgida*		1	2
Oenopota bergensis	9	8		*Colus holboelli*	11	10	*Toledonia limnaeoides*	2	3					
Anatoma crispata	10			*Obtusella tumidula*	9		*Pleurotomella packardi*	1	1	2				
Rugulina fragilis	9			*Eumetula* n. sp.	6		*Colus* cf. *sabini*		3					
Philine lima	8			*Skenea* aff. proxima	2		*Turrisipho* cf. *dalli*		3					
Cylichna alba	2	6		*Velutina lanigera*	2		*'Alvania' incognita*		2					
Philine cf. *catena*	6			*Velutina* n. sp. E	2		*Alvania* aff. *moerchi*		2					
Eumetula arctica	6			*Buccinum oblitum*	1		*Turrisipho voeringi*		2					
Oenopota cf. *assimilis*	5	1					*Cima* cf. *cuticulata*	1	1					
Admete viridula	4	1					*Crinolamia dahli*	1		1				
Skenea trochoides	3						*Volutopsius* sp.		1					
Philine scabra	3						*Colus islandicus*		1					
Cerithiella metula	3													
Laeocochlis sinistratus	2													
Puncturella noachina	2													
Oenopota trevelliana		2												
Euspira pallida	1													
Mitrella rosacea	1													
Amphissa acutecostata	1													
Spirotropis modiolus	1													
Melanella cf. *orphanensis*	1													
Liomesus ovum		1												
Metzgeria alba		1												
Oenopota elegans		1												

Numbers are total number of specimens within each depth zone for total data set (95 stations; species only found on the shelf, on the Iceland-Faroe Ridge or in the Faroe-Shetland Channel not included).

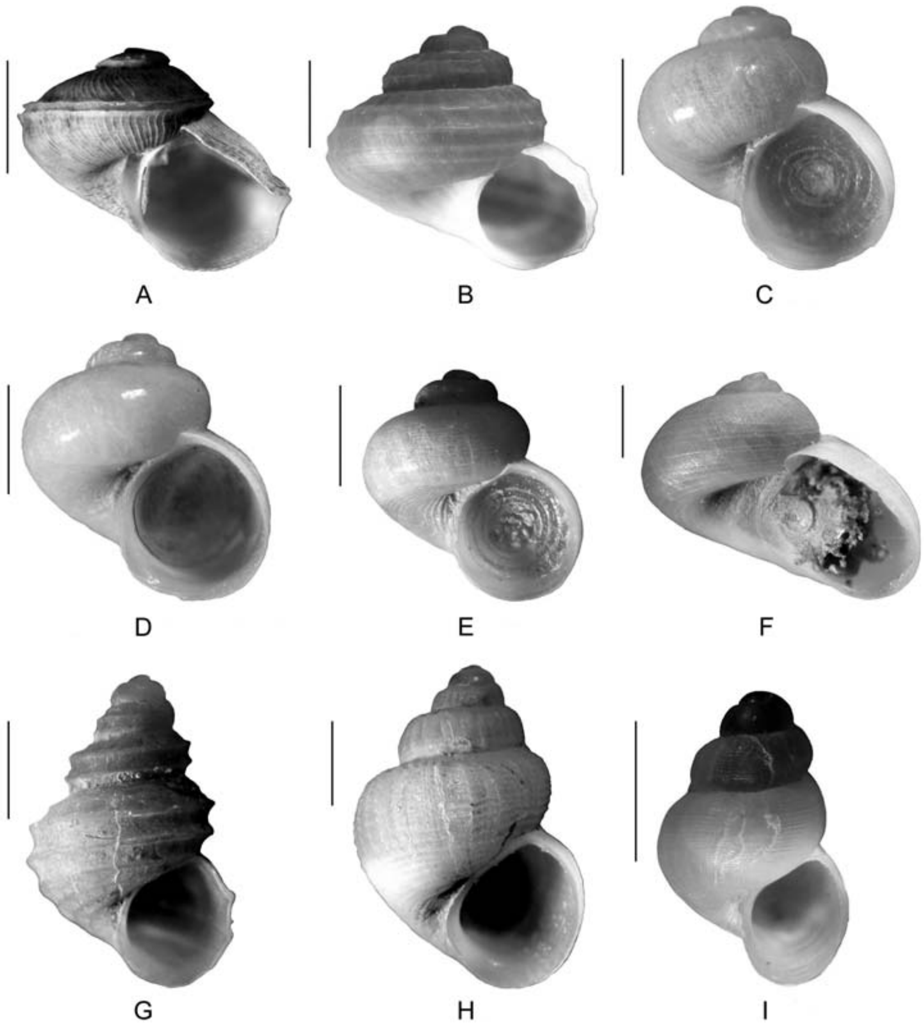

Figure 6. A. *Anatoma crispata* (Fleming, 1828), *c.* 545 m. **B.** *Solariella obscura* (Couthoy, 1838), *c.* 500 m. **C.** *Skenea peterseni* (Friele, 1877), *c.* 600 m. **D.** *Skenea* aff. *proxima* (Tryon, 1888), *c.* 600 m. **E.** *Skenea* n. sp. A, 830 m. **F.** *Rugulina fragilis* (G.O. Sars, 1878), *c.* 710 m. **G.** *Alvania moerchi* (Collin, 1886), *c.* 605 m. **H.** *Alvania wyvillethomsoni* (Friele, 1877), *c.* 600 m. **I.** *Obtusella tumidula* (G.O. Sars, 1878), *c.* 500 m. Scale bars = 1 mm.

between 490 and 750 m. This group is best represented in a few samples with high diversity and abundance, from around 600 m, in the middle of a depth zone exposed to diurnal internal waves. Samples from the slope below 750 m (which in this part of the Norwegian Sea is exposed to constant sub-zero temperatures) have generally much lower abundances, and many of the species in these samples (the slope group) are found in all depth zones from 500 to at least 2,000 m. Faunistically, there is thus no basis for distinguishing between middle and lower slope.

With only one or two exceptions, the 'ecotone' group species have not previously been recorded from the Norwegian shelf, and if recorded from depths below 750 m at all, then only as scattered specimens. Some of these species have their closest records on the upper slope north of the Faroes. These (e.g. *Alvania moerchi* and *Onoba islandica*) are found in high numbers also in the single sample from 400 m on the Iceland-Faroe Ridge, and have previously been found frequently on the shelf and slope of Iceland (Warén, 1996). The remaining species (except for the undescribed ones) are primarily known from shallow waters in the Arctic.

Alvania wyvillethomsoni and *Laona finmarchica* are the two dominating species on both the upper and lower slope, but with higher abundance above 750 m than below. These two species have a wide distribution, and have been mentioned as common to abundant both in the bathyal zone of the Norwegian Sea, and on the Arctic Shelf (e.g. Grieg, 1915; Schiøtte, 2005).

Thirty-one of the species taken in one or more of the samples from between 490 and 750 m are known from the shelf of western Norway or the Norwegian Trench, and are here regarded as shelf species. Especially intriguing are the three or four species of *Oenopota*, all fairly common on the Norwegian shelf, that are here found in rather high numbers on the slope, both below and above 700 m. In the deep sea south of the Wyville-Thomson Ridge, conoideans not found on the shelf further north constitute a numerically important part of the species pool (Olabarria, 2006). (This may be an indication that their distribution is limited by factors other than temperature.) This faunal component seems to be replaced by these shelf species of *Oenopota*, together with the deeper living *Oenopota ovalis*, in the Norwegian Sea. *Pleurotomella packardi*, which is known from positive-temperature water in the depths of the North Atlantic, is the only other conoidean in the deep basins of the Norwegian Sea.

The samples from deeper than 2,000 m are characterized by low species diversity, but surprisingly high abundance, of a few near-endemic species, as earlier reported by Bouchet & Warén

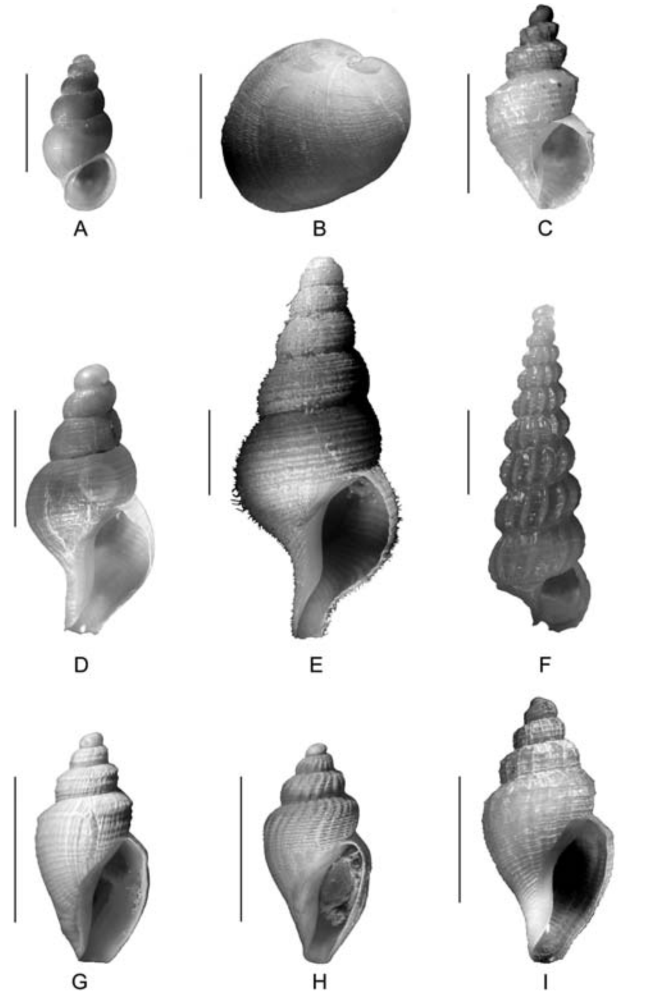

Figure 7. A. *Onoba islandica* (Friele, 1886), *c.* 605 m. **B.** *Velutina undata* J. Smith, 1839, *c.* 650 m. **C.** *Admete* n. sp., *c.* 605 m. **D.** *Colus latericeus* (Møller, 1842), *c.* 600 m. **E.** *Turrisipho lachesis* (Mørch, 1869), *c.* 600 m. **F.** *Eumetula* n. sp., *c.* 605 m. **G.** *Oenopota violacea* (Mighels & Adams, 1842), 800 m. **H.** *Oenopota tenuicostata* (G.O. Sars, 1878), 800 m. **I.** *Oenopota bergensis* (Friele, 1886), *c.* 500 m. Scale bars = 4 mm, except **A** and **F** = 2 mm.

(1979). In 33 samples taken at 11 stations from depths between 2,470 and 3,710 m, they identified some 90,000 specimens of shell-bearing molluscs, of which 5,653 were gastropods belonging to 15 species. In addition to the seven species listed in Table 3 above (see also Supplementary material Tables S1, S2), they found the following species: *Anatoma crispata*, *Skenea profunda*, *Pseudosetia semipellucida*, a few juveniles of *Torellia delicata*, and *Cylichnium africanum*. The last of these and *Anatoma crispata* are the only species not included in the present material or other material I have seen from below 2,000 m in the Norwegian Sea. (I have however seen specimens of another, presumably undescribed species of *Anatoma*.) A species not represented in their material but apparently confined to the abyssal of the Norwegian Sea, is '*Rissoa*' *griegi* Friele, 1879 (generic assignment unclear) which is associated with *Teredo*-bored pieces of sunken wood, a habitat it appears to share with *Skenea profunda*, and it also seems to be abundant at hydrothermal vents (C. Schander, personal communication). In the stations from below 2,000 m in my material, only 28 specimens of *Alvania wyvillethomsoni*, six of *Diaphana hiemalis* and 33 of *Laona finmarchica* (Table 3) belong to species not included in Bouchet & Warén's (1979) group of abyssal species. These three are all much more numerous on the slope, and in all likelihood are only incidental guests in the abyssal depths of the Norwegian Sea.

Recently a British and a Dutch research group have both published a number of articles on the habitats and fauna in the Faroe-Shetland Channel, specifically the West Shetland Slope (Bett, 2001; van Raaphorst *et al.*, 2001; Bonnin *et al.*, 2002; Narayanaswamy, Bett & Gage, 2005; Witbaard *et al.*, 2005). The results from both groups (based on the total macrofauna by Bett, 2001, the polychaetes by Narayanaswamy *et al.*, 2005 and on the molluscs by Witbaard *et al.*, 2005) indicate that the species diversity peaks at around 400 to 500 m, declining rapidly below 500 m, and that the fauna below about 500 m is very different from the one above 400 m (Bett, 2001; Narayanaswamy *et al.*, 2005; Witbaard *et al.*, 2005). Both groups implicate internal waves in the thermocline zone between the Norwegian Sea sub-zero deep water and Atlantic water in the upper slope current flowing northwards.

The British group found a high correlation between species diversity and the temperature range in the upper part of the depth zone where temperature fluctuates between positive and negative values. Thus the maximum diversity is found at 400 to 450 m, where the temperature occasionally is below zero, and the range is 5–6°. Further up on the slope, where the range is equally high but the temperature stays consistently above zero, the diversity is lower, at the same level as found on the shelf. Further down, where the temperature is only occasionally positive, the diversity falls off rapidly with depth (Bett, 2001; Narayanaswamy *et al.*, 2005). Narayanaswamy *et al.* (2005) concluded that in the Faroe-Shetland Channel temperature replaces depth as the dominant variable influencing the polychaete community on a large scale.

The Dutch group emphasize alternative potential effects of internal waves on the sea bed. The wave energy is supposedly dissipated by turbulent mixing at or close to the sloping bottom, leading to local resuspension of fluffy organic-rich sediment, or the creation of a nepheloid near-bottom layer (Witbaard *et al.*, 2005). These authors recorded a higher proportion of filter-feeders than either above or below on the slope, which they claim supports the theory.

My data from the North Sea Fan suggest a diversity pattern very similar to the ones reported from the Faroe-Shetland Channel, but with the maximum pushed about 200 m deeper, to around 600 m. This depth zone coincides with the zone where the 'core' ecotone group species are most abundant (Supplementary material Table S2), and where my few scattered temperature measurements indicate the highest temperature range where both negative and positive values are equally represented (Fig. 2).

The diversity peak around 400 to 500 m is generally interpreted as an overlap of the upper and lower boundaries of two distinct assemblages (Bett, 2001; Gage, 2004). This might partly be the case also for my material, but in addition a considerable proportion of the gastropod assemblage in question has not been recorded from either above or below this zone. The only published species list permitting a direct comparison is table III of Witbaard *et al.* (2005), showing the distribution with depth of the 13 most abundant bivalves from the West Shetland Slope in the Faroe-Shetland Channel. In this list four species have their lower boundaries at 600–700 m, but all of them, except *Rhinoclama notabilis* are found (if sparingly) also in the 200–300 m zone, in positive-temperature water. If this absence of a specialized ecotone fauna among the bivalves is due to methodological differences, to different environments or to a genuine difference between bivalve and gastropod faunas is hard to tell. The total absence of all the species I have classified as 'core' ecotone gastropods (except for *Turrisipho lachesis*) in the species list of Witbaard *et al*. (2005) argues for either a methodological difference or differences in the habitats.

My results support the conclusions of Bett (2001), Gage (2004), Narayanaswamy *et al*. (2005) and Olabarria (2006), recently endorsed also by Stuart & Rex (2009), that depth-related species diversity patterns vary geographically. The postulated global pattern in which species diversity varies parabolically with depth with a maximum at around 1,200 m (Rex *et al*., 2005b) is thus not tenable.

Recently Stuart & Rex (2009) compared gastropod species diversities from 10 lower bathyal to abyssal basins in various parts of the Atlantic Ocean. They included (as one basin) four widely separated stations in the Norwegian Sea. Based on the data in Bouchet & Warén (1979), they concluded that the species richness in the abyssal basins of the Norwegian Sea was significantly lower than that which they had earlier reported from similar depths in the western Atlantic (Rex *et al*., 2005b). As the depth range of their eight samples (two from each station) was low (2,500–3,200 m) they were unable to make a comparison with the total depth- related pattern in the western Atlantic. They did indicate, however, a decreasing diversity with depth. When the remaining material of Bouchet & Warén (1979) is taken into account, this decreasing diversity with depth is no longer apparent (two localities, at 3,210 and 3,500 m, respectively, yielded six and five species). Neither is it reflected in my data based on 25 stations from 2,019 to 3,900 m. An observation not available from the data of Bouchet & Warén (1979) is the marked increased dominance of the two *Mohnia* species deeper than 2,500 m, and the fact that *Mohnia danielsseni* was only found below 2,300 m.

Only three species in my material have a depth distribution that make them candidates for the source-sink hypothesis of Rex *et al*. (2005a). All the remaining apparently have self-sustaining populations. But, as the population densities of the typical abyssal species in this ocean appear surprisingly high, there might not be a need for an explanation. Nevertheless, the question of the immigration route for the abyssal fauna is still unresolved. *Pleurotomella packardi* and *Oenopota ovalis* are both present in the bathyal zone south of the Wyville-Thomson Ridge, with presumed maximal abundances at around 1,300–1,700 m (Olabarria, 2006). The others have so far only been recorded from the abyssal or bathyal zones of the Norwegian Sea, although congeners have been found either in the Arctic or in the North Atlantic bathyal.

A possible reason for the 'ecotone' group and its principal members having been unnoticed for so long may be the sparsity of samples from this particular depth zone in earlier investigations. In the Norwegian North Atlantic Expedition, 1876–1878, the molluscs were studied from only a single sample in the relevant depth stratum, i.e. stn 124 at 640 m, 66°41′N (Friele & Grieg, 1901). Friele (1903) looked at material from 16 stations in the Norwegian Sea, of which none was from the relevant depth zone on the slope outside Norway. Grieg (1915) analysed two samples in the centre of the North Sea Fan, but from 800 and 1,400 m, respectively, therefore below the 'ecotone'.

'*Alvania*' *incognita* was described from several specimens on a piece of sunken driftwood, and has since been found (together with *Alvania* aff. *moerchi*) in a sample from Håkon Mosby mud volcano (A. Warén, personal communication). This indicates the presence on the slope of cold seeps or biodegradeable substrates harbouring a specialized fauna not likely to be taken in regular sledge hauls. Warén has indicated that several additional species otherwise only known from hot vents or sunken biogenic material are present in various localities on the slope.

This should caution against any over-interpretation of my results. The region is vast, and vastly undersampled. The hydrography and bottom morphology are complex, and the recently discovered presence of several hydrothermal vents and methane seeps with their own faunas should guarantee a rich source of future modifications of my simplified zonation pattern.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Molluscan Studies* online.

ACKNOWLEDGEMENTS

Without the resourcefulness and persistent collecting efforts of Torleiv Brattegard throughout the 1980s, the material for this study would have been nonexistent. Jon Anders Kongsrud and Tom Alvestad of the Zoological Museum in Bergen have contributed with complete sorting of a majority of the samples from the *Håkon Mosby* cruises. During early stages of the work Anders Warén supplied invaluable assistance in identifying individuals of gastropods unknown to me, without always agreeing on my final decisions; he also kindly looked through an earlier version of the manuscript. Michael Rex and an anonymous referee have provided helpful comments on the manuscript. I thank Elin Holm for preparing Figures 1 and 2.

REFERENCES

BETT, B.J. 2001. UK Atlantic Margin Environmental Survey: introduction and overview of bathyal benthic ecology. *Continental Shelf Research*, **21**: 917–956.

BONNIN, J., VAN RAAPHORST, W., BRUMMER, G.-J., VAN HAREN, H. & MALSCHAERT, H. 2002. Intense mid-slope resuspension of particulate matter in the Faeroe-Shetland Channel: short-term deployment of near-bottom sediment traps. *Deep-Sea Research I*, **49**: 1485–1505.

BOUCHET, P. & WARÉN, A. 1979. The abyssal molluscan fauna of the Norwegian Sea and its relation to other faunas. *Sarsia*, **64**: 211–243.

BOUCHET, P. & WARÉN, A. 1980. Revision of the North-East Atlantic bathyal and abyssal Turridae (Mollusca, Gastropoda). *Journal of Molluscan Studies*, *Suppl*. **8**: 1–119.

BOUCHET, P. & WARÉN, A. 1985. Revision of the Northeast Atlantic bathyal and abyssal Neogastropoda, excluding Turridae (Mollusca, Gastropoda). *Bollettino Malacologico*, *Suppl*. **1**: 123–296.

BOUCHET, P. & WARÉN, A. 1986. Revision of the Northeast Atlantic bathyal and abyssal Aclididae, Eulimidae, Epitoniidae (Mollusca, Gastropoda). *Bollettino Malacologico*, *Suppl*. **2**: 299–576.

BOUCHET, P. & WARÉN, A. 1993. Revision of the Northeast Atlantic bathyal and abyssal Mesogastropoda. *Bollettino Malacologico*, *Suppl*. **3**: 579–840.

BRATTEGARD, T. & FOSSÅ, J.H. 1991. Replicability of an epibenthic sampler. *Journal of the Marine Biological Association of the United Kingdom*, **71**: 153–166.

FRIELE, H. 1877. Preliminary Report on Mollusca from the Norwegian North Atlantic Expedition in 1876. *Nyt Magazin for Naturvidenskaberne*, **23**: 1–10.

FRIELE, H. 1879. Catalog der auf der norwegischen Nordmeer-expedition bei Spitzbergen gefundenen Mollusken. *Jahrbücher der Deutschen Malakozoologischen Gesellschaft*, **6**: 264–286.

FRIELE, H. 1882. Mollusca I. Buccinidae. *Norwegian North-Atlantic Expedition, 1876–1878*, **3** Zoology (8): 1–38.

FRIELE, H. 1886. Mollusca II. *Norwegian North-Atlantic Expedition, 1876–1878*, **3**(16): 1–35.

FRIELE, H. 1903. Mollusken der ersten Nordmeerfahrt des Fischereidampfers 'Michael Sars' 1900 unter Leitung von Herrn Dr. Johan Hjort. *Bergens Museums Aarbog*, **1902**(3): 1–18.

FRIELE, H. & GRIEG, J. 1901. Mollusca III. *Norwegian North-Atlantic Expedition*, *1876–1878*, **7**(5): 1–129.

GAGE, J.D. 2004. Diversity in deep-sea benthic macrofauna: the importance of local ecology, the larger scale, history and the Antarctic. *Deep-Sea Research II*, **51**: 1689–1708.

GRIEG, J. 1915. Evertebratfaunaen paa havdypet utenfor 'Tampen'. *Bergens Museums Aarbok*, **1914**(3): 1–26.

HØISÆTER, T. 2009a. Distribution of marine, benthic, shell bearing gastropods along the Norwegian coast. *Fauna Norvegica*, **28**: 1–106.

HØISÆTER, T. 2009b. Reappraisal of *Cerithiella danielsseni* (Gastropoda: Caenogastropoda: Cerithiopsidae): a taxon confined to negative temperatures in the Norwegian Sea. *Journal of the Marine Biological Association of the United Kingdom*.

NARAYANASWAMY, B.E., BETT, B.J. & GAGE, J.D. 2005. Ecology of bathyal polychaete fauna at an Arctic-Atlantic boundary (Faroe-Shetland Channel, North-east Atlantic). *Marine Biology Research*, **1**: 20–32.

NYGÅRD, A., SEJRUP, H.P., HAFLIDASON, H. & BRYN, P. 2004. The glacial North Sea Fan, southern Norwegian Margin: architecture and evolution from the upper continental slope to the deep-sea basin. *Marine and Petroleum Geology*, **22**: 71–84.

NYGÅRD, A., SEJRUP, H.P., HAFLIDASON, H., LEKENS, W.A.H., CLARK, C.D. & BIGG, G.R. 2007. Extreme sediment and ice discharge from marine-based ice streams: New evidence from the North Sea. *Geology*, **55**: 395–398.

OLABARRIA, C. 2006. Faunal change and bathymetric diversity gradient in deep-sea prosobranchs from Northeastern Atlantic. *Biodiversity and Conservation*, **15**: 3685–3702.

PRIMER 6 – Version 6-1-6. Primer-E Ltd.

REX, M.A., MCCLAIN, C.R., JOHNSON, N.A., ETTER, R.J, ALLEN, J.A., BOUCHET, P. & WARÉN, A. 2005a. A source-sink hypothesis for abyssal biodiversity. *American Naturalist*, **165**: 163–178.

REX, M.A., CRAME, J.A., STUART, C.T. & CLARKE, A. 2005b. Large-scale biogeographic patterns in marine mollusks: a confluence of history and productivity. *Ecology*, **86**: 2288–2297.

SARS, G.O. 1878. *Bidrag til Kundskaben om Norges arktiske Fauna. I. Mollusca Regionis Arcticae Norvegiae. Oversigt over de i Norges arktiske region forekommende bløddyr*. Universitetsprogram for første halvaar 1878, Christiania.

SCHIØTTE, T. 2005. Marine, benthic molluscs common to North Greenland and the Faroes: a first investigation of a previously unrecognized North Atlantic fauna element. *BIOFAR Proceedings* **2005** (BIOFAR Symposium, Torshavn, 24–26 April 2003): 94–108.

SNELI, J.A. 1998. A simple benthic sledge for shallow and deep-sea sampling. *Sarsia*, **83**: 69–72.

SNELI, J.A., SCHIØTTE, T., JENSEN, K.R., WIKANDER, P.B., STOKLAND, Ø. & SØRENSEN, J. 2005. The Marine Mollusca of the Faroes. *Annales Societatis Scientiarum Færoensis*, *Suppl*. **42**: 15–176.

STUART, C.T. & REX, M.A. 2009. Bathymetric patterns of deep-sea gastropod species diversity in 10 basins of the Atlantic Ocean and Norwegian Sea. *Marine Ecology*, **30**: 164–180.

VAN RAAPHORST, W., MALSCHAERT, H., VAN HAREN, H., BOER, W. & BRUMMER, G.-J. 2001. Cross-slope zonation of erosion and deposition in the Faeroe-Shetland Channel, North Atlantic Ocean. *Deep-Sea Research I*, **48**: 567–591.

WARÉN, A. 1989. New and little known mollusca from Iceland. *Sarsia*, **74**: 1–28.

WARÉN, A. 1991. New and little known Mollusca from Iceland and Scandinavia. *Sarsia*, **76**: 53–124.

WARÉN, A. 1993. New and little known Mollusca from Iceland and Scandinavia. Part 2. *Sarsia*, **78**: 159–201.

WARÉN, A. 1996. New and little known Mollusca from Iceland and Scandinavia. Part 3. *Sarsia*, **81**: 197–245.

WITBAARD, R., DAAN, R., MULDER, M. & LAVALEYE, M. 2005. The mollusc fauna along a depth transect in the Faroe Shetland Channel: is there a relationship with internal waves? *Marine Biology Research*, **1**: 186–201.